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COMMENTARY / OPINION

Insights into Parental Care from Studies on Non-mammalian Vertebrates

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Abstract

Parental care has attracted attention from both proximate and ultimate perspectives. While understanding the adaptive significance of care has been the focus of work in diverse organisms in behavioral ecology, most of what we know about the proximate mechanisms underlying parental care behavior comes from studies in mammals. Although studies on mammals have greatly improved our understanding of care, viewing parental care solely through a mammalian lens can limit our understanding. Here, we draw upon examples from non-mammalian vertebrate systems to show that in many ways mammals are the exception rather than the rule for caregiving: across vertebrates, maternal care is often not the ancestral or the most common mode of care and fathering is not derivative of mothering. Embracing the diversity of parental care can improve our understanding of both the proximate basis and adaptive significance of parental care and the affective processes involved in caregiving.

Keywords Evolution of care · Male uniparental care · Proximate mechanisms of care · Toolkit hypothesis · Social decision-making network

Parental Care as an Affective Process

Affective processes play a central role in mediating interactions between caregivers and their dependents. For example, becoming a parent is associated with dynamic changes in emotion, which allow parents to assess and respond to the changing needs of their offspring and promote adaptive development (reviewed in Dix, 1991). This ability of parents to perceive and respond to the needs of their offspring relies upon fascinating neuroendocrine machinery (reviewed in Pereira & Ferreira, 2016). Therefore, by studying the proximate mechanisms of caregiving, we can gain insight into the neural mechanisms underlying affective processes. For example, studies on maternal brains during caregiving have revealed the importance of the mesocorticolimbic dopamine system and medial preoptic area in motivation (reviewed in Pereira & Ferreira, 2016 and Numan, 2007), the role of the medial amygdala in aversion (reviewed in Numan, 2007), and the role of the medial preoptic area in attraction (reviewed in Numan, 2007). However, much of what we know about the neuroendocrine basis of care comes from studies on mammals and maternal care. In this article, we argue that a non-mammalian perspective can change the way we think about parental care, especially our understanding of the proximate mechanisms of paternal care (i.e., care provided by fathers).

Limitations of an Exclusively Mammalian Perspective on Parental Care

Non-human mammalian models for parental care such as mouse, *Mus musculus* (e.g., Kohl & Dulac, 2018), rats, *Rattus norvegius* (e.g., Numan 1994, 2007; Champagne & Meaney, 2007), several species of *Microtus* voles (e.g., McGuire & Novak, 1984, 1986; McGraw & Young, 2010),

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and rhesus macaques, *Macaca mulatta* (e.g., Suomi, 1997, Mastripieri, 1998, Stevens et al., 2009) have played an important role in shaping our understanding of parental care and its underlying neural, genetic, endocrine, and molecular basis. Here, we argue that thinking about parental care in a broader evolutionary context, specifically by considering the diversity of caregiving among vertebrates, challenges some of the assumptions about care that an exclusive focus on mammalian models might lead us to believe. In particular, non-mammalian models have an important role to play in changing the way we think about fathers.

Because paternal care is rare in mammals, and mothers experience dramatic and fascinating neuroendocrine changes associated with pregnancy and lactation, a mammalian perspective on caregiving often focuses primarily on females. When mammalian fathers do provide care, it is alongside females, i.e., as biparental care, and this may have contributed to the perception that paternal care is derivative of and inferior to maternal care (e.g., Kinsley & Amory-Meyer, 2011). This problem is compounded because it is challenging to study fathers independent of mothers in mammals. For example, studies seeking to isolate the effect of fathers on offspring behavior might remove the father and then look at consequences for offspring (e.g., McGuire et al., 1992; Harrison et al., 2009). However, in biparental systems, mothers may alter their behavior to compensate when fathers are removed (McNamara et al., 2003), or may allocate care depending on the father's attributes (e.g., Curley et al., 2011), which makes it difficult to identify the specific contributions of fathers. In addition to being biparental, mammalian models for paternal care are also often monogamous and form pair bonds (e.g., prairie voles, *Microtus ochrogaster*, Wang et al., 1999; California mouse, *Peromyscus californicus*, Zhao & Marler, 2014; titi monkeys, *Callicebus cupreus*, Bales et al., 2017), making it difficult to parse the mechanistic basis of paternal care from the formation of pair bonds. Another approach to studying paternal care in mammals is to focus on species where virgin males provide alloparental care (e.g., Table 1 in Bales & Saltzman, 2016) and/or when male care is a lab artifact rather than a naturally occurring behavior (e.g., gray-tailed voles, *Microtus canicaudus*, and meadow voles, *M. pennsylvanicus*, reviewed in Wolff, 2003). However, it can be difficult to interpret the findings of these studies because the ecological relevance of male caregiving in these systems is not always clear.

Many of these pitfalls can be avoided by studying the mechanisms of male caregiving in species that show male uniparental care and by leveraging natural variation in caregiving (e.g., poison frogs, Roland & O'Connell, 2015; Fischer et al., 2019). Studies in non-mammals can provide a new perspective on parental care, especially with respect to fatherhood. In this paper, we first summarize the diversity of modes and forms of care that have evolved in each of the major vertebrate lineages to address some common assumptions about care that come from a mammal-centric view. For brevity, we will not discuss care in invertebrates but note that the tremendous diversity of caregiving in insects and other invertebrates is highly deserving of further study (reviewed in Trumbo, 2012). Second, we provide an overview of the commonalities between male and female caregivers in the forms of care provided and the mechanisms underlying care behavior to show that paternal care is not as distinct from maternal care as a mammalian perspective may lead us to believe. We also summarize growing evidence that care behavior is typically regulated by the same underlying mechanisms regardless of taxa. Finally, we conclude by arguing that embracing the diversity of parental care across vertebrates can improve our understanding of both the proximate basis and adaptive significance of parental care.

Parental Care Is Diverse and Widespread in Vertebrates

As humans we think of caregiving as lactation, intimate mother-offspring tactile interactions, and long periods of dependence. Although care may not manifest exactly like this in other taxa, other animals also go to great lengths to promote the survival of their offspring. For example, poison frog parents piggyback their tadpoles to water and provision them with unfertilized eggs (Schulte et al., 2020) and some species of teleosts (e.g., *Tilapia*) fan their pectoral fins to circulate oxygen-rich water over their developing embryos (Perrone & Zaret, 1979). Several species of passerine birds incubate their broods and provision their begging nestlings (Wang & Richter, 2021), and some python snakes incubate their eggs by shivering (Shine, 1988).

Although parental care is ubiquitous among mammals and birds (except for ~1% of bird species that are brood parasites, Antonson et al., 2020), care is evolutionarily rare when considering all vertebrate species. Only ~30% of fish families, 6–15% of anurans (frogs and toads), and ~20% of salamander species exhibit parental care (Balshine, 2012). Care in reptiles is also extremely rare; only ~3% of 938 squamate reptile genera exhibit care (Reynolds et al., 2002), although care is present in all 24 crocodilian species (Murray et al., 2020). When animals do provide care, the roles and responsibilities of parents are highly variable within and across taxa. In some species, the burden of care falls on only the mothers (female uniparental care) or only the fathers (male uniparental care). In other species, both mothers and fathers provide care (biparental care). Occasionally, care is provided by individuals who are not the parents, i.e., alloparental care and cooperative breeding (e.g., mammals and birds, Riedman, 1982; fishes, Wisenden, 1999).

In mammals, female uniparental care is the ancestral state. Biparental care has evolved from female uniparental care nine times and has been lost (returning to female uniparental care) three times (Reynolds et al., 2002). Therefore, in mammals, the only way that male care has evolved is during the evolutionary transition from female uniparental care to biparental care, i.e., the only route to fathering behavior in mammals is to go through mothers first. The evolution of the placenta and internal fertilization (and possibly lactation, see Balshine, 2012) may have made it unlikely for male uniparental care to evolve in mammals, because male mammals cannot gestate or lactate. As a result, the view that paternal care is distinct from and supplementary to maternal care may be at least partially true for mammals: male care is always derived from female care, always occurs alongside female care, and care often occurs in ways that are "female-specific."

In contrast, in non-mammalian vertebrates, the assumption that paternal care is lesser than and/or inherently different from maternal care is far from true. Some paternal care strategies even take the form of typical "maternal" care such as pregnancy or lactation. For example, in seahorses and pipefishes (Stölting & Wilson, 2007) and Darwin's frog, *Rhinoderma darwinii* (Goicoechea et al., 1986), males undergo "pregnancy," and in ring doves (*Streptopelia risoria*) and blue discus fish (*Symphysodon aequifasciatus*), fathers produce "milk" to provision their offspring (Schradin & Anzenberger, 1999), via the same mechanism (prolactin) as lactation in mammals! Indeed, in some non-mammalian vertebrate lineages, fathering is not exclusively an evolutionary offshoot of mothering and is often ancestral to maternal care. For example, male uniparental care has evolved multiple times from no care: at least 30 times in fishes (Mank et al., 2005, Sutton & Wilson, 2019) and at least 22 times in anurans (Fig. 1, Reynolds et al., 2002).

In addition, in non-mammalian vertebrates, uniparental female care is often the exception rather than the rule for parental care. For example, 90–95% of bird species are biparental (Balshine, 2012), and both sexes perform similar behaviors such as nest building, incubation, and provisioning of offspring (Wang & Richter, 2021). In fishes, male uniparental care is the "rule," as this is the most common mode of care (apart from no care; Balshine, 2012). There are also some species of birds and amphibians in which males are the sole caregiver (Reynolds et al., 2002). For example, in the wattled jacana bird (*Jacana jacana*), males provide extensive care to their offspring in the form of incubation, provisioning, and defense; females neither incubate nor provision except in cases where the male has been killed (Emlen & Wrege, 2004). At least in these species with male uniparental care, we clearly cannot assume that fathers are supplementary to mothers.

While uniparental female care is the dominant mode of caregiving in mammals, parental care is highly evolutionarily labile in non-mammalian vertebrate lineages (Reynolds et al., 2002). Evolutionary transitions between four modes of parental care (no care, female uniparental, biparental, male uniparental) have occurred in fishes and amphibians, often in both directions (Fig. 2). In birds, there have been at least four transitions from biparental to male uniparental care and at least seven transitions from biparental to female uniparental care (Reynolds et al., 2002). Parental care is generally understudied in reptiles (Doody et al., 2013), but it is known that some species show female uniparental care (e.g., squamates, Halliwell et al., 2017) and/or biparental care (e.g., crocodilians; Lang et al., 1986; Whitaker, 2007) and several have no care (Reynolds et al., 2002). No reptiles are known to show male uniparental care (Shine, 1988).

This brief evolutionary survey of caregiving in vertebrates suggests that male care, although rare in mammals, is widespread in other vertebrates. It is not just mothers who take extraordinary measures to care for their offspring; fathers do it too, often in similar ways as mothers (offspring provisioning, nest building, and even "pregnancy"). This brief survey of the evolutionary lability of caregiving in vertebrates also suggests that there are many independent origins of care, and once care evolves, it seems harder to lose, likely due to coevolution between offspring and parents that make offspring reliant on care (Reynolds et al., 2002; Royle et al., 2012). Although rare, there are a few cases of evolutionary losses of care in vertebrates and invertebrates (i.e., transitions from female uniparental, male uniparental, or biparental care to no care, e.g., white stickleback fish, *Gasterosteus aculeatus*, Blouw, 1996; burying beetles, *Nicrophorus vespilloides*, Jarrett, Evans et al., 2018; Jarrett, Rebar et al., 2018; avian brood parasites, Antonson et al., 2020). These systems offer a great opportunity to understand whether the proximate and ultimate mechanisms favoring the evolution of care can work both forwards and backwards (e.g., Lynch et al., 2020). This evolutionary perspective on care also shows us that different modes of care can swap back and forth, but there are constraints that influence what can happen next (e.g., the evolution of internal fertilization can favor the evolution of maternal care and disfavor male uniparental care; Mank et al., 2005).

The Neuroendocrine Mechanisms Underlying Parental Care Show Similarities Across Taxonomic Groups and Between the Sexes

Given this diversity in strategies for providing care, it is remarkable that many of the underlying molecular, genetic, hormonal, and neural mechanisms appear to be highly conserved. Interestingly, the literature has repeatedly implicated the same molecules (e.g., galanin, prolactin, oxytocin) and the same brain region (the preoptic area [POA] of the hypothalamus) in caregiving in vertebrates (O'Connell & Hofmann, 2011; Dulac et al., 2014). For example, prolactin promotes not only lactation in mammals, but also caregiving behavior and the

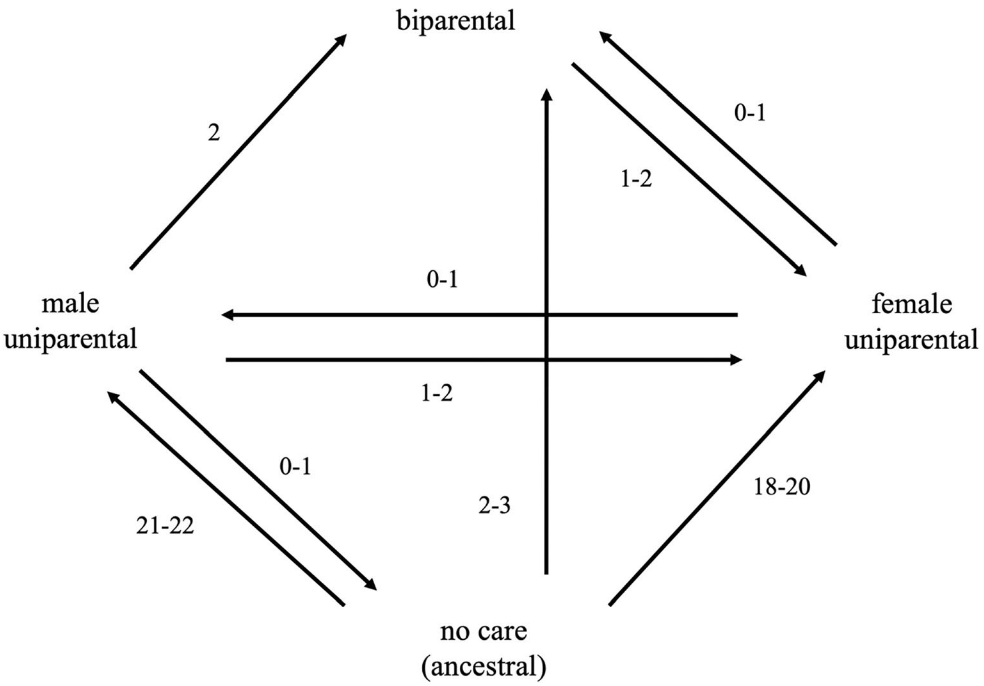

Fig. 1 The number and direction of evolutionary transitions between four modes of parental care in anurans (frogs and toads). Arrows represent the direction of the evolutionary transition from one mode of care to another and the number by each arrow represents the number of transitions in that direction. For example, biparental care has evolved from male uniparental care 2 times and from no care 2–3 times. The number of evolutionary transitions is often represented as a range, because these numbers depend on how the phylogeny was resolved. Figure modified from Reynolds et al. 2002.

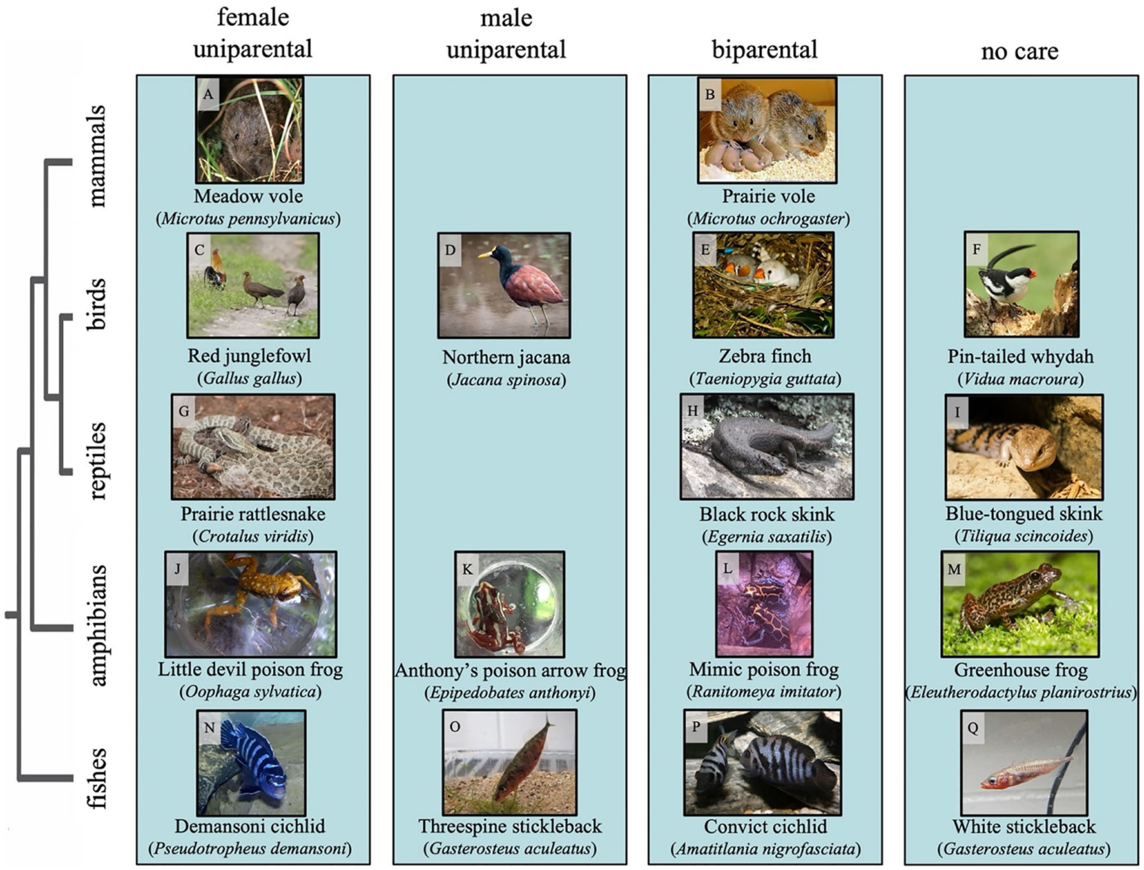

Fig. 2 Simplified phylogeny showing examples of different modes of parental care (female uniparental, male uniparental, biparental, no care) that exists within each of the major vertebrate lineages. Figure modified from Dulac et al. 2014. The "no care" column specifically shows species that have evolutionarily lost parental care. Photo credits: Phil Myers (A), Todd Ahern (B), Lip Kee (C), Becky Matsubara (D), William Warby (E), Alan Manson (F), Jared Tarbell (G), Peter Shanks (H), Eric Kilby (I), Eva Fischer (J, K), Jenn Moss (L), Brian Gratwicke (M), Lee Nachtigal (N), Colby Behrens (O, Q), Dean Pemberton (P). Photos (A)–(I), (M), (N), (P) were obtained from creativecommons.org

development of crop milk in birds (Farrar et al., 2021). This growing evidence suggests that the mechanisms underlying caregiving are evolutionarily ancient, and caregiving may have evolved convergently via the co-option of conserved molecular mechanisms at each independent origin, i.e., the toolkit hypothesis for social behavior (Toth & Robinson, 2007, Rittschof & Robinson, 2016, Bukhari et al., 2019).

The mechanisms underlying care behavior are also often conserved between the sexes (e.g., see Rogers & Bales, 2019). Hormones like prolactin, follicle-stimulating hormone, and luteinizing hormone that were named for their effects in females on lactation and ovarian follicles also play roles in male caregiving. For example, in threespine stickleback fish (*Gasterosteus aculeatus*) which provide male uniparental care, prolactin is associated with incubation behavior (fanning) in fathers (Páll et al., 2004). Indeed, there is growing evidence in vertebrates that the same molecular mechanisms are activated regardless of who is providing care: mother, father, sibling, non-relative (Stagkourakis et al., 2020). For example, neuropeptide signaling can activate the same neural pathways in both mothers and fathers (Wynne-Edwards & Timonin, 2007). In male stickleback, the genes that are differentially expressed in the brain as a father proceeds through the stages of caregiving (territorial defense, nest building, incubating eggs, caring for newly-hatched offspring) are also differentially expressed in the brains of female mice as they transition from pregnancy to the post-partum periods (Bukhari et al., 2019). In poison frogs (*Ranitomeya imitator*, *Oophaga sylvatica*, *Dendrobates tinctorius*), there is a signature of "care" in the brain (i.e., increased neural activity in the medial pallium and preoptic area during tadpole transport), irrespective of whether the caregiver is male or female (Fischer et al., 2019). Despite this evidence for important similarities between male and female caregivers, there are of course important processes that are unique to each sex, e.g., processes associated with pregnancy and lactation in mammalian females. Nonmammalian models of care have an important role to play in improving our general understanding of care because they offer many diverse examples of care that can make it easier to isolate the signal of care independent of the strong signal of lactation and pregnancy.

In summary, there is growing evidence that the mechanisms underlying care and the forms of caregiving (e.g., provisioning, defense, nest building, and even pregnancy) are often conserved across the sexes and across taxa. This suggests that caregiving in both sexes and across vertebrate taxa likely evolved via the co-option of conserved mechanisms.

Conclusions and Areas for Future Research

In this article, we argue that viewing parental care from a nonmammalian perspective can change the way we think about the lability of behavior both between the sexes and during evolution. Parental care is closely linked with affective processes (e.g., emotion, motivation, attraction, aversion); therefore, studying care can also inform our understanding of the proximate basis and evolution of affective processes. Broadening the array of taxa considered as subjects can help fill in gaps in our understanding of the proximate basis for care for at least three reasons. First, there are some behaviors or breeding systems (e.g., male uniparental care) that simply are not available to study in traditional mammalian models; therefore, a comprehensive understanding of the proximate basis and adaptive significance of parental care requires a large cast of characters as subjects. Studying care in male uniparental systems is also valuable because it provides an opportunity to understand the affective processes involved in caregiving, independent of pregnancy and lactation. Second, nonmammalian taxa like fishes and anurans that have experienced several transitions between four modes of parental care provide a gold mine of opportunities to understand how mechanisms for care evolve when modes of caregiving change among close relatives. Third, because the mechanisms underlying the great diversity of parental care in vertebrates are deeply conserved across taxa and between the sexes, diversity offers an opportunity to understand how mechanisms can be tweaked to generate phenotypic variation. In other words, how do behaviorally divergent organisms differ at a mechanistic level, and at what level of biological organization are such tweaks evident? At the ligand or receptor level? In different brain areas? Cell types? During development? In gene regulatory mechanisms that confer specificity, e.g., only expressed in a key cell type at a key moment in time? Answers to these questions can provide fundamental insights into how mechanisms of behavior work and evolve.

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