CHAPTER 4

Patterns of parental care in vertebrates

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4.1   Introduction

Understanding parental care behaviour has remained a core research area in evolutionary behavioural ecology. Why the fascination with parental behaviour? Many human cultures have a strong focus on children and parenting and our extensive and prolonged care for our own young undoubtedly contributes to our fascination with parental care in other animals. Also by studying parental care, behavioural scientists can gain a useful window on the social dynamics of family groups, providing insights on sexual conflict (Chapter 9), parent–offspring conflict (Chapter 7), sibling rivalry (Chapter 8), and kin-mediated cooperation (Emlen 1994, 1997). The strong link between parental effort and mating effort (and sexual selection patterns in general) has also driven the ever-growing interest in parental behaviour (Williams 1966; Trivers 1972; Emlen and Oring 1977; Kokko and Jennions 2008).

Parental care varies widely between species. While costly parental feeding of offspring is a near hallmark feature of birds and mammals, many species of fishes, amphibians, and reptiles also provide care for young by simply but vigorously guarding young against predators. Whether it is the mother or the father that defends the brood also varies widely between species. Understanding the key ecological factors selecting for care and explaining the plethora of parental care forms across different taxa has remained an enduring challenge in evolutionary behavioural ecology (Lack 1968; Gross 2005; Kvarnemo 2010). Empirical research has shown that providing care benefits parents by increasing offspring survival and increasing their reproductive success. However, parental care also has three potential costs: 1) a decrease in parental survival, 2) decreased growth and associated fecundity reduction, and 3) fewer remating opportunities (Gross and Sargent 1985). Scientists have used these costs and benefits to better understand when care will evolve and which sex will provide care (Maynard-Smith 1977; Balshine-Earn and Earn 1997; Houston et al. 2005). Vertebrate groups that show great variation in care types, like teleost fishes and shorebirds, have been particular useful models in the search for a better understanding of the evolution of parental behaviour.

Since Clutton-Brock (1991) published his encyclopedic bible on parental care, two new technological advances (both molecular) have helped to further invigorate parental care research. First, phylogenetically based, comparative studies are now commonly employed in the study of parental care. The molecular revolution has facilitated the wide scale availability of molecular phylogenies, and analysis that links behaviour to these (Goodwin et al. 1998). These phylogenetic studies have strongly augmented and guided the more traditional behavioural ecology approach of experimental manipulation (Wright and Cuthill 1989). Second, the growth of genomic and bioinformatic studies has facilitated investigations into the divergence or conservation of genes, gene networks, and gene regulation across species or genera that share similar behaviour. Both these new directions have been made possible because of the rapid expansion of molecular data and because of impressive computational improvements that have facilitated large-scale database creation and analysis. In general, the molecular revolution is providing deep insights

into the evolutionary and physiological mechanisms underlying parental behaviour.

In the next section, I provide an overview of the forms of care are generally observed across fishes, amphibians, reptiles, birds, and mammals and examine the factors that are thought to have selected for the evolution of viviparity and lactation. Then I discuss the evolution of male care, female care, and biparental care as well as the evolutionary transitions between these care states. I conclude the chapter with a brief overview of the patterns of parental care in humans. Whenever possible, I highlight new comparative and molecular studies in order to shed light on the evolution and maintenance of parental care and link care patterns across the different species and classes of vertebrates.

4.2   Forms of care

Some researchers prefer to use the term 'parental care' to refer only to only post-mating behaviours (such as care of eggs, larvae, or young after fertilization; see Chapter 1). However, some behaviours that occur before or during mating, such as nest building, egg provisioning, provisioning of the female with nuptial gifts or courtship feeding, are often still regarded as parental care as they lead to higher offspring survival. Here I describe the various forms of parental care in its broader sense.

4.2.1   Preparation of the physical rearing environment

The simplest form of parental care is the preparation of a territory to receive eggs or young (Fig. 4.1). Species differ in terms of whether they merely occupy an existing structure to receive young, or they modify these structures, or even create new structures *de novo*. Regardless, the preparation and construction of a nest, den, cavity, or burrow constitutes a basic but important aspect of parental behaviour that strongly influences the survival probabilities of young (Clutton-Brock 1991). These structures provide insulation and protection for young from adverse environmental conditions (such as low temperatures, rain, or desiccation)

and may prevent predation. However, building such structures can be costly to the parent in terms of energy, time, and predation risk (Gauthier and Thomas 1993). Such costs are better born by some individuals than others, and hence the nest or burrow has become much more than the place where young are looked after and can be thought of as an extension of the individual's phenotype (Dawkins 1982; Soler et al. 1998). Females in many species have been shown to prefer males that build big, elaborate or particularly well-constructed nests (Soler et al. 1998; Östlund-Nilsson 2001). For example, male penduline tits (*Auriparus flaviceps*) build complex domed nests and these nests attract females, and males with the largest nests are most likely to mate, mate earlier, and have partners that faithfully look after young (Grubbauer and Hoi 1996; Szentirmai et al. 2005, Fig. 4.1a). Female choice is based on nest size even when male quality and habitat quality was held constant (Grubbauer and Hoi 1996). It turns out that the larger nests have a better insulation capacity, thereby reducing temperature fluctuations and promoting embryonic development (Grubbauer and Hoi 1996).

In mammals, den or burrow building may have evolved for purposes other than the rearing of young (Fig. 4.1b). These year round structures that provide insulation and protection are extremely commonly used among carnivore, rodent, insectivore, and lagomorph species, all of whom are subject to an intense predation pressure (Birks et al. 2005). For example, some species of deer mice (genus *Peromyscus*) build complex burrows that contain nest chambers, specific holes used as an entrance, and several long escape tunnels that minimize predation. The same burrow is used for both sleeping and looking after young. Recently behavioural experiments have mapped burrowing behaviour onto a *Peromyscus* molecular phylogeny to reveal consistent differences between species in the shape and frequency of burrow making, and that species with complex burrows with many escape tunnels have evolved from species with simpler burrowing behaviour (Weber and Hoekstra 2009).

Birds are without a doubt the master builders of the vertebrate world, using a diverse range of nesting materials and building nests of many different

Figure 4.1   Preparing for eggs and young. (**a**) A male Pendeline tit, *(Auriparus flaviceps)* with a domed shaped nests; females prefer large, well constructed nests. (**b**) A rabbit burrow with five kits. (**c**) An African weaver bird (Ploceidae) with its flask shaped nest. (**d**) The mud nest of a cliff swallow (*Petrochelidon pyrrhonota*). (**e**) A male three-spined stickleback (*Gasterosteus aculeatus*) observing a female entering his nest. (**f**) A male and female cichlid fish from Lake Tanganyika (*Cyathopharynx furcifer*) spawning in a crater nest.

shapes and sizes. Most bird species build or modify a nest in which they deposit and incubate the eggs. Some species build open nests (e.g. American robins, *Turdus migratorius*), others excavate a cavity (e.g. downy woodpecker, *Picoides pubescens*), while some bird species simply take over the cavities made by other species lining the chamber with moss grass, moss, feathers, and hair to cushion the eggs inside (e.g. burrowing owls, *Athene cunicularia*; Martin and Li 1992). African weaver birds (Ploceidae) build dramatic nests that look like flasks hanging by woven loops from branches of trees. Each nest contains hundreds of strands of grass, twigs, or leaf fibres woven tightly together, and each contains a long downward facing, narrow entrance tunnel (Hansell 2000; Fig. 4.1c). Cliff swallows (*Petrochelidon pyrrhonota*) too build complicated nests that are

made of mud mixed with bird saliva and are shaped like pottery jugs (Fig. 4.1d). A comparative phylogenetic analysis of the entire swallow family reveals that cavity nesting and nesting in mud-made structures evolved from simple burrowing (Winkler and Sheldon 1993; Sheldon et al. 2005). While most bird nests are short seasonal structures that are constructed to protect eggs, a few bird species like some of the larger raptors and megapods and some weavers have nests that last for many years and can be metres in diameter and height (Stone 1989). For example, nests of the colonial social weavers (*Philetairus socius*) not only last long but are also huge, often covering an entire tree. These multi-chambered colony-wide nests are honeycombed in shape and serve as a breeding area for hundreds of bird pairs (Bartholomew et al. 1976).

Some reptiles, amphibians, and fish construct nests. Female iguanas (e.g. *Iguana inguana*) and snakes (e.g. *Pituophis melanoleucus*) can spend a considerable amount of time (many days) as well as substantial energy excavating a burrow in hard compact soils into which they deposit fertilized eggs (Doody et al. 2009). Similarly turtles and crocodiles make burrows in which they hide their eggs. (Shine 1988). Nest building has arisen a number of times in frogs. For example, in *Hyla boan*, the nest building gladiator frogs of Brazil, males build deep nests out of sand or clay within which the fertilized eggs undergo early development (Martins et al. 1998). Other frogs are also known to make floating bubble or foam nests on the surface of ponds, streams, or the axils of terrestrial bromeliads (Haddad and Prado 2005). Fish are also known to build nests. While simple pits or (redds) are dug by many fish, like female salmon, other species like the Lake Tanganyika's cichlid *Cyathopharynx furcifer*, and three-spined sticklebacks, *Gasterosteus aculeatus*, construct remarkable nests. *Cyathopharynx furcifer* digs a crater shaped nest up to 2 metres in diameter and sticklebacks weave elaborate nests of plant material carefully glued together with a special kidney glycoprotein secretion known as spiggin (Balshine and Sloman 2010; Fig. 4.1e and 4.1f).

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Although the costs and benefits of building these structures in specific ways have not yet been fully elucidated or manipulated experimentally, the watershed of new molecular phylogenies now available are providing insights on the evolutionary pathways and trajectories for nest building. These studies are shedding light on which nest building behaviours and nest types were ancestral and which are derived. In general, these studies show that the evolutionary trajectory towards fewer, higher quality offspring has been associated with increased selection for extensive pre-natal nest preparation. This makes sense because larger offspring represent 1) a greater lure for predators and 2) a greater proportion of a parent's lifetime reproductive output, that is too valuable to leave to chance.

4.2.2   Defence of offspring

Typically species that significantly modify the substrate on which they lay eggs (nest, cavity, and burrow builders) will also vigorously defend their young against predation. Animals that defend young usually do so in territories around their nests. Many species also protect and defend their young by keeping them in or attached to the parent's body (Fig. 4.2a). For example developing young can be kept in the parents' mouths (e.g. marine catfishes and many cichlids), stomachs (e.g. myobatrachid frogs), ventral pouches (e.g. marsupials, seahorses, and pipefishes), embedded in skin
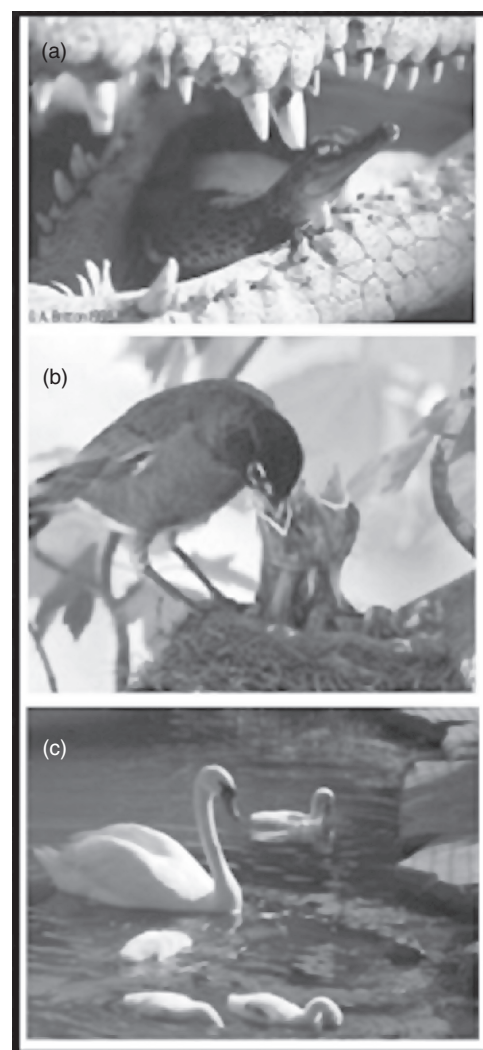

Figure 4.2   Post hatching care. (a) A Nile crocodile protecting and transporting its young in its mouth cavity (b) A robin feeding young at the nest. (c) A parent Bewick swan socially assisting its four cygnets by ensuring they have access to feeding sites.

(e.g. American banjo catfish and seadragons), or inside the gills (e.g. cave fish). Most commonly, young remain inside the females reproductive tract. Live bearing or viviparity (see below) has evolved 21–22 times across fishes (Goodwin et al. 2002), at least once in amphibians, 102–115 times in reptiles, and 1–2 times in mammals (Reynolds et al. 2002). Internal brooding is an extremely effective method of protection because the only way a predator can capture or kill the young is to injure or kill the parent or force the parent to eject or drop its young.

4.2.3 Provisioning

4.2.3.1 Provisioning of gametes
All females provision their eggs with nutrient rich yolk stores but the degree of egg provisioning varies dramatically within and across species. Eggs vary wildly across species in terms of their size, yolk, albumen hormones, and nutrient composition. Among birds, for example, the African ostrich (*Strutihio camelus*) has the largest eggs (21 cm in length and 1.4 kg), while the vervain hummingbird (*Mellisuga minima*) of Jamaica has the smallest (1 cm in length and 0.375 g) but each egg represents 16% of the female's total body mass (Bird 2004). Eggs vary not only between species but also among females within a species or population. In general, young that hatch from larger eggs have higher probability of survival especially if born in challenging environments (Nager and van Noordwijk, 1992, but see Christians 2002). But not all females make eggs of the same size, and egg size is influenced by many factors, including clutch size, the mother's phenotypic quality, environmental conditions such as food availability and density, as well as the predictability of the environmental conditions (Smith and Fretwell 1974; Christians 2002; Kindsvater et al. 2011). Parental care itself also appears to have co-evolved with egg size; species that provide intense care for longer periods tend to have only a few, large eggs, while species that do not provide care or that provide less intense care for more young tend to produce smaller eggs (Shine 1988; Sargent et al. 1987; but see Summers 2007).

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It is often assumed that the costs of provisioning and protection of young are much greater than the costs of egg production. However, a careful study on lesser black-backed gulls (*Larus fuscus*) revealed that even a small increase in the cost of making an extra egg can have substantial impacts on how much energy parents will have to rear offspring (Nager et al. 2000). Even so, some researchers still do not accept that gamete provisioning is a truly a form of parental care, preferring to use the term parental care to refer only to behaviours that follow fertilization (see also Chapter 1). Once the retention of embryos within the female reproductive tract (termed viviparity, see below) evolved, additional provisioning or nourishment of developing embryos was possible beyond gamete provision.

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4.2.3.2 Provisioning inside the parent and the evolution of live birth
In viviparous animals, the embryo develops within the mother's reproductive tract and the mother gives birth to live young, as opposed to the young developing in an egg outside of the mother's reproductive tract (known as oviparity). Viviparity can be as simple as embryo retention until hatching, or as complex as provision of nutrients by either direct absorption or by a specialized placental blood-vessel link (Reynolds et al. 2002). Viviparity has evolved among all vertebrate groups other than birds. Viviparity has the benefits of increasing offspring survival, but carries associated costs of reducing fecundity and mobility and increasing metabolic demands due to carrying offspring within the female (Wourms and Lombardi 1992; Qualls and Shine 1995). It has been argued that viviparity evolved 1) as an adaptation to cold and other rigorous climates (Tinkle and Gibbons 1977) or 2) as a way to deal with vastly unpredictable environments (Wootton 1990).

Across vertebrates, viviparity appears to have evolved independently 132 times (Blackburn 1995; Reynolds et al. 2002). A direct exchange of nutrients between mother and offspring via placenta-like structures is probably the most efficient way to provision developing offspring. However, viviparity provides offspring with direct access to maternal physiology, and selection may act on offspring to develop mechanisms for extracting resources more effectively from parents. Therefore, the placenta has been viewed as the battleground site where mother and offspring may fight over control of nutrients and the allocation of resources (Haig 1993).

Viviparity is found in all mammal species except for the five monotremes:, the platypus (Ornithorhynchidae) and the four species of spiny anteater (Tachyglossidae), which all lay a single egg. The length of time that a female mammal will carry an embryo varies enormously from 12 days in the American opossum (*Didelphis virginiana*) to 660 days in African bush elephant (*Loxodonta africana*) (Hayssen 1993). Placental mammals have long pregnancies, followed by a relatively short lactation period (see below). In contrast, marsupials have much shorter pregnancies, followed by an extended period of lactation. Viviparity has been observed in 20% of the world's reptiles. It has arisen in many different reptile families, but is especially common among lizards and snakes (evolving some 102–115 times in the squamate reptiles; Shine 1985; Reynolds et al. 2002). The retention of developing embryos with maternal provisioning (live-bearing) has evolved in all three orders of Amphibians. Live bearing remains rare in frogs and toads (Anura) and in salamanders and newts (Urodela) (less than 1% of species), but is very common in the caecilian amphibians (occurring in 3 of 9 families and about 75% of all species; Wake 1993). It is thought to have evolved from egg laying and to represent a single evolutionary origin (Wilkinson and Nussbaum 1998). Viviparity has evolved from egg laying 21–22 times across all fishes (Dulvy and Reynolds 1997), and 12 times in teleost fishes (Goodwin et al. 2002). Interestingly, viviparity is the most common form of reproduction among sharks and rays (Elasmobranches). Viviparous fish species have larger offspring than egg laying fish but surprisingly do not have fewer young (Goodwin et al. 2002). Perhaps the most famous and odd case of viviparous fish is observed in seahorses and pipefish. In these fishes, females lay the eggs in the male's enclosed brood pouch within which the eggs are fertilized, and then aerated and nourished for several weeks (Kvarnemo 2010). The male seahorses eventually give birth via a series of forward and backwards muscular contortions to one young at a time (Vincent and Sadler 1995).

4.2.3.3   *Provisioning offspring outside the parent's body*

Many researchers have argued that the most energetically costly of parental behaviours is the feeding of newly hatched or born young (Fig. 4.2b; Drent and Daan 1980; but see Nager 2006). Food supplementation studies across different taxa have amply demonstrated that increased food availability results in young that emerge earlier, grow better, and have higher survival rates (Martin 1987; Christians 2002). In many small bird species, parents make more than 500 return feeding trips to the nest each day (Norberg 1981). All female mammals feed young with milk. Although hooded seal pups (*Cystophora cristata*) nurse for only 4 days, their mothers fast during this period and transfer an astonishing 8 kg of milk each day. In just four days, pups drinking this high fat (60%) milk manage to double their body mass (from 22 kg at birth to 45 kg at weaning). This species breeds on ice floes that often break up, and these unstable ecological conditions are thought to have selected for such intensive lactation (Boness and Bowen 1996).

Female mammals secrete milk from their mammary glands. How and why did lactation evolve in mammals? Although the duration of lactation varies wildly across mammals, ranging from 4 days in hooded seals to nearly three years in chimpanzees, *Pan toglodytes* (Gittleman and Thompson 1988; Hayssen 1993), recent comparative genomics and transcriptomics studies have revealed that all three mammalian lineages share highly conserved milk protein genes known as caseins (Lefèvre et al. 2010). The highly conserved nature of these genes suggests that it is likely that the origins of lactation, and the mammary gland itself, predate the common ancestor of living mammals. Molecular and fossil evidence suggests that the first mammal-like-reptiles called therapsids appeared at the end of the Triassic or the beginning of the Jurassic (166–240 million years ago). Along with the ability to lactate, therapsids possessed many mammalian traits such as endothermy, hair, and large brains (Hayssen 1993).

The mammary gland is thought to have evolved from a sweat or skin gland and the nipple from an associated hair follicle. Four major theories have been proposed to explain why these original secreting skin cells evolved into modern day mammary glands: 1) to keep the parchment-like eggs of early mammals moist (Oftedal 2002); 2) to provide extra nutrients to young (Hayssen 1993); 3) to keep offspring free from infection and provide immuno-

logical protection (Vorbach et al. 2006); and 4) to reduce juvenile mortality by maintaining a close mother–offspring contact (Hayssen 1993). These hypotheses are not necessarily mutually exclusive. Living monotremes, like the platypus, still produce parchment-shelled eggs and feed young milk that is secreted onto a patch of skin not a nipple. Lactation reduces the importance of provisioning the offspring with nutrients for growth through additional allocation of yolk to eggs. Indeed, the egg has been completely abandoned in the marsupial and placental mammals in favour of the placenta (Oftedal 2002).

Only female mammals lactate the young. Given that young fed from maternal energy reserves are well buffered from environmental fluctuations in food supply, a number of researchers have questioned why male lactation has not evolved? In fact, males have been shown to produce small amount of milk in two species of bats; *Dyacopterus spadecius* from Malaysia and *Pteropus capistrastus* from Papua New Guinea (Francis 1994). Physiological barriers to male lactation include 1) the need for androgen suppression at puberty so that aromatase can orchestrate mammary gland development, and 2) the need for a change in the estrogen to progesterone ratio which in turn influences prolactin release and milk letdown (Daly 1979; Kunz and Hoskens 2009). While these proximate barriers clearly can be and have been surmounted in two species of male bats, functional lactation is unlikely to have been selected for in male mammals because of the high costs to males of associating with young via lost mating opportunities and paternity uncertainty (Kunz and Hoskens 2009).

Although rare, parental feeding of young among fish and amphibian species has also been reported. The young of the cichlid fish *Symphysodon discus* ingest the epidermal mucus from their parents' body (Buckley et al. 2010). Similarly, both male and female parents of the Central American convict cichlid, *Cichlasoma nigrofasciatum*, carefully lift up fallen leaves for their young providing them with benthic prey underneath the leaf litter. In Dendrobates frogs from Central America, females feed tadpoles unfertilized trophic eggs (Brust 1993).

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4.2.3.4   Nutritionally independent young and social support

The most long-lasting parental care behaviour found in vertebrates is undoubtedly the continued support provided for nutritionally independent young. This type of care is typically found only in long-lived social vertebrates. Parents can continue to help their offspring and influence their fitness by providing them access to good feeding areas (Bewick swans, *Cygnus bewickii*; Scott 1980 Fig. 4.2c), by helping them acquire and defend a territory of their own (tree-toed sloths; Montgomery and Sunquist 1978), teaching skills, and by preventing conspecific attacks (Engh et al. 2000). In cercopithecine primates, such as Japanese macaques (*Macaca fuscata*), as well as in the spotted hyaena (*Crocuta crocuta*), offspring often remain for their entire lives in the same social group

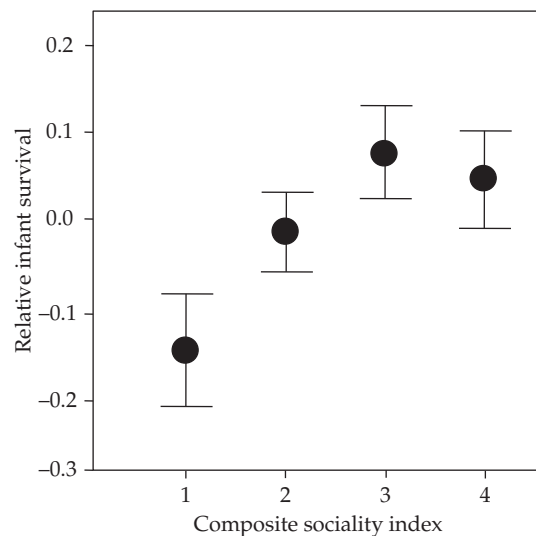**Figure 4.3**   Redrawn from Silk et al. 2003, which is based on a 16 year study of savannah baboons in Kenya. In this study there was a strong positive effect of sociality on infant survival. The percentage of surviving infants increased with the mother's composite sociality score. The composite sociality score was based on three separate measures: 1) the time spent within 5 m of another adult conspecifics, 2) how much the mother was groomed by other adults in the group, and 3) how much time she spent grooming other adults. Females with high scores were considered more socially integrated than the average female and those with low scores less socially connected. Infant survival was calculated as the proportion of that female's infants that survived to 1 year of age. The main period of strong infant dependency is 1 year. Redrawn with permission from AAAS.

as their mothers, and social rank is inherited. Based on a 16-year study on savannah baboons (*Papio cynocephalus*), in Amboseli, Kenya, Silk et al. (2003) showed that socially integrated females that had many living female relatives in the group were more likely to have their infants survive than females that scored low on the sociality index (Fig. 4.3). The fitness effects of sociality via infant survival were independent of the effects of dominance rank, and environmental conditions. In some long-lived social vertebrates, known as cooperative breeders, some members of a social group forgo reproduction and help raise offspring (Emlen 1994). Such helpers may derive direct and indirect fitness benefits from living in the social group (Wong and Balshine 2010). For example, in the Tanganyikan cichlid *Neolamprologus pulcher*, sexually mature young continue to be vigorously guarded by parents or the dominant breeders of the social group (Wong and Balshine 2010).

4.3   Transitions in care

Our understanding of parental care evolution has been greatly enhanced by reconstructing the historical transitions in patterns of care across taxa and in particular considering the variation in which sex provides parental care.

4.3.1   Parental care in fishes

Fishes provide care in a diverse fashion ranging from simple hiding of eggs, to guarding young in elaborately prepared structures or in/on the parent's body, and even the feeding of young (Balshine and Sloman 2011; Fig. 4.1e and 4.1f). However most fish species do not provide any post-fertilization parental care. Only about 30% of the 500 known fish families show some type of parental care. Most often (in 78% of all cases) care is provided by only one parent (Gross and Sargent 1985; Reynolds 2002) and male care (50–84%) is much more common than female care. Biparental care is the least common form of care in fishes (Mank et al. 2005). In some species, such as Galilee St. Peter's fish (*Sarotherodon galileaus*) and the brown bullhead (*Ameiurus nebulosus*), patterns of care are labile and paternal, maternal, and biparental care all co-exist (Blumer 1979; Balshine-Earn 1995). Based on a recent family

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level supertree for all ray-finned fishes, Mank et al. (2005) showed that male-only care has emerged at least 22 times (always within lineages with external fertilization), that biparental care arose at least 4 times, and that female-only care evolved independently at least 16 times. There have been at least 13 transitions to internal fertilization (and viviparity) all of which are associated with female care. The correlation between the mode of fertilization and the pattern of parental care suggests that there are two distinct pathways to male versus female care in fishes with the mode of fertilization (external versus internal) being the diverging starting point (Mank et al. 2005; Fig. 4.4a).

It is perhaps surprising, given that there are over 400 different fish families, that only one comparative analysis has investigated patterns of parental care within fish families (Goodwin et al. 1998). This study shows that among cichlid fishes there have been 21–30 changes from biparental to female only care, but that there have many fewer transitions in the other direction. This study supports the traditional route for parental care evolution, according to which male care evolves from none, that biparental care evolves from male care, and that female care evolves from biparental care (Gittleman 1981).

4.3.2   Parental care in amphibians

Most amphibian species abandon their eggs after laying them, but a few species display amazing parental care strategies. Some kind of parental behaviour is observed in 6–15% of the approximately 5000 anuran species (with male care being ancestral) and in 20% of around 500 salamander species (Summers et al. 2006; Summers and Earn 1999; Wells 2007). In total, parental care is thought to have evolved at least 41 times independently in this taxonomic class (Summers et al. 2006; Brown et al. 2010; K. Summers personal communication; Fig. 4.4b). The forms of parental care in amphibians are extraordinarily varied, including behaviours such as guarding the developing eggs, and carrying of eggs and tadpoles on the parents backs, on their hind legs, in dorsal pouches, vocal sacs, and even in the stomach (Corben et al. 1974). For example, male *Rhinoderma darwini* frogs carry eggs and young in their vocal sac until they have developed into
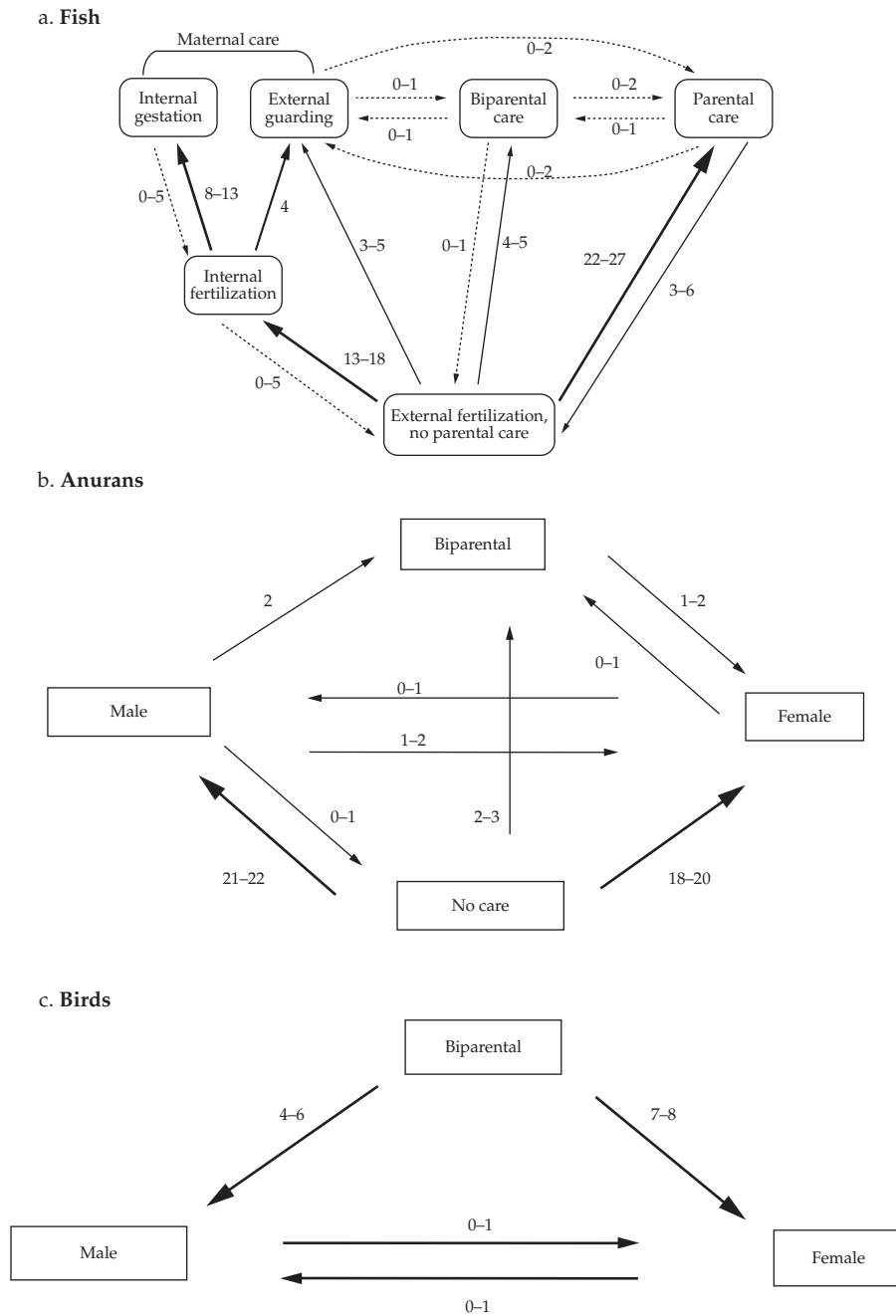
a. **Fish**

b. **Anurans**

c. **Birds**

Figure 4.4   The most recent and well-accepted evolutionary models for transitions among parental care states in **a.** fishes (taken from an analysis based on data for 228 families of ray-finned fishes Mank et al, 2005); **b.** amphibians (based on estimates from Reynolds et al. 2002, Summers et al. 2006, and Brown et al. 2010) and **c.** birds (taken from Reynolds et al. 2002). There are four possible states of parental care: no care, male, female, or biparental. The solid arrows show the likely direction of evolution among states. The number by each arrow refers to the minimum and maximum number of possible transitions. The dashed arrows refer to the selective factors promoting transitions in care. The percentage of families in each state is shown, and families including species in more than one state are counted more than once.

adults (Lutz 1947). In *Dendrobates pumlico*, another frog species from Central America, both parents will transport their young on their backs from one small water body to another and the females feed the growing tadpoles daily with unfertilized trophic eggs (Weygoldt 1987). As in fishes, patterns of parental care are varied, including male-only, female-only care and biparental care (Gross and Shine 1981; Crump 1996).

Care among amphibians is most common in tropical species where high predation rates may have forced parents to smaller water bodies that are free of many predators (Magnusson and Hero 1991), but where there is likely to be greater fluctuations in water levels, temperature, oxygen levels, and food availability (Wells 2007). Parental care could ameliorate such harsh fluctuating conditions because parents can move young around to better sites as the environmental conditions deteriorate (Bickford 2004). The size of the breeding pool size is associated with the evolution of parental care in frogs (Brown et al. 2010), and the most intensive form of parental care observed in frogs, feeding of trophic eggs to tadpoles, evolved in concert with the use of extremely small breeding pools and biparental care (Summers and Earn 1999; Brown et al. 2010).

4.3.3   Parental care in reptiles

Like fishes and amphibians the most common pattern in reptiles is the complete absence of care. Maternal care occurs only in about 1% of oviparous lizards and 3% of oviparous snakes (Shine 1988; De Fraipont et al. 1996). Care is usually limited to nest guarding, though some pythons coil around clutches and generate heat to incubate the eggs by means of shivering (Shine 1988). However maternal care is widespread in crocodilians, with the females of all 8 species guarding nests and young (Ferguson 1985; Lang 1987). Care by the male alone has never been recorded in a reptile (Shine 1988). There is currently no robust or comprehensive estimate for the number of times care has evolved in reptiles.

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4.3.4   Parental care in birds

In most bird species (90–95%) both parents look after the young chicks, while in 4–8% of bird species females alone look after young, and in 1–2% males alone do so (Silver et al. 1985; Cockburn 2006). Typically birds provide parental care by building a nest, incubating eggs, and then defending and feeding the chicks. Why do males and females birds commonly provide joint care? Males tend to provide care when the fitness derived via offspring survival is greater than benefits of abandoning young to seek out new mates (Székely et al. 1999). In many species, if males do not help raise young, some or even all the young chicks perish (Reynolds and Székely 1997). In many bird species, chicks are completely helpless at hatching, requiring constant feeding and warmth in order to grow and develop. Male and female birds are equally capable of building a nest, incubating, and feeding young (Ketterson and Nolan 1994). There are little anatomical or physiological sex specific specializations (in contrast to mammals) that would predispose one sex to provide parental care over the other sex. Simple biparental care with identical care roles, which is common in birds, may ensure that each parent can replace the other should the other die or leave (Oring 1982).

Given how common biparental care is across birds, scientists have long assumed that it is the most primitive form of care, and have concentrated their efforts in explaining how male or female care could have possibly evolved from this ancestral state (Lack 1968; Emlen 1994; Emlen and Oring 1977; Oring 1982; Székely and Reynolds 1995; Owens 2002). However, more recently researchers have argued that male-only care in the form of egg guarding is the most likely ancestral form of care in birds and that biparental and female care are derived from it (Wesołowski 1994; Varricchio et al. 2008). Initially, there was a strong rejection of the suggestion that male-only care evolved first (Burley and Johnson 2002; Tullberg et al. 2002), but in recent years the idea has received substantial support from molecular, taxonomical, and paleontological studies. First, the fossil record shows that the clutch volume to adult boy mass of three theropod dinosaurs (considered to be either closely related to birds or direct ancestors of birds) matches closely that of birds that show paternal care (Varricchio et al. 2008). Second, in the most primitive of all living birds known collectively as paleognaths (e.g. ratities and

tinamous; Harshman et al. 2008, Phillips et al. 2010), all but 2 of the 60 species in this group have male-only care (Handford and Mares 1985). The proponents of the 'male-care-evolved-first' hypothesis argue that care first evolved in males and not in females because 1) females would have been energetically constrained by producing large eggs, 2) care would have significantly decreased future female fecundity, and 3), as in fishes, territorial males could combine egg protection and the attraction of additional mates, thereby lowering the costs of paternal care to males (Ah King et al. 2004). Biparental care probably evolved from male-only care due to harsh environmental conditions favouring the constant presence of one parent for incubation or protection. Such simple biparental care would in turn provide the platform from which role specialization, uniparental double-clutching, and then male-only or female-only care emerged as environmental conditions became more benign (Wesołowski 1994, 2004). Although a formal analysis of transitions in care across bird species has yet to be conducted, a preliminary analysis based on a partly resolved tree suggests that of eight independent transitions towards female care all but one occur through a biparental care intermediate step (Reynolds et al. 2002; Fig. 4.4c). The origins of care patterns in bird continue to be an area of great excitement, stimulating lots of empirical and theoretical work.

4.3.5   Parental care in mammals

In mammals, females always provide care and they usually do so alone or as part of a kin group. In monotremes, females lay and incubate a single egg in the female's abdominal pouch (echidnas, Tachyglossidae) or in a burrow (platypus, Ornithorhynchidae). Female monotremes do not possess nipples, but instead their milk oozes out of their skin and young lick milk from the milk-soaked fur (Brawand et al. 2008). Female marsupials provide care for their extremely altricial young within a pouch or skin fold that contains a mammary gland to which the offspring remains permanently attached as the teat swells in its mouth (Long 1969). Although marsupials have very short gestational periods (4–5 weeks), the young are nursed

for nearly a year (Russell 1982). In the placental mammals, there is a wide range of parental care by females after birth. In some species such as the guinea pig, *Cavia porcellus*, the young are extremely precocial. In this species, the young are active soon after birth, can feed themselves and do not require a parent to keep warm (Laurien-Kehnen and Trillmich 2003). Other species, such as most other rodents, cats, and dogs, have highly dependent young that need to be warmed, fed and protected.

Males assist in care in only 9–10% of mammalian genera, including primates, carnivores, and rodents (Kleiman and Malcolm 1981). The general assumption is that female care among mammals is primitive and that biparental care is derived (Reichard and Boesch 2003). When males provide care, they typically carry, feed, warm, and guard the young against predators. In Siberian hamsters, *Phadopus campbelli*, males assist in the female's delivery, clear the nostrils to open the pups' airways, and lick and clean the pups of membranes immediately after birth (Jones and Wynne-Edwards 2000). In the California mouse, *Peromyscus californicus*, the removal of the male results in lower offspring survival (Cantoni and Brown 1997). The decreased survival is not a result of a reduction in care but the presence of infanticidal intruders who try to mate with the mother. Although biparental care is certainly rare in mammals, it appears to have evolved from female care 9 times and to have been lost 3 times (Reynolds et al. 2002). Males will care more or less depending on the costs of lost mating opportunities, and reduced mobility or foraging success caused by looking after young (Woodroffe and Vincent 1994).

4.4   Parental care in humans

Compared with other mammals, *Homo sapiens* provide intensive and long lasting post-natal parental care for a relatively small number of offspring. Human mothers provide nutrition and protection during the 9 months of pregnancy and supply milk from their own reserves during infancy, and both parents usually continue to support their offspring for their entire lifespan. There are at least three distinctive characteristics of human parental care behaviour that is rarely observed in other mammals

and that require explanation: 1) the exceptionally long period of parental care, 2) the considerable amount of male care, and 3) kin support in rearing young (Hill and Kaplan 1999).

4.4.1 Exceptionally long parental care duration

Humans look after their offspring through infancy, childhood, puberty, and often well after sexual maturity. This represents an unusually long period of dependence, even among primates (Hill and Kaplan 1999). For example, human parents continue to provide financial and emotional support for their offspring, even after their offspring have become parents in their own right. What event in hominid evolution selected for this long parental care period? The fossil record suggests that over the last 4 million years, brain volume has increased threefold and this change is associated with a doubling in the developmental period (Alexander 1979). Dunbar (1993) proposed that large brains were necessary early in hominid evolution to deal with the complexities of social life and in support of this idea he demonstrated that brain size covaries with group size among non-human primates. The long developmental period that arose with large brains would have enabled sufficient time to learn how to deal with the complexities of social living (coalition and cooperation) and such skills would have be necessary to control access to resources and to coordinate competition with other groups (Dunbar 2000). Parenting by both mothers and fathers would have supported this long developmental period and selected for the efficient acquisition of social skills and competences (Geary and Flinn 2001).

4.4.2 Male care and support

Although male care is extremely rare among mammals, male humans care for young in every culture studied to date (Marlowe 2000). Men provide social protection and material resources to their wives and children (Marlowe 2000). In some cultures, men spend time holding and babysitting their children. For example, Hadza men from Tanzania protect their offspring by remaining close to them for 12%
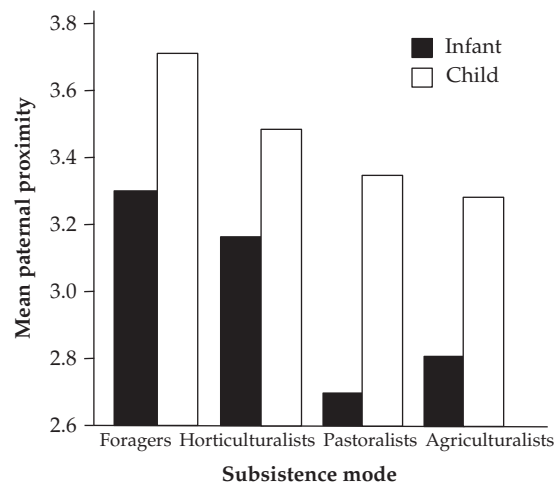

Figure 4.5 Data of the average father–offspring proximity according to major subsistence mode, based on an original sample of 186 Standard Cross Cultural societies, and redrawn from Marlowe 2000.
Hunter-gatherers or foragers (n = 42) practice no agriculture; Horticulturalists (n = 70) get the majority of their diet from agriculture; Pastoralist (n = 17) acquire the majority of their diet from domesticated animals; and Agriculturists (n = 57) practice intense forms of agriculture using irrigation, fertilization, and plows. Used with permission from Elsevier.

of the daytime and 100% of time of the nighttime (Marlowe 1999). The degree of male involvement with children varies widely with ecological and social circumstances. For example, men in foraging societies tend to provide the most child care, interacting closely and regularly with their children for much longer periods than men in horticulturalist, agriculturist, and pastoralist societies (Marlowe 2000; Fig. 4.5).

Why do male humans always provide some type of care? Two main hypotheses have been put forth: 1) paternal care in humans was selected for by the need for male provisioning especially during lactation or gestation periods when women could not hunt efficiently (Washburn and Lancaster 1968; Deacon 1997); 2) paternal care was selected as biproduct of mate guarding (van Rhijn 1991; Hawkes 2004). A number of authors have argued that men may end up providing parental care as a consequence of protecting a mate against harassment from other males (Smuts 1987; Hawkes 2004). The parental care via mate guarding hypothesis has received more support from the available ethnology

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and human behavioural ecology data than the provisioning hypothesis (Kelly 1995). Male provisioning and defence of offspring appears to have had more to do with attracting mates and competing with other men over mates rather than providing care for children (Hill and Kaplan 1988). For example, a hunter's family rarely receives more food than the rest of the village or social group (Hill and Kaplan 1988). Hence, male hunting and defence are effectively a kind of public good, as these characteristics do not only help the man's wife and his offspring but benefit the whole social group (Hawkes and Bliege Bird 2002). Great hunters and fighters develop reputations and gain more mates. The costly signals of male quality demonstrated via hunting capacity appear to more strongly line up with status and mating access than with male parental provisioning *per se* (Hawkes and Bliege Bird 2002). In essence, what appears to be a form of male parental care may in fact be represent a form of male mating effort.

4.4.3   Support from constellations of kin

While women and their children clearly form the nucleus of a family, human families are typically embedded in wider kin networks that provide a considerable amount of assistance in the provisioning, protection, and socialization of children (Hrdy 2009). Humans are unusual among mammals in their strong reliance on extended kin assistance for rearing offspring. The kin that help rear offspring are often an older, non-reproductive sibling or an older relative like a grandmother or an aunt (Hawkes et al. 1998; Shanley and Kirkwood 2001). These relatives operate as a 'helper at the nest' significantly increasing reproductive success of their breeding relatives (Hrdy 2009). It has been hypothesized that menopause (the cessation of ovarian function and female fertility, that occurs between the ages of 40–60) is an adaptation to extend post-reproductive lifespan and increases investment by older females (Hawkes 2003; Lahdenpera et al. 2004; but see Tang 1996). Older females with extensive experience of both social and physical environments can increase the fitness of their children and grandchildren by transferring valuable social survival skills and connections and

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teaching them how to better compete and negotiate social environments within a kin network (Hawkes 2003).

4.4.4   Humans as a study system for parental care

Although humans are unique in their long parental care duration and in the degree to which kin help raise offspring, humans, like other species, allocate their investment in offspring judiciously considering factors such as parentage, offspring quality, and parental resources. These patterns are best demonstrated in studies of the cross-cultural variation in parental neglect, offspring abandonment, and infanticide (Daly and Wilson 1988). Collectively they show that parentage, offspring quality, and the availability of parental resources all influence care in our own species. Parentage matters: human parents spend the most money on genetic children from current relationships and least on their stepchildren, especially those from relationships that have already ended (Anderson et al. 2007). It turns out that having a step-parent is the most powerful epidemiological risk factor for child abuse, suggesting that parental investment is strongly influenced by relatedness (Davis and Daly 1997; Westneat and Sherman 1991; but see Temrin et al. 2000 and Daly and Wilson 2001). Among the Aché Indians, a traditional hunter-gather tribe from Paraguay, children who have lost their natural fathers have a significantly increased risk of dying before the age of 15 compared to children whose fathers remain around (Hill and Kaplan 1988). These children are apparently commonly killed by adult men from within their social group who do not want to provide for young that are not their own (Hill and Kaplan 1988). Offspring quality matters: although very much a strategy of last resort, parents will sometimes abandon or even kill their own offspring. The frequency of infanticide increases if the offspring is seriously ill, has major birth defects, severe physical deformities, and hence poor probable future fitness (Daly and Wilson 1988). Parental resources matter: when the social and physical costs of raising a child are too high, humans across different societies will commit infanticide or simply abandon offspring (Daly and Wilson 1988). In this

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way infanticide can be seen as a strategic allocation decision occurring more regularly when a second baby is born soon after the last one or when there are too few resources to raise a child. In Canada, France, and England, infanticide is more common among unwed mothers (Daly and Wilson 1988). Interestingly, while the practice of twin killing is rare (1%) in societies where mothers regularly get help from their female relatives in rearing children, it is a fairly common practice (43%) in societies where mothers have to carry the bulk of the parenthood burden alone (Granzberg 1973).

These cross-cultural studies of infanticide demonstrate further that environments can pose differential costs associated with parental provisioning (Daly and Wilson 1984). For example, in agricultural and pastoral societies in African, infanticide rates are extremely low (Hrdy 1994). In many of these societies, women are calorically self-sufficient, direct paternal investment is small, and the temporary fostering or more permanent adoption of children to kin is extremely common (Hrdy 1994; Marlowe 2000). In contrast, in New Guinean and Amazonian hunter-gather tribal societies, infanticide rates are much higher (12–38%). In these societies adoption and fostering is not a viable option because when foraging conditions worsen everyone in the group faces the same deteriorating foraging conditions (Hill and Kaplan 1988). Also, in these societies, men invest a great deal in care, and children are heavily dependent on male input as the lack of paternal support increases the risk for infanticide (Hill and Kaplan 1988).

In summary, in humans the importance of group solidarity and cooperation, in the face of intense intergroup competition has apparently selected for a very long care duration, as well as group and biparental care of offspring. In addition, the evolution of menopause and the presence of non-reproductive helpers with little incentive to disperse has dramatically changed the cost–benefits ratio for providing care in humans.

4.5 Concluding remarks

The most obvious conclusion to draw from this review is that parental care is highly dynamic and variable. Although, we have a fairly solid understanding of factors that determine whether a parent will or will not provide care, we still need to develop a firm theoretical foundation to understand the variation that exists in parental care form. Why, for example, do some species look after their young in a nest while other species do so on or in the parental body? Several promising developments (all comparative and based on molecular revolution) are already significantly advancing our understanding of the evolution of parental care. From a theoretical prospective, the explosion of recent studies on sexual conflict over the extent of care for young will undoubtedly shed light on the generality of how life history and ecological variables interact to mediate levels and types of parental behaviour. More experiments and broad-scaled phylogenetically based comparative anslyses are needed to explore if particular forms or types of care are associated with high or low levels of sexual conflict over care. Further progress is highly likely if we continue to combine broad-scale approaches and the levels of analysis on which we investigate parental care (i.e. adaptive function, proximate mechanisms, evolutionary history, and development).

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