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Chapter 11

c0011 Parental Care, Sexual Selection, and Mating Systems in Neotropical Poison Frogs

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s0005 INTRODUCTION

p0010 The neotropical poison frogs of the family Dendrobatidae are distributed from Nicaragua in Central America to Brazil and Bolivia in South America. These frogs have received considerable attention from scientists and laymen alike, mainly because of the extreme toxicity and bright coloration in many species that has evolved in the context of aposematism (Myers and Daly, 1976, 1983). However, many species in this clade also show elaborate and conspicuous social behaviors, particularly in the contexts of mating strategies and parental care (Summers, 1992a; Summers and McKeon, 2004; Wells, 2007). Whether these conspicuous behaviors have evolved in part because toxicity has permitted the evolution of such behaviors, or because bright coloration provides a visual signal that can then evolve in response to evolutionary forces in the context of sexual selection, is an open question. We note, however, that there are many species of frogs in this family that are not, in fact, toxic or brightly colored, yet do display elaborate and conspicuous patterns of territoriality, courtship, mating, and parental care (some of these species will be discussed below). The presence of these complex yet observable social interactions have made dendrobatid frogs a focal point of interest for researchers interested in the influence of ecological and social factors on the evolution of parental care and mating strategies. In this chapter we review some general theoretical developments focused on the interrelationships of sexual selection and parental care, focusing on the work of Trivers (1972) (see also Requena *et al.*, Chapter 8 of this volume), and then explore how research on neotropical poison frogs has contributed to our understanding of specific issues of special interest in this broad area.

Sexual Selection. http://dx.doi.org/10.1016/B978-0-12-416028-6.00011-6

s0010 THEORETICAL BACKGROUND

p0015 Building on key insights by Bateman (1948) concerning the relationship between the gamete size dimorphism that defines male and female identities and the effect of multiple mating on fecundity in males and females, and Williams (1966) on the effect of parental care on sex roles, Trivers (1972) developed the general argument that sexual selection is controlled by patterns of relative parental investment between the sexes. Trivers (1972) argued that if one sex provides substantially more parental investment per offspring (defined as investment that reduces the parents' ability to produce other offspring), that sex will become a limiting resource for which the opposite sex will compete. In most species that have been studied, females provide more parental investment than males, and males compete intensely for mating opportunities (Andersson, 1994). This argument has dominated the discussion of this topic in the literature ever since, and although various alternative viewpoints have been presented (see, for example, Tang-Martinez and Ryder, 2005; Roughgarden *et al.*, 2006), Trivers' general argument continues to be the dominant paradigm of sexual selection (Kokko and Jennions, 2008).

p0020 Trivers (1972) proposed that key empirical tests of the hypothesized relationship between parental investment and mating systems would come from species in which the typical patterns of parental investment are reversed (i.e., males invest substantially more per offspring than females). Under these circumstances, he predicted that females would evolve to be the more competitive sex, and males should be relatively selective about mating. In this review, we highlight work on sexual selection and parental investment in several species of poison frogs that provide an alternative perspective on how parental investment and sexual selection can interact.

p0025 Following Trivers' (1972) paper, a number of key contributions highlighted other factors that influence sexual selection. Emlen and Oring (1977) emphasized the effect of ecological factors on the "environmental polygamy potential", and developed the concept of the operational sex ratio (OSR) as a key influence on sexual selection and mating systems. While some authors have advocated the OSR (and related statistics) as a key measure of the strength of sexual selection (e.g., Shuster and Wade, 2003), there are significant problems with this approach (reviewed in Klug *et al.*, 2010). However, the role of ecological factors in the evolution of both parental care and mating systems has continued to be a major theme in behavioral ecology and evolution (e.g., Okuda, 1999; Kokko and Monaghan, 2001; Kokko and Rankin, 2006).

p0030 Clutton-Brock and Vincent (1991) developed the concept of the "Potential Reproductive Rate", which was argued to be a bridge between relative parental investment and sexual selection, but more easily measured than parental investment. Several authors (e.g., Clutton-Brock and Parker, 1992; Arnold and Duvall, 1994) developed mathematical models of the influence of relative parental investment on sexual selection, focusing on the idea of "time-out" from the mating pool. The results of these models strongly supported the logic developed by Trivers in his 1972 paper. More recent mathematical models (e.g., Kokko and Jennions, 2008) support many of Trivers' (1972) original arguments, although with some differences concerning the effect of sexual selection on the evolution of parental care (see below).

p0035 It should be noted that the relationship between parental investment and sexual selection was only one among many important concepts that have emerged from Trivers' (1972) paper. For example, the paper also made major contributions to our understanding of the evolution of parental care (Kokko and Jennions, 2008), and to sexual conflict (Lessells, 2012).

p0040 With regard to the evolution of parental care (and specifically which sex should provide care when care is provided), Trivers (1972) made three major arguments: first, that high levels of investment in nutrient-rich eggs by females would make them more likely than males to provide care; second, that higher uncertainty of parentage for males would militate against male parental care; and third, that sexual selection acting on males would select against paternal care.

p0045 Each of these arguments has generated substantial controversy. Dawkins and Carlisle (1976) contended that the first argument involved a "Concorde Fallacy", in that previous investment (in gametes) does not reliably predict future returns on subsequent investment (in parental care). They proposed instead that the sex which has the opportunity to desert first will do so. The Concorde Fallacy argument has been influential, although some authors have pointed out that past investment will predict likely future returns on investment under certain circumstances (e.g., Coleman and Gross, 1991). With regard to the effect of opportunities for desertion, substantial empirical evidence contradicts the predictions of this hypothesis (Clutton-Brock, 1991).

p0050 The second argument was criticized extensively by Maynard Smith (1978) and Werren *et al.* (1980), who argued that, assuming paternity remained constant across broods, uncertainty of paternity should not influence the evolution of male care. This argument was in turn criticized as incomplete (e.g., Westneat and Sherman, 1993). In 1997, Queller developed a simple yet elegant model that demonstrated the general validity of Trivers' (1972) original argument that uncertainty of paternity will select against the evolution of male parental care. More recent modeling efforts have confirmed this general point (e.g., Kokko and Jennions, 2008). Large-scale comparative analyses have produced results consistent with a strong influence of certainty of paternity on the evolution of male versus female parental care (e.g., Møller and Cuervo, 2000; Arnold and Owens, 2002; Ah-King *et al.*, 2005; Mank *et al.*, 2005), and there is substantial evidence from experimental studies that uncertainty of paternity does influence the likelihood and extent of male parental care in some species (e.g., Neff and Gross, 2001; Neff, 2003). However, numerous exceptions to this trend have been identified (e.g., Alonzo and Heckman, 2010; Brennan, 2012; Kamel and Grosberg, 2012; reviewed in Sheldon, 2002; Alonzo, 2010). Recent theoretical models have identified factors that can drive the evolution of male parental care in spite of low paternity, such as female choice for caring males (e.g., Alonzo, 2012). Researchers have also identified various factors that may mitigate the impact of uncertainty of paternity on the evolution of parental care (reviewed in Alonzo and Klug, 2012).

p0055 Queller (1997) also developed a model that confirmed Trivers (1972) arguments concerning the influence of sexual selection on the evolution of male parental care, demonstrating that males that are successful in intrasexual competition for matings should be less inclined to perform parental care, whereas unsuccessful males are not in a position to provide care. This result was confirmed by a more extensive model developed by Kokko and Jennions (2008), although they emphasize that the effect of asymmetric parental investment on the operational sex ratio should actually favor increased parental care by the sex that is present in excess, and this may override the effect of sexual selection to reduce care under some circumstances.

p0060 As mentioned above, another major contribution made by Trivers (1972) was to emphasize the importance of sexual conflict. This phenomenon has become the subject of a separate field of investigation in its own right (e.g., Parker, 1979; Arnqvist and Rowe, 2005), and has led to many important insights into the evolution of mating systems and parental care (Davies, 1989; Brown *et al.*, 1997; Lessells, 2012).

p0065 Below we review the evolution of parental care in neotropical poison frogs in the context of previous conceptual developments concerning sexual selection and the evolution of parental care.

s0015 THE EVOLUTION OF PARENTAL CARE IN TROPICAL FROGS

p0070 The reproductive strategies of frogs are highly diverse. While many are familiar with the life cycle of the leopard frog and other common temperate species, which involves short annual bouts of mating in the spring and the deposition of unattended eggs in aquatic habitats, this is only one tiny part of the stunning diversity of reproductive strategies practiced by frogs (Duellman and Trueb, 1986). These strategies have been arrayed into a plethora of reproductive modes (at least 39: Duellman and Trueb, 1986; Haddad and Prado, 2005; Wells, 2007), including variation in egg deposition site, parental care behaviors, and developmental modes, among other features.

p0075 Parental care is rare in frogs (occurring in about 10–20% of extant species: McDiarmid, 1978; Lehtinen and Nussbaum, 2003), but it has evolved multiple times across the evolutionary tree of the Anura (Summers *et al.*, 2006, 2007; Gomez-Mestre *et al.*, 2012). Latitude stands out as a key correlate of the evolution of parental care in frogs: most species with parental care occur in tropical latitudes (Duellman and Trueb, 1986; Magnusson and Hero, 1991). Why this is the case has been the subject of considerable speculation, and a number of authors have proposed that it may have been associated with a trend toward terrestrial reproduction in tropical frogs (e.g., Salthe and Duellman, 1973; McDiarmid, 1978; Crump, 1995). Predation in aquatic environments has been frequently proposed as a key factor favoring the evolution of terrestrial reproduction (Lutz, 1947; Goin and Goin, 1962; Duellman and Trueb, 1986). Research on anuran species in the Brazilian Amazon indicated that predation by other anuran larvae was likely a key factor that may have favored the evolution of terrestrial reproduction in neotropical frogs (Magnusson and Hero, 1991). The risk of desiccation is also a key factor that is likely to have affected the evolution of terrestrial reproduction (Touchon and Warkentin, 2008), with wetter, more humid conditions likely favoring terrestrial reproduction. Recently, Touchon (2012) summarized data on aquatic and terrestrial egg mortality in the neotropical hylid frog *Dendrosophus ebbracatus*, a species that shows variation in reproductive mode (aquatic versus terrestrial). This research revealed that predation and desiccation are the major factors impacting the relative fitness of these reproductive modes, providing a rare intraspecific window into the factors that are likely to have influenced the evolution of terrestrial reproduction.

p0080 Terrestrial reproduction does not necessarily involve the evolution of parental care, but the two traits are strongly associated in a phylogenetic context (Gomez-Mestre *et al.*, 2012). Hence, terrestrial reproduction has evolved repeatedly in tropical frogs, and in many cases this is associated with the evolution of male, female, or biparental care (Duellman and Trueb, 1986). This trend is seen in the Neotropics as well as the Old World tropics.

p0085 In many taxa (e.g., mammals, reptiles, insects) male parental care is rare and female care is the predominant form of care when care is provided (Clutton-Brock, 1991). In contrast, uniparental male care is the most common form of care in teleost fish (Gross, 2005; Mank *et al.*, 2005; Balshine, 2012). Frogs show an intermediate pattern, with similar numbers of species showing male and female parental care (Wells, 2007).

p0090 Given the fact that external fertilization is the rule rather than the exception in frogs, a number of authors have argued that certainty of parentage may have played a role in the relatively high frequency of male parental care in frogs (reviewed in Clutton-Brock, 1991). A comparative analysis of parental care and mode of fertilization by Beck (1998) concluded that parentage did not influence the evolution of male versus female care in frogs (assuming certainty of paternity is higher with external fertilization), but there were significant problems and deficiencies in this analysis (reviewed in Wells, 2007) and the issue is not resolved. In fish, the results of comparative analyses do suggest a role for certainty of paternity (Ah-King *et al.*, 2005; Mank *et al.*, 2005), but it is also clear that male parental care exists in many species that have substantial frequencies of sneaker males and associated compromises in paternity (Alonzo and Klug, 2012).

p0095 The evolution of parental care in fish has received more theoretical and empirical attention than in any other taxa (reviewed in Balshine, 2012), and provides a valuable starting point to consider the evolution of sex-specific parental care patterns in tropical frogs.

p0100 A number of researchers focused on the evolution of parental care in fish have argued that male parental care is particularly likely to evolve in circumstances where females lay eggs directly on a territory defended by a male (Williams, 1975; Ridley, 1978; Perrone and Zaret, 1979; Baylis, 1981; Gross and Sargent, 1985). There are likely several inter-related reasons for this association. The first is simple direct association: when the eggs are laid on the male's territory, they are readily available to receive care (Williams 1966). This association also means that some forms of parental care are likely to have a relatively low cost for male fish in terms of lost mating opportunities (Loiselle, 1978; Blumer, 1979; Gross and Sargent, 1985): they can continue to attract and mate with females while simultaneously performing some forms of care (e.g., defending clutches from interspecific and intraspecific predation). In fact, parental care in association with territory defense may actually enhance male mating success in some cases: there is evidence that females in some species prefer to mate with males that have clutches from previous matings (Marconato and Bissaza, 1986; Knapp and Sargent, 1989), and some authors have argued that intersexual selection may have a strong influence on the evolution of male care (e.g., Tallamy, 2000 for arthropods). Recent theory confirms the logic of the argument that intersexual selection via female choice can be a powerful and general selective agent favoring the evolution of male parental care (Alonzo, 2012). Comparative analyses (Ah-King *et al.*, 2005) support the argument that male parental care is likely to evolve following the evolution of male territoriality and pairwise-spawning (which likely increased certainty of paternity relative to group-spawning systems). Other researchers have emphasized the importance of differential costs of parental care to males and females (Gross and Sargent, 1985; Gross, 2005). In species with indeterminate growth, parental care may have higher costs to female lifetime reproductive success, in terms of reduced fecundity, than to males. This is another factor that may have favored the evolution of uniparental male parental care in fish.

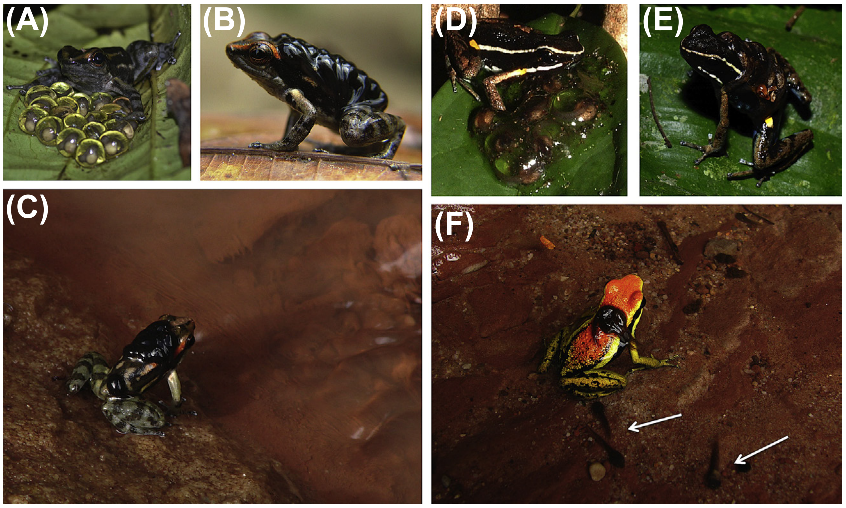
p0105 In frogs, territoriality may also play a crucial role in the evolution of male versus female parental care (Wells, 1977, 1981, 2007). Just as in fish, the defense of territories that include oviposition sites may result in a low cost of parental care in terms of reduced mating opportunities. However, this hypothesis has not been tested in a comparative phylogenetic framework, as it has been in fish. The costs of parental care to females may be particularly high in frogs (as in fish), owing to the effect of indeterminate growth on fecundity (Gross, 2005). Again, further work is required to test this hypothesis. Wells (2007) hypothesized that male parental care may be especially likely to evolve in species in which males defend elevated sites (e.g., treeholes or leaf axils). This may expose clutches to particularly dry conditions, hence favoring the evolution of specialized oviposition sites that provide a humid microenvironment. Such sites are expected to be in short supply, and hence attractive to females and economically defendable by males (Townsend, 1989). The association of male parental care with economically defendable small territories centered on oviposition sites could also be consistent with a role for certainty of paternity in the evolution of male parental care, but there are few comparative data on paternity between territorial and non-territorial species, or between species with or without paternal care. In fact, there has only been one study of paternity in a species of frog with male parental care outside of poison frogs (see below): *Kurixalus eiffingeri* in Taiwan, a rhacophorid treefrog that breeds in micropools in bamboo (Chen *et al.*, 2011). In this species, mixed paternity was found in spite of the presence of uniparental male care, although there was a positive relationship between parental investment by caring males and levels of paternity in the clutches attended.

s0020 PATTERNS OF PARENTAL CARE IN NEOTROPICAL POISON FROGS

p0110 Nearly all members of the neotropical poison frogs (families Aromobatidae and Dendrobatidae) have some form of parental care, at a minimum involving the transport of tadpoles from terrestrial egg clutches to bodies of water. It is thought that the ancestors of poison frogs lived and dwelled along streams, as seen in *Aromobates nocturnus*, a basal lineage, which are nocturnal, stream-dwelling frogs (Myers *et al.*, 1991; Summers and McKeon, 2004). Many poison frogs can be classified as terrestrial- or stream-breeders; typically, egg clutches are laid terrestrially and often attended by a parent. When the eggs hatch, one of the parents, usually the male, transports the tadpoles on his back to a terrestrial pool of water or a stream. Most members of the family Aromobatidae display this pattern of reproduction and parental care; however, phytotelm breeding (Bourne *et al.*, 2001) and endotrophic, nidicolous tadpoles that are not transported (Juncá *et al.*, 1994; Caldwell and Lima, 2003) have evolved in this family. Terrestrial breeding with tadpole transport is also characteristic of the genera *Ameerega*, *Epipedobates*, *Colostethus*, *Hyloxalus*, and *Silverstoneia* in the family Dendrobatidae (Figs 11.1 and 11.2).

p0115 Phytotelm breeding has evolved at least three times in poison frogs (see Fig. 11.3), and is characterized by the deposition of tadpoles in arboreal pools of water that collect in leaf axils (such as those of bromeliads, *Heliconia*, *Xanthosoma*, and *Dieffenbachia*), treeholes, bamboo stalks, palm fronds, fallen fruit husks, etc. For a nearly exhaustive list of patterns of parental care and tadpole habitat among dendrobatid frogs, see Wells (2007: Ch.11). An ancestral state reconstruction using parsimony suggests that terrestrial breeding and male parental care are ancestral to the clade, with phytotelm breeding, as well as biparental care and uniparental female care, being derived states (Summers and McKeon, 2004; see also Fig. 11.3).

p0120 A variety of factors have been posited to influence the transition to phytotelm breeding, including predation by fish and aquatic invertebrates, egg predation by tadpoles, competition, and possibly parasites in larger terrestrial



f0010 **FIGURE 11.1 Parental care in stream- and terrestrial-breeding dendrobatids.** (A–C) *Hyloxalus nexipus* is a stream-breeding species with male parental care. (A) A male *H. nexipus* attends an egg clutch of ~16 eggs laid on a leaf on the forest floor, and (B) transports all the tadpoles from one clutch on his back. (C) A male *H. nexipus* with tadpoles next to a flowing stream where the tadpoles will be deposited. (D–F) Many members of the genus *Ameerega* are classified as terrestrial breeders. (D) A male *A. hahneli* attends a clutch of seven eggs, and (E) transports them once they hatch. (F) A male *A. bassleri* deposits tadpoles in a terrestrial pool; arrows indicate tadpoles already in the water. See color plate at the back of the book. *Photographs courtesy of Jason Brown (B, D), Adam Stuckert (A, E), and Evan Twomey (C, F).*

pools and streams, as well as abiotic factors such as pool-drying (Summers and McKeon, 2004; McKeon and Summers, 2013). Recent work on Peruvian populations of *Allobates femoralis*, a species that breeds in terrestrial pools on the ground, highlights the potential importance of predation and indirect effects on the transition to phytotelm breeding (McKeon and Summers, 2013). Experiments with artificial basins placed in the forest investigated the effects of both pool size and presence of a large belostomatid insect predator on tadpole deposition in this species. Large pools were preferred for tadpole deposition, but, surprisingly, pools with the large predators were also preferred. This puzzling result coincided with the observation that these large sit-and-wait predators significantly reduced the presence of a major small, active predator (the dytiscid beetle), which also preys on tadpoles. It appears that the preference of *Allobates* for pools containing belostomatids is caused by the indirect effects of these predators on another, more common predator (a case of "my enemy's enemy is my friend"). In experiments on the colonization by predators of pools of the same size placed at different heights in the forest, it was found that dytiscids (and other predators) rarely colonize pools that are raised above the forest floor. This result is consistent with previous surveys of predator abundance in phytotelmata (Summers, 1990, 1999; Summers and

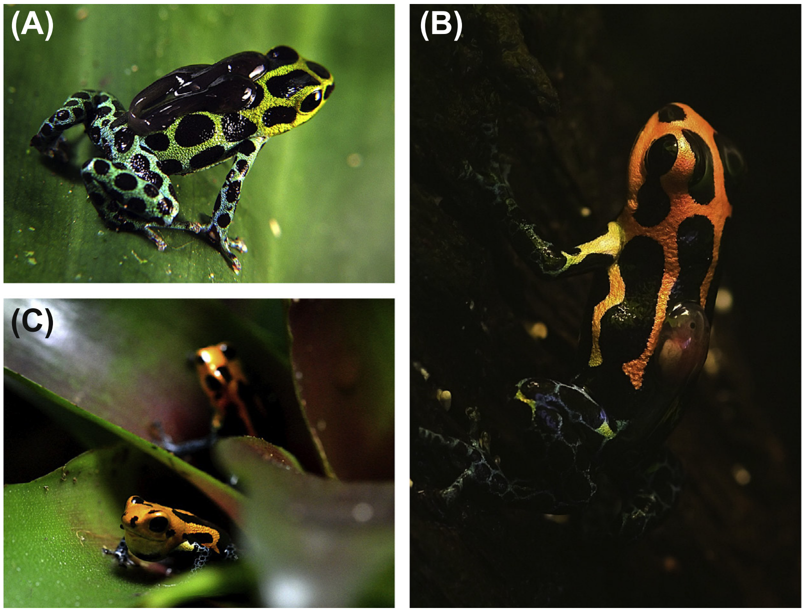


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FIGURE 11.2 Parental care in phytotelm breeders. (A) A male *Ranitomeya variabilis* transports three tadpoles that will be deposited in phytotelmata such as bromeliad axils. Similar to terrestrial- and stream-breeders, no further care is provided after tadpole deposition. (B) A male *R. imitator* transports each tadpole from a clutch, individually, to small, nutrient-poor phytotelmata. (C) After tadpole deposition the male calls to the female, leads her to the pools occupied by their offspring, and continues to call, stimulating her to provision tadpoles with unfertilized trophic eggs. See color plate at the back of the book. *Photographs courtesy of Jason Brown (A), James Tumulty (B), and Adam Stuckert (C).*

McKeon, 2004). Hence these pools are likely to serve as a refuge from predation, and this may have been a critical factor favoring the evolution of phytotelm breeding in dendrobatid frogs. While the most important factors driving the transition to phytotelm breeding are still under investigation, this transition has undoubtedly had profound impacts on parental care, sexual selection, and mating systems in these frogs.

s0025 Evolution of Male Care

p0125 As stated above, many authors have suggested that male territoriality is an important correlate of paternal care in externally fertilizing taxa (Williams, 1975; Wells, 1977; Ridley, 1978; Baylis, 1981). When males are territorial to attract females, and oviposition occurs within a male's territory, males could be selected to care through association with the offspring, especially if it is beneficial for the male to maintain his territory to attract future mates and thus less costly for the male to remain with the offspring than the female (Ridley, 1978). This scenario has also been developed in detail by Kent Wells, who suggests

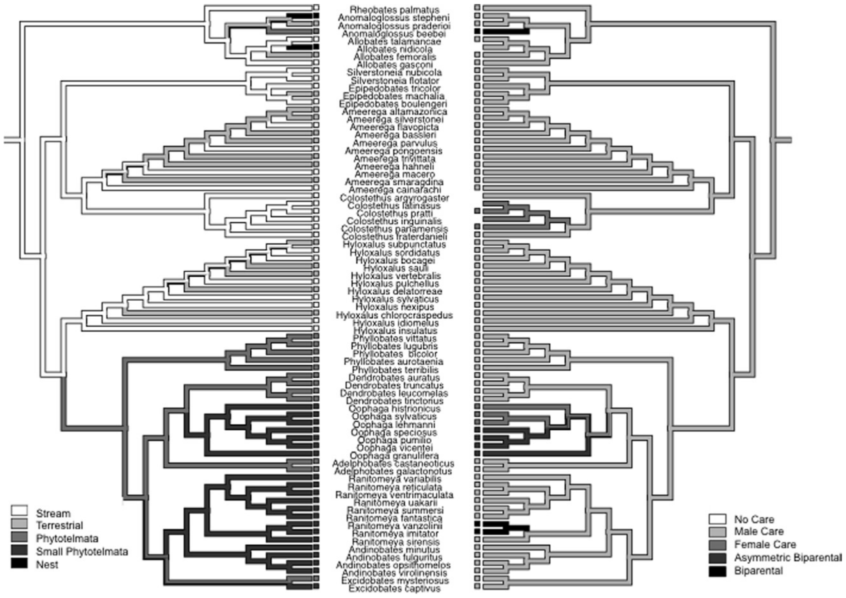

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FIGURE 11.3 Mirror tree illustrating the evolution of parental care and breeding site in dendrobatid frogs. The topology of the tree is based on Brown *et al.* (2011) (for relationships within and between *Dendrobates*, *Oophaga*, *Ranitomeya*, *Adelphobates*, *Andinobates*, and *Excidobates*) and Pyron and Wiens (2011) (for the rest of the tree). Character states for each species were taken from the literature (see Wells, 2007, for a summary). Ancestral character states were estimated using parsimony in the software package Mesquite (Maddison and Maddison, 2011), and the mirror tree was constructed with that package. Note that in some species that have generally been considered to have male parental care, females have also been observed to transport tadpoles well (see Grant *et al.*, 2006). Here we assign the character state generally associated with a particular taxon (summarized in Wells, 2007).

that paternal care in anurans is likely an "outgrowth" of territorial defense of oviposition sites (Wells, 1977, 1981, 2007). Currently we lack the power to investigate this hypothesis from a comparative perspective within poison frogs, as male care is ancestral to the clade (Summers and McKeon, 2004). Nevertheless, some observations appear consistent with this hypothesis and are worth noting.

p0130 An important assumption of this hypothesis is that parental care should not preclude mating success – i.e., males should be able to attract additional mates while attending egg clutches within their territory. This assumption is valid for male poison frogs, many of which continue to call while attending eggs, and males have been found guarding multiple clutches (Summers, 1989; Roithmair, 1992; Juncá *et al.*, 1994; Pröhl and Hödl, 1999; Ursprung *et al.*, 2011). However, this is not a general rule, as male *Rheobates* (=*Colostethus*) *palmatus* were observed to sit on eggs constantly and ceased calling throughout the entire period of egg development (Lüddecke, 1999).

p0135 Another complication, noted by Wells (1981), is that these predictions about territoriality and egg attendance may not apply to selection for tadpole transport, as tadpoles usually need to be transported well outside a male's territory. Thus, a male will have to leave his territory, and his venue for attracting females, to transport tadpoles. However, confidence of parentage is likely to be an important consideration; females who oviposit in male territories but do not remain with egg clutches may have low confidence of maternity when males guard clutches from multiple females, and selection may still favor male tadpole transport on account of higher confidence of paternity on the part of the male. Furthermore, field observations show that males that transport tadpoles outside of their territory often return and continue territory defense shortly thereafter, thus the cost of tadpole transport to territory defense may not be that great (Summers, 1989; Ringler *et al.*, 2009). This complication also may not apply to male phytotelm breeders defending territories that include tadpole deposition sites (Summers and Amos, 1997; Poelman and Dicke, 2008; Brown *et al.*, 2009). However, costs of tadpole transport in species with particularly strong male–male competition for territories could have driven the evolution of female tadpole transport in *Colostethus panamensis* and closely related congeners (see below).

p0140 Along a separate, but not mutually exclusive, line of reasoning, male parental care could correlate with increasing certainty of paternity. Males should only care for offspring for which they have high confidence of paternity (Trivers, 1972), and defending a territory would prevent other males from fertilizing eggs laid in their territory. Relative to other taxonomic groups, multiple paternity has not been widely documented in anurans, but evidence has been accruing (e.g., Laurila and Seppa, 1998; Prado and Haddad, 2003; Lodé and Lesbarrères, 2004; Vieites *et al.*, 2004; Chen *et al.*, 2011). The fact that multiple paternity is not widely documented in anurans is in part due to the lack of genetic analyses of paternity of egg clutches. Given the dense breeding aggregations of many anuran amphibians, it seems likely that multiple paternity is widespread in this order, and the territorial spacing of species with male parental care could be an adaptation to avoid cuckoldry. Consistent with this hypothesis in poison frogs are observations of some males being most vigilant in egg attendance in the first few days after oviposition and subsequently spending less time with the eggs and more time calling as the risk of fertilization decreases (*Ameerega picta*, Weygoldt,1987; *Anomaloglossus stepheni*, Juncá, 1998). Furthermore, genetic analysis revealed no evidence of multiple paternity in *Allobates femoralis*, a species with male care and male territoriality (Ringler *et al.*, 2012). More recently, observations of *Oophaga pumilio* males that adopted a satellite strategy and followed courting pairs to oviposition sites provide evidence that cuckoldry could indeed be a selective force favoring territoriality in species with male care (Meuche and Pröhl, 2011).

s0030 Evolution of Female Care

p0145 Our ancestral state reconstruction (Fig. 11.3) indicates that female care has evolved once in stream-breeding frogs of the genus *Colostethus*, and is characterized by female tadpole transport (Wells, 1980a, 1981); and has evolved three times independently in phytotelm breeders, being characterized by the provisioning of tadpoles with trophic eggs (Brust, 1993; Bourne *et al.*, 2001; Brown *et al.*, 2008a).

p0150 Several species in the *Oophaga* group have asymmetric biparental care, in which the male attends the clutches periodically, but the female carries out the far more intensive care involved in carrying the tadpoles to phytotelmata and returning to feed them over the course of tadpole development (Weygoldt, 1980; Brust, 1993). The asymmetric biparental care of the genus *Oophaga* is a derived state within the family Dendrobatidae (Summers *et al.*, 1999). Given the ancestral state and widespread prevalence of male-only care, the evolutionary transitions to biparental and female care are of considerable interest. The *vanzolinii* clade is characterized by biparental care; males typically attend eggs and transport tadpoles, then males call to females and stimulate them to provision tadpoles with unfertilized trophic eggs throughout tadpole development (Caldwell and de Oliveira, 1999; Brown *et al.*, 2008b).

p0155 The selective forces favoring the evolution of female tadpole transport in stream breeders *Colostethus panamensis* and its close relatives are unclear, but Wells (1981, 2007) pointed to the costs of transporting tadpoles while defending a territory. Comparisons between *C. panamensis* and *Mannophryne trinitatis* revealed similar breeding ecologies but different sex roles of parental care and territory defense (Wells, 1980a, 1980b). *Mannophryne trinitatis* breed along streams in the mountains of Trinidad and Venezuela; males transport tadpoles, and females are highly territorial and aggressive during the reproductive season (Test, 1954; Sexton, 1960; Wells, 1980b). In contrast, *C. panamensis* also breed along streams, but in this species males defend large reproductive territories and females transport tadpoles (Wells, 1980a). He hypothesized that it is costly to defend a territory while transporting tadpoles due to potential injury to the offspring, and that the sex responsible for tadpole transport will not be the sex that defends territories (Wells, 1980a, 1980b, 1981). This pattern breaks down, however, in many other poison frogs in which males defend territories and transport tadpoles (Summers, 1989, 1992a, 1992b, 1999, 2000; Roithmair, 1992; Summers and Amos, 1997; Summers and McKeon, 2004). Nevertheless, this factor could be most relevant when male–male competition for territories is particularly intense and/or tadpoles are carried for long periods of time (Wells, 1981, 2007).

p0160 Future research on the costs and benefits of tadpole transport in relation to territory defense is needed to understand this relationship. One useful test of these costs could be conducted in a species where both sexes transport tadpoles but only one is territorial, such as *Allobates femoralis*, where males are territorial and are predominantly responsible for tadpole transport but females also sometimes transport (Weygoldt, 1987; Ursprung *et al.*, 2011).

p0165 Summers and Earn (1999) discussed the evolution of female parental care from male or biparental care, and developed game-theoretic models to investigate the influence of a cost of polygyny on the evolution of female care. They reviewed four different factors that might drive the evolution of female care: the cost of polygyny; resource dispersion; reproductive parasitism by females; and the use of pools of small size with decreased nutrient content.

s0035 *The Cost of Polygyny*

p0170 Zimmermann and Zimmermann (1984, 1988) argued that female parental care in the *Oophaga histrionicus* group evolved from shared ancestry with members of the *Ranitomeya variabilis (ventrimaculata)* group, which also shows female care in the form of trophic egg-feeding. Frogs in this group breed in small phytotelmata, and tadpoles are highly cannibalistic (Summers, 1999). Weygoldt (1987) speculated that females in species in this group suffered a high cost of polygyny when males fed the offspring of some mates to the tadpoles of others. He argued that this could have selected for the evolution of female parental care. More recent phylogenetic analyses (e.g., Summers *et al.*, 1999; Grant *et al.*, 2006; Santos *et al.*, 2009; Brown *et al.*, 2011) indicate that female parental care as found in the *histrionicus* clade (with asymmetric biparental and uniparental female care) evolved independently from female parental care in the *variabilis* (*ventrimaculata*) clade (with biparental species). Nevertheless, the question of whether a cost of polygyny could drive the evolution of female care remains valid, and this could have been an important factor in one or more of the clades where female care has evolved. Game-theoretic analyses indicate that a cost of polygyny on its own is unlikely to drive the evolution of a pure uniparental female care strategy from male-only care. However, given specific assumptions (Summers and Earn, 1999), a high cost of polygyny could drive the evolution of biparental care, and it could also interact with a cost of lost mating opportunities in males in a synergistic manner, ultimately resulting in the evolution of a pure female care strategy.

p0175 There is evidence for substantial costs of polygyny in several species of dendrobatids that have been studied intensively (Summers, 1989, 1990, 1992a, 1992b; Summers and Amos, 1997), but variation in the cost of polygyny does not appear to be associated with the evolution of parental care in a comparative context (Fig. 11.3). *Ranitomeya imitator*, which shows biparental care with relatively equal male and female parental effort (Brown *et al.*, 2008a), appears to have a low cost of polygyny (Brown *et al.*, 2010a; Tumulty *et al.*, unpublished observations). This does not rule out the possibility that a high cost of polygyny selected for biparental care ancestrally in this lineage, but it does indicate that it is unlikely that a cost of polygyny would drive a transition from biparental to pure female care. In the *histrionicus* lineage, there is both asymmetric biparental care, in which the male performs some care (clutch attendance) but the female puts substantially more time and effort into parental care without the assistance of the male, and pure female care. Ancestral reconstructions of the evolution of parental care in this clade (Fig. 11.3) do not clearly support the prediction from the cost of polygyny hypothesis that female parental care evolved from biparental care rather than the reverse. Further, the nature of asymmetric biparental care in this group is such that a cost of polygyny is unlikely to exist under this pattern of parental care, given that the male has been completely disconnected from tadpole transport and feeding. Hence, it appears that a high cost of polygyny is unlikely to have driven the evolution of female parental care in these groups of poison frogs, although it is likely to have had a profound influence on the mating systems of some species (see below).

s0040 *Resource Dispersion*

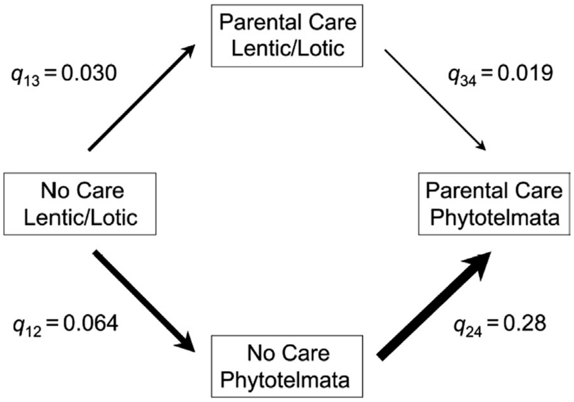
p0180 It is possible that a change in the dispersion of resources critical to reproduction could have favored male desertion and the evolution of female parental care. However, males do not appear to monopolize reproductive resources (i.e., breeding pools or oviposition sites) in species with female parental care (e.g., *Oophaga pumilio*; Pröhl and Hödl, 1999, and references above). Hence, this hypothesis seems unlikely.

s0045 *Reproductive Parasitism by Females*

p0185 Reproductive parasitism by females could also drive the evolution of female care (theoretically) and shift the balance of selection in favor of male desertion, leading to uniparental female parental care by default. Reproductive parasitism, in which males attempt to place tadpoles into pools that contain embryos of other individuals that can be cannibalized, has been demonstrated to occur experimentally in *Ranitomeya variabilis* (Brown *et al.*, 2009), and it is possible that females engage in similar behavior. However, female transport of tadpoles in species with male parental care is rare, and it seems unlikely that females would engage in this behavior frequently enough to drive selection in favor of male desertion.

s0050 *Use of Pools of Small Size with Decreased Nutrient Content*

p0190 Female parental care may have evolved in the context of the use of pools of small size with decreased nutrient content (Summers and Earn, 1999; Brown *et al.*, 2010a). Small pools are widely available in many tropical rainforests, yet the ability of frogs to use them is limited because of their extremely low nutrient content. The evolution of trophic egg-feeding may have been a “key innovation” that allowed poison frogs to exploit a new ecological niche (extremely small phytotelmata) (Brown *et al.*, 2010a). This innovation depended on the evolution of female care, because only females can provide trophic eggs. Phylogenetic reconstructions suggest that this innovation has evolved at least twice in the poison frogs (Summers *et al.*, 1999; Summers and McKeon, 2004; Fig. 11.3),



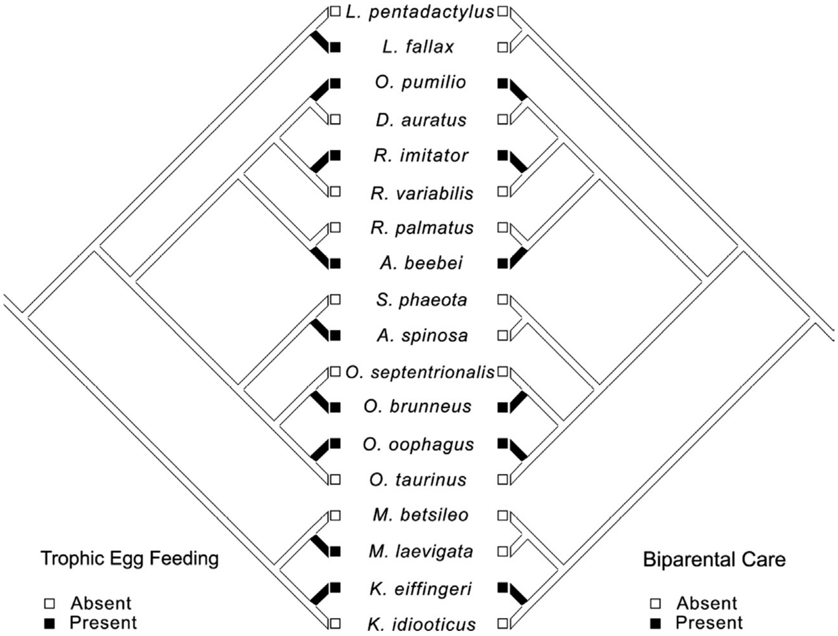
f0025

FIGURE 11.4 Path diagram of evolutionary pathways from ancestral terrestrial-breeding strategies (lentic – pool-breeding; lotic –stream-breeding) to phytotelm breeding, and from ancestral breeding strategies without parental care, to breeding with parental care, across the order Anura (frogs). The *q* values indicate the transition rate for that transition, estimated via maximum likelihood (Pagel, 1994). Statistical analyses using likelihood ratio tests indicate that the most common pathway involved the evolution of phytotelm breeding first, followed by the evolution of parental care. *Figure reprinted from Brown* et al. *(2010a), with permission from the American Society of Naturalists.*

and may have evolved in *Anomaloglossus beebei* as well (Bourne *et al.*, 2001). Comparative analyses across all frogs indicate that the evolution of small-pool use is associated with the evolution of parental care (Brown *et al.*, 2010a). Furthermore, directional analyses using maximum likelihood methods (Pagel, 1994) indicate that transitions to phytotelm breeding (from stream/pond breeding) preceded the evolution of parental care, rather than the reverse, indicating that this key ecological factor drove the evolution of parental care, rather than the reverse (Brown *et al.*, 2010a; Fig. 11.4). These comparative analyses also revealed a significant association between the use of extremely small pools (phytotelm breeding) and the evolution of egg-feeding by females (Brown *et al.*, 2010a; Fig. 11.5). Hence, current research indicates that the transition to the use of extremely small phytotelmata was probably a major factor selecting for the evolution of female parental care in the context of both biparental care and uniparental female care.

s0055 Territoriality and Mating Systems

p0195 Territoriality and complex courtship seem to be important correlates of terrestrial reproduction and parental care in Dendrobatidae, Aromobatidae, and other anuran families. In contrast to lek-breeding frogs, which usually defend short-term calling sites and oviposit elsewhere, many terrestrial-breeding poison frogs that have been studied defend long-term, multipurpose territories that include calling sites, venues for courtship, oviposition sites, and feeding



f0030 **FIGURE 11.5 Mirror tree illustrating the correlation between the evolution of egg-feeding and the evolution of biparental care across all frogs (order Anura).** Each taxon with egg-feeding and/or biparental care is paired with one outgroup taxon that does not show the trait. A concentrated changes test (Maddison, 1990) indicates a highly significant correlation between the evolution of egg-feeding and biparental care. *Figure reprinted from Brown* et al. *(2010a), with permission from the American Society of Naturalists.*

grounds (Pröhl, 2005), while some phytotelm breeders defend territories that also include tadpole deposition sites (Bourne *et al.*, 2001; Poelman and Dicke, 2008; Brown *et al.*, 2009).

p0200 Despite the general observation that poison frogs often defend multipurpose territories, it is not always clear what exactly is being defended (Pröhl, 2005). Pröhl (2005) identified two categories of territories in dendrobatid frogs: non-reproductive territories that include feeding sites, access to moisture, and retreat sites, as seen in some stream breeders (Wells 1980a, 1980b); and reproductive territories for attracting and courting mates, which are defended specifically against intraspecific competitors (Pröhl, 2005, and citations therein). The most conspicuous and commonly documented territorial behaviors relate primarily to reproduction. Species defending reproductive territories do not seem to defend feeding grounds (but see Meuche *et al.*, 2011) as generally only one sex (usually the male) is territorial (e.g., Crump, 1972; Wells, 1980a; Roithmair, 1992, 1994; Summers, 1992b, 1999; Juncá, 1998); both sexes would be expected to benefit from territorial behavior if a primary function of territoriality was defense of feeding grounds. Furthermore, male territoriality is often only directed at other calling males. For example, male *Allobates femoralis* attacked calling males but ignored non-calling males foraging in their territories (Roithmair, 1992), indicating that the primary role of territory defense relates to intrasexual competition for mates.

p0205 Given the reliance of poison frogs on terrestrial resources for reproduction, it is reasonable to speculate that these resources may be limiting and, as such, should be defended. Male territoriality in this case could be classified as resource defense polygyny, where males can monopolize females through defense of resources needed by females for reproduction (Emlen and Oring, 1977). In North American bullfrogs, for example, large males control high-quality oviposition sites needed by females, and experiments show that these sites have lower egg mortality (Howard, 1978). Oviposition sites for poison frogs, however, are usually dead leaves on the forest floor that are generally assumed to be too plentiful to be worth defending (Roithmair, 1992, 1994; Pröhl, 2005). The same is probably true of calling sites themselves, which usually take the form of raised microhabitats such as logs, leaves of understory plants, branches, and raised tree roots (Pröhl, 2005). In contrast, many authors conclude that the main function of territory defense by male poison frogs is the defense of an area in which males can advertise to and court females without interruption from rivals (reviewed in Pröhl, 2005), and male mating success is often correlated with territory size and overall calling activity (Roithmair, 1994, 1992; Pröhl, 2003).

p0210 Phytotelmata used for tadpole deposition, however, can be a limiting reproductive resource for phytotelm breeders (Donnelly, 1989a, 1989b; Poelman and Dicke, 2008; Brown *et al.*, 2009). The strawberry poison frog *Oophaga pumilio* is a phytotelm breeder in which females provide the majority of the parental care. Females transport tadpoles to small phytotelmata and provision them with unfertilized eggs throughout development (Limerick, 1980; Weygoldt, 1980; Brust, 1993). Donnelly (1989a, 1989b) examined the effect of reproductive resource limitation on adult density by manipulating the density of oviposition sites (leaf litter) and tadpole-rearing sites (bromeliads) in the field. The density of males and females increased in bromeliad addition plots, but there was no difference in adult densities between leaf litter plots and controls, indicating that tadpole-rearing sites are limiting but oviposition sites are not (Donnelly, 1989b). Male *O. pumilio* exhibit strong intrasexual competition, defending territories vocally as well as through physical aggression (Bunnell, 1973; Weygoldt, 1980; Pröhl, 1997; Bee, 2003). This led Donnelly (1989a, 1989b) to hypothesize that males defend limiting phytotelmata needed by females in order to monopolize access to mates. Others have pointed out, however, that it is unlikely males are defending phytotelmata, as male territories often do not include these tadpole-rearing sites (McVey *et al.*, 1981; Pröhl, 1997; Pröhl and Hödl, 1999). In a more detailed spatial analysis of male and female *O. pumilio*, females were shown to have a clumped distribution around tadpole-rearing sites whereas males did not (Pröhl and Berke, 2001). Furthermore, females were often observed transporting tadpoles to pools outside of the range of the male parent, and even to pools in the ranges of males with whom they had not mated (Pröhl and Berke, 2001). Thus, it appears that resource defense polygyny does not characterize *O. pumilio*, and the space-use pattern seems better explained by females settling around tadpole-rearing sites and males advertising in areas of high densities of females (Pröhl and Hödl, 1999; Pröhl and Berke, 2001; Meuche *et al.*, 2012).

p0215 There is some evidence that female *Oophaga pumilio* defend the phytotelmata in which they are caring for tadpoles (Haase and Pröhl, 2002). These observations are consistent with other egg-feeding species that defend territories closely associated with phytotelmata (Caldwell and de Oliveira, 1999; Brown *et al.*, 2009). The risk of larval and egg cannibalism in small phytotelmata can be extreme (Summers and Amos, 1997; Summers, 1999; Poelman and Dicke, 2007; Brown *et al.*, 2009). In *Ranitomeya variabilis (ventrimaculata)*, multiple embryos and tadpoles often wind up in the same pools and larger tadpoles consume eggs deposited at or below the water line as well as newly hatched smaller tadpoles (Summers and Amos, 1997; Summers, 1999). In fact, Brown *et al.* (2009) documented tactical reproductive parasitism in a Peruvian population of this species; males preferentially deposited tadpoles in pools that already contained embryos, and newly hatched tadpoles were quickly cannibalized. Given this risk, it is not surprising that species in which parents provision tadpoles with trophic eggs should be especially protective of phytotelmata containing their offspring. Consistent with this is the lack of territorial behavior in species that breed in small phytotelmata but do not provision tadpoles (Brown *et al.*, 2008a; 2009; Werner *et al.*, 2010; see also Poelman and Dicke, 2008). Additionally, mate guarding may also be an important function of territorial behavior in species with biparental care and pair bonding (Brown *et al.* 2008a, 2010a).

s0060 Parental Investment and Sexual Selection

p0220 In the genus *Oophaga*, females put more effort into parental care than do males. Females transport tadpoles when they hatch, and deposit them in small, nutrient-poor phytotelmata, to which they return to provision the tadpoles with unfertilized trophic eggs (Weygoldt, 1980; Brust, 1993). Observations of egg-feeding in *Oophaga pumilio* suggest that females respond to cues given by the tadpoles; tadpoles were observed wriggling and nibbling at females when they entered the water, possibly signaling hunger (Brust, 1993). This tactile stimulation appears to be important for initiating trophic egg-feeding, as has been demonstrated in the egg-feeding treefrog *Anotheca spinosa* (Jungfer, 1996). Female removal experiments in *Oophaga pumilio* confirm the need for female trophic egg provisioning of tadpoles in these small pools (Brust, 1993). In contrast, male parental care in *O. pumilio* is limited to egg attendance (Weygoldt, 1980; Pröhl and Hödl, 1999). This pattern of parental investment is similar to mammals, where females invest substantially more into offspring post-fertilization than do males, including nutritive provisioning. This pattern is also predicted to result in a similar mating system to many mammals with a highly skewed operational sex ratio (OSR), where males compete intensely for access to females and display a high level of polygyny (Trivers, 1972; Emlen and Oring, 1977).

p0225 Pröhl and Hödl (1999) quantified the potential reproductive rates (Clutton-Brock and Vincent, 1991; Clutton-Brock and Parker, 1992) of male and female *Oophaga pumilio* in the field. Calculations of "time out" of the mating pool for each sex – time mating and performing parental care – revealed that the ratio of female to male "time out" was over 73 : 1, mostly due to the 22 days that females spend caring for tadpoles, during which time they do not mate (Pröhl and Hödl, 1999). Males, on the other hand, could mate sequentially with multiple females even on the same day (Pröhl and Hödl, 1999). The mating system was polygamous, with sequential and simultaneous polygyny and sequential polyandry. Strong intrasexual competition (male territoriality) and high variance in male mating success, as well as the observations of females sampling males, indicates strong sexual selection on males (Pröhl and Hödl, 1999). Male mating success correlated most strongly with overall calling activity, a condition-dependent trait (Pröhl, 2003).

p0230 The distribution of phytotelmata used for tadpole deposition was found to have an important effect on the mating system of *Oophaga pumilio*. Pröhl (2002) compared the population densities and adult sex ratios of two sites: a primary forest site with relatively few phytotelmata (bromeliads and *Dieffenbachia*), and a secondary forest site with a high density of potential tadpole habitats (mainly *Heliconia* and banana plants). The adult sex ratio (ASR) was more highly skewed towards females in the secondary forest, presumably as a result of females clumping around the available phytotelmata. Male density, on the other hand, may be limited by territorial spacing; males defending small territories in areas of high female density are generally in better condition than those defending larger territories in areas of low female density (Meuche *et al.*, 2012). Taking into account potential reproductive rates, the more even ASR of the primary forest resulted in a more highly male-skewed OSR, and greater opportunity for sexual selection, in the primary forest than the secondary forest (Pröhl, 2002). These results demonstrate the intimate linkage between the limiting ecological trait of phytotelmata and the mating system of these frogs.

p0235 Sexual selection on males, in the form of intrasexual competition between males and female mate choice, is also common in many poison frogs with male-only parental care (Summers, 1989, 1992a, 1992b, 1999; Roithmair, 1992, 1994). As shown above, this usually manifests itself as male territory defense of venues for attracting and courting females. When explaining the phenomenon of sexual selection acting more strongly on males despite male paternal care, it is important to realize that male-only care does not necessarily mean that male parental investment is greater than that of females (Wells, 1981). Territorial males often continue to advertise to females while attending egg clutches, and can care for multiple clutches from several females; thus the reproductive rate of males need not be substantially limited by parental care (Summers, 1989; Ursprung *et al.*, 2011).

p0240 Strong male–male competition has apparently led to non-choosy females in *Allobates femoralis*, a terrestrial breeder with male egg attendance and tadpole transport. Using molecular markers to conduct parentage analysis of individual frogs over 2 years, Ursprung *et al.* (2011) were able to track the reproductive success of males and females as measured by the number of offspring they produced that reached adulthood in the next generation. More males than females obtained zero matings, due to the failure of these males to hold territories, but among breeders no difference in reproductive success was found between males and females (Ursprung *et al.*, 2011). Their analysis revealed high levels of polygynandry and found that females displayed site fidelity (Ringler *et al.*, 2009), mainly mating with nearby males (Ringler *et al.*, 2012). They concluded that strong intrasexual competition between males for territories, as well as “bet-hedging” benefits of sequential polyandry, have selected against restrictive female choice in this species (Ringler *et al.*, 2012).

s0065 Parental Investment, Sex Role Reversal, and Sexual Conflict

p0245 Trivers (1972) originally cited *Dendrobates auratus*, the green poison frog, as a possible example of sex role reversal, based on evidence for extensive paternal care and active courtship of males by females cited in the literature. Wells (1977) attempted to test this hypothesis, and discovered that females were more active in courtship than males, and that females competed aggressively for males in captivity. Hence, this species was considered a promising example of sex role reversal. However, Summers (1989, 1990, 1992a, 1992b) tested the sex role reversal hypothesis and concluded that it was not supported in this case. Time budgets derived from long-term observations in the field indicated that males did not spend more time caring for each offspring than the time required for females to produce them. In fact, males could care for multiple clutches simultaneously, and frequently did so. Male territoriality was associated with attracting females to a high-quality habitat and maintaining an area, free of other males, in which courtship and breeding could occur. In contrast, females did not defend specific areas, but rather specific males (see below). Females were highly aggressive, but female–female aggression was not more frequent or intense than male–male aggression. Female–female aggression resulted from mate guarding: large females remained in the territory of a specific male, and attacked any other female that attempted to approach that male (Summers, 1989). This provides a clear example of sexual conflict, because the male (in all cases) would actively court both females when approached by two females simultaneously. Comparative studies of closely related species with male (*Dendrobates leucomelas*) and female (*Oophaga sylvatica*) parental care support this interpretation of female aggression and sexual conflict (Summers, 1992a). The underlying cause of the conflict appears to be costs of polygyny to females, in terms of reduced quality of paternal care.

p0250 There are a number of possible sources for such costs, but Summers (1990) focused on the potential costs of multiple tadpole deposition. *Dendrobates auratus* males carry offspring individually to small pools (phytotelmata) that form in treeholes. Males do not have access to an unlimited number of such pools and so they return to pools where they have previously deposited tadpoles, carrying additional ones, especially if they are caring for multiple clutches from multiple females. Experiments on the effect of multiple deposition showed that increasing the number of tadpoles significantly reduced the average growth rate. Furthermore, tadpoles are highly cannibalistic, and pools generally have only a single surviving tadpole when multiple tadpoles overlap in the same pool (Summers, 1990). From the male's perspective, cannibalism may be a case of sacrificing one offspring for the benefit of another, but from the perspective of the female parent that has a tadpole eaten by another (unrelated) female's offspring, such cannibalism imposes a severe fitness cost with no compensating benefit. Note that *D. auratus* tadpoles readily attack and cannibalize both related and unrelated tadpoles (Gray *et al.*, 2009).

p0255 One interesting feature noted by Wells (1977) was that females appear to be more active during courtship than males. This was confirmed by Summers (1989), who observed multiple complete courtships in the field. During courtship, males lead females through the leaf litter, searching for an oviposition site. The female follows the male, actively stroking, nudging, and even jumping on him as they proceed through the leaf litter. This process can be lengthy (over 6 hours). However, active courtship by the female does not necessarily indicate that the female is less selective about mating than the male (which is predicted in sex role reversal: Trivers, 1972). In the case of *D. auratus*, active courtship by the female is ultimately not a good indicator of willingness to mate in a particular male–female interaction, and female rejection of males is significantly more common than male rejection of females (Summers, 1989, 1992a). In some cases, females appear to use active courtship as a mechanism to distract males from courting other females that approach them. When a mate-guarding female detects another female approaching the male she is guarding, she will alternate between attacking the second female and actively courting the male. The male actively calls at and courts both females, but ultimately the mate-guarding female prevails and drives away the secondary female and continues to actively court the male for approximately 20–30 minutes. However, guarding females often discontinue courting the male in these interactions while the male pursues and courts the female, but to no avail. It appears that the female is unwilling to mate in such types of interaction, although she will ultimately mate with that male at a later date. This kind of behavior parallels similar tactics seen in some species of birds involving increased solicitation of copulations to prevent males from engaging in extra-pair copulations (e.g., Eens and Pinxten, 1996), although external fertilization prevents the use of complete copulations for this purpose in frogs. Courtship in this context is apparently a form of deception, used by the female to prevent the male from mating with other females that he has attracted to his territory (Summers, 1992b).

p0260 The mating system of *D. auratus* appears to be polygynandrous (both males and females may have multiple partners), but is also characterized by high levels of sexual conflict. Females, in particular, suffer costs from male polygyny, and some females (presumably those with high fighting ability) attempt to guard specific males that control high-quality territories. Hence, although sex roles are not reversed, sexual conflict exerts a strong influence on the mating system of this species. In this regard, *D. auratus* shares similarities with various species of birds that exhibit sexual conflict over paternal care, such as dunnocks (Davies, 1985) and starlings (Eens and Pinxten, 1995; Smith and Sandell, 2005). The importance of sexual conflict in structuring mating systems and mating strategies was developed in a seminal paper by Davies (1989) and further discussed by Brown *et al.* (1997). The mating system of *Dendrobates auratus* provides an excellent example of the effects of sexual conflict over paternal care in a non-avian vertebrate (Summers, 1992b).

s0070 Biparental Care and Monogamy

p0265 Frogs in the *vanzolinii* clade have apparently experienced a decrease in sexual conflict, as both sexes provide substantial investment into offspring (Figs 11.2, 11.3). Biparental care and long-term pair bonding have been documented in both *Ranitomeya imitator* (Brown *et al.*, 2008a) and its sister species *R. vanzolinii* (Caldwell, 1997; Caldwell and de Oliveira, 1999), and further genetic parentage analysis has revealed that *R. imitator* is genetically monogamous (Brown *et al.*, 2010a). Biparental care has long been recognized as an important factor favoring the evolution of monogamy (e.g., Lack, 1968; Kleiman, 1977; Wittenberger and Tilson, 1980), but empirical support has been largely limited to birds (Møller, 2000) and some mammals (e.g., Gubernick and Teferi, 2000). Monogamy is extremely rare among ectothermic vertebrates, and *R. imitator* and *R. vanzolinii* have offered unique examples of biparental care and monogamy in amphibians.

p0270 In *Ranitomeya imitator* and *R. vanzolinii*, egg clutches are laid in arboreal oviposition sites, and are usually attached to phytotelmata above the water level (Caldwell and de Oliveira, 1999; Brown *et al.*, 2008a) or laid in leaf axils that do not necessarily hold water (J. Tumulty, personal observation). Males attend egg clutches and transport tadpoles individually (Fig. 11.2), depositing them in small phytotelmata – water-filled cavities of saplings and vines in *R. vanzolinii* and *Dieffenbachia*, and *Heliconia* axils in *R. imitator*. Females have also been observed to occasionally attend egg clutches and transport tadpoles in *R. imitator* when males were experimentally removed (Tumulty *et al.*, unpublished observations), but observations of unmanipulated pairs show that males predominantly perform these parental behaviors. Throughout their development tadpoles are provisioned with unfertilized trophic eggs, but, unlike *Oophaga*, males coordinate provisioning events by leading females to individual phytotelmata while calling and stimulating them to lay trophic eggs in a way that appears similar to courtship (Caldwell and de Oliveira, 1999; Brown *et al.*, 2008a; Fig. 11.2). However, in contrast to egg clutches resulting from courtship, trophic eggs are laid in the water and are not fertilized (Caldwell and de Oliveira, 1999; Brown *et al.*, 2008a). Observations of parent–tadpole interactions show similarities to egg-feeding behavior in *O. pumilio*, in that tadpoles are often observed wriggling and nibbling against parents when they enter the water (Brown *et al.* 2008a).

p0275 Brown *et al.* (2008a, 2008b, 2009, 2010b) compared phytotelm size, parental care strategy, and the mating system of *R. imitator* with that of a sympatric close relative, *R. variabilis*, to demonstrate the critical importance of pool size in the evolutionary transition to biparental care and monogamy in *R. imitator*. In contrast to *R. imitator*, *R. variabilis* has uniparental male care characterized by male tadpole transport, and a promiscuous mating system; there was no evidence of mate fidelity, neither sex defended territories, and males displayed scramble competition for phytotelmata (Brown *et al.*, 2008a, 2009).

p0280 This striking difference in parental care strategies and mating systems of these two species is associated with the use of different sized pools for tadpole deposition. *Ranitomeya imitator* typically breed in *Heliconia* and *Dieffenbachia* host plants, which retain an average of 24 mL of water in their axils (Brown *et al.*, 2008a). In contrast, *R. variabilis* deposit tadpoles in bromeliads axils averaging 112 mL in volume (Brown *et al.*, 2008a). Brown *et al.* (2008b) conducted a pool choice experiment using pairs of artificial pools differing in size attached to vegetation throughout a field site in Peru to compare the tadpole deposition preferences of *R. imitator* with that of *R. variabilis*. When given a choice between small and medium sized pools, and between medium and large sized pools, *R. variabilis* males preferentially deposited tadpoles in larger pools. *R. imitator* preferred smaller pools for tadpole deposition, and avoided both medium and large sized pools.

p0285 One longstanding hypothesis for the evolution of monogamy posits that when biparental care becomes crucial for offspring survival, males and females can obtain greater reproductive success through exclusive cooperation in the care of mutual offspring than either can from polygamy (Wittenberger and Tilson, 1980). Brown *et al.* (2010a) and Tumulty *et al.* (unpublished observations) tested this hypothesis by examining the adaptive value of male and female care in *R. imitator*. Reciprocal transplants of tadpoles in natural pools revealed that trophic egg provisioning, and hence female parental care, is critical for growth of *R. imitator* tadpoles in the small nutrient-poor pools typically used by this species (Brown *et al.*, 2010a). While tadpoles of both species grew moderately well in the large pools typically used by *R. variabilis*, neither species showed substantial growth when placed in the small pools typically used by *R. imitator* and not provisioned with trophic eggs. Brown *et al.* (2010a) accomplished this by placing a screen over the phytotelmata of *R. imitator* tadpoles so that adults could not access the pool to provision tadpoles, which showed significantly lower growth than control tadpoles that continued to be fed trophic eggs. More recent male removal experiments have revealed the critical importance of male care throughout tadpole development in *R. imitator*. Males were removed 3 weeks after tadpole deposition, and tadpoles in this removal treatment experienced significantly lower growth and survival over the following 3 weeks compared with unmanipulated control pairs (Tumulty *et al.*, unpublished observations). Although a few females were apparently able to provision tadpoles with trophic eggs without male stimulation, as shown by the presence of trophic eggs in the pools of several tadpoles shortly after male removal, the lower growth and survival of tadpoles indicates that females did not maintain provisioning at the level of control parents.

p0290 Coupled with the results of a comparative analysis across all frogs, showing the critical importance of pool size in driving the evolution of parental care in anurans (Fig. 11.4), and the association between trophic egg-feeding and biparental care in small pools (Fig. 11.5), these results make a strong case that the transition to breeding in small phytotelmata drove the evolution of biparental care and monogamy in *R. imitator* (Brown *et al.*, 2010a). The extended high levels of biparental investment necessary to rear tadpoles in small nutrient-poor pools are apparently enough to make polygamy unprofitable for *R. imitator*. Pairs were not observed to produce additional fertilized egg clutches while caring for tadpoles, indicating that rates of egg production limit reproductive rate as well as the number of tadpoles that can be cared for simultaneously (Tumulty *et al.*, unpublished observations). This limitation likely prevents females from practicing simultaneous polyandry. The importance of male care, as revealed by the male removal experiments, also shows that males may be limited in the number of offspring they can rear. It could also be difficult for males to monopolize more than one female, given their role in defending territories, surveying pools, and coordinating feeding events. Based on genetic analyses, 1 out of 12 males in monitored pairs was polygynous (Brown *et al.*, 2010a), so it is possible, although apparently very difficult, for a male to monopolize two females. It would indeed be interesting to compare the reproductive success of polygynous and monogamous male *R. imitator*, and the potential cost of polygyny to females, but the rarity of polygynous males in this species makes this sort of study unfeasible.

p0295 While the territorial nature of male *R. imitator*, and occasional observations of female–female aggression observed in captivity (Brown *et al.*, 2008a), indicate that mate guarding could be an important factor in the mating system of this species, it is unlikely to be a sufficient explanation for maintenance of monogamy. As shown in the previous section, male territoriality and intense female mate guarding characterizes several species with uniparental male care, yet these frogs still maintain a polygynandrous mating system (Summers, 1989, 1990, 1992a). Instead, the salient feature that uniquely characterizes monogamy in *R. imitator* is cooperative biparental care of eggs and tadpoles, with similar high levels of parental investment by males and females.

s0075 CONCLUSIONS AND FUTURE RESEARCH

p0300 Much remains to be learned about parental care and sexual selection in dendrobatids. To date, only a handful of species have been the subject of long-term studies of behavior in the field. Many surprises may await us in terms of the interaction of parental care and mating strategies in these frogs. The costs of parental care to males and females have been difficult to investigate, and it remains an important challenge for the future to quantify these costs in the field. There are intriguing hints of links between parental care and territoriality in frogs (similar to those in fish), and comparative analyses would be useful to illuminate the interaction between these two categories of behavior. As mentioned above, few studies have quantified uncertainty of parentage in anuran mating systems, yet this factor may have an important impact on both patterns of parental care and mating strategies in dendrobatid frogs and other species of anurans. Detailed research on particular species (e.g., Pröhl and Berke, 2001) indicate strong influences of ecological factors on sexual selection and mating systems, but research on a wider range of species is needed before general conclusions can be reached. Sexual conflict is known to have an important impact on mating strategies in some species (Summers, 1992b), but the nature and extent of sexual conflict is not known for most species.

p0305 One area that has been receiving increasing attention in the past few years is the interaction of sexual selection and population divergence in the poison frogs. For example, the strawberry poison frog *Oophaga* (*Dendrobates*) *pumilio* shows extreme color pattern divergence among populations in the Bocas del Toro region of Panama, and on the nearby mainland (Daly and Myers, 1967). Summers *et al.* (1997) demonstrated that this diversity arose very rapidly in the recent past, and posited that sexual selection in the form of female mate choice for different colors in different populations could have driven such rapid divergence. Subsequent research has confirmed the plausibility of sexual selection as a diversifying force acting on these populations (Summers *et al.*, 1999; Reynolds and Fitzpatrick, 2007; Rudh *et al.*, 2007, 2010; Maan and Cummings, 2008, 2009; Brown *et al.*, 2010b; Tazzyman and Iwasa, 2010; Richards-Zawacki and Cummings, 2011; Richards-Zawacki *et al.*, 2011; Gehara *et al.*, 2013). Whether sexual selection acts to increase color pattern divergence between populations in other species of poison frogs is currently unknown, but there are a number of species with high levels of color pattern variation among populations in which sexual selection may play a role in diversification (e.g., Roberts *et al.*, 2007; Yeager *et al.*, 2012).

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Abstract
Tropical frogs exhibit an extraordinary diversity of reproductive strategies, including complex patterns of parental care and mating behavior. The neotropical poison frogs (families Dendrobatidae and Aromobatidae) have parental care in almost all species, and many different types of parental care have evolved, including male, female, and biparental care. These different patterns of care are associated with various aspects of ecology and life history, and with diverse mating strategies and systems. We discuss the ecology and evolution of parental care in the neotropical poison frogs in an evolutionary and ecological context, and discuss how sexual selection affects and is affected by parental care in this clade. We also review theoretical and empirical research on the evolution of parental care, sexual selection, and mating systems. We describe the patterns of parental care and sexual selection in poison frogs in the context of previous theoretical and empirical studies. Finally, we suggest potentially productive directions for future research.

Keywords: Anura; Dendrobatidae; South America; Central America; reproductive strategies; phytotelmata