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THE EVOLUTIONARY ECOLOGY OF PHYTOTELMATA USE IN NEOTROPICAL POISON FROGS

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ABSTRACT

We review research on the evolutionary ecology of phytotelmata-breeding in neotropical poison frogs (dendrobatids). Recent advances in systematic analysis make it possible to develop a preliminary hypothesis concerning the evolutionary relationships within the family Dendrobatidae. This phylogenetic tree suggests that the evolution of phytotelmata-breeding has been conservative, evolving only a few times and being restricted largely to the genus *Dendrobates*. We review ecological factors that could potentially have driven the evolution of phytotelmata-breeding. We then review how the evolution of phytotelmata-breeding has influenced aspects of dendrobatid life history, including parental care, mating strategies, and egg and clutch size. Finally, we discuss evidence linking patterns of phytotelmata use to dendrobatid abundance and community structure.

Key Words: reproductive strategy, pool, Dendrobatidae

INTRODUCTION

Research on the ecology and evolutionary biology of tropical anurans has lagged behind work on their temperate counterparts, although great strides have been made in the recent past (*e.g.*, Savage, 2002). Research on the evolution and ecology of phytotelmata use in tropical species has been especially sparse until recently. As this symposium volume demonstrates, the ecology and evolution of phytotelmata use provide a wealth of stimulating opportunities for research, an excellent source of data for comparative analyses, and a host of new and intriguing questions relevant to fundamental biological issues.

The Neotropical poison frogs of the family Dendrobatidae display a diversity of reproductive strategies involving phytotelmata that make them excellent subjects for research on current issues in evolutionary biology and ecology. For example, many species display complex forms of parental care associated with the use of small pools, and this has important effects on the nature and intensity of sexual selection (Wells, 1978; Summers, 1989, 1990, 1992*a*,*b*). This review will focus on the evolution of phytotelmata-breeding in dendrobatid frogs, and will explore several aspects of life history that were profoundly affected by that transition. As yet, relatively little research has been done on these connections, and many of the results discussed here are preliminary. Nevertheless, the range of life history strategies within the family offers opportunities to address a variety of interesting ecological and evolutionary questions.

MATERIALS AND METHODS

For the most part, this article reviews and analyzes previously published research in a comparative framework. However, we will present results from original research on phytotelmata use in three species of poison frogs: *Dendrobates ventrimaculatus* from Amazonian Ecuador, and *Dendrobates minutus* and *Dendrobates auratus* from eastern Panama. Summaries of the methods used to study each of these species are presented in Appendix 1. For further details on methodology, see Summers (1999) and Summers *et al.* (2000). We also present comparative analyses of data on reproductive characteristics (*e.g.*, egg and clutch size) as they relate to phytotelmata-breeding, using data gathered from the literature.

RESULTS AND DISCUSSION

Evolutionary Relationships in the Dendrobatidae. Understanding phylogenetic relationships among the poison frogs is critical if we are to correctly infer patterns of trait evolution, such as phytotelmata-breeding. Silverstone's monographs (1975, 1976) established the framework for subsequent systematic treatments of the aposematic members of the Dendrobatidae. Charles Myers and John Daly have made numerous contributions to our understanding of the systematic relationships within the Dendrobatidae (*e.g.* Myers and Daly, 1976; Myers *et al.*, 1995). Myers *et al.* (1991) identified *Aromobates nocturnus* as the basal lineage to other members of the family Dendrobatidae. Despite significant efforts by Edwards (1971, 1974), research on the evolutionary relationships of the cryptic species within Dendrobatidae (placed in the genera *Colostethus, Mannophryne and Nephelobates*) has lagged behind research on the more brightly colored taxa, and the systematics of this group are controversial (Coloma, 1995).

Recent studies of poison frog systematics have utilized molecular phylogenetic analysis (Clough and Summers, 2000; Vences *et al.*, 2000; Symula *et al.*, 2001, 2003). Researchers have also begun to include members of the genus *Colostethus* (*sensu lato*) in molecular phylogenetic analyses (La Marca *et al.*, 2002; Vences *et al.*, 2003). The resulting phylogenetic hypotheses allow us to investigate the relationships between

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ecological factors and life history traits in an evolutionary context.

Figure 1 shows a composite phylogeny that is derived from several of the recent molecular phylogenetic analyses mentioned above. Most studies have supported similar phylogenetic tree topologies, which should enhance our confidence that they are identifying actual historical relationships. Some taxa that were not included in any molecular analyses were placed on the tree on the basis of previous systematic analyses using morphological characters. For example, samples of *A. nocturnus* were not available for molecular systematic analyses. However, a suite of morphological characteristics indicates that this species represents the basal lineage of the dendrobatids (Myers *et al.*, 1991).

The Evolution of Phytotelmata-breeding. *Aromobates nocturnus* is a stream-dwelling, nocturnal frog that shares several key morphological features with other members of the Dendrobatidae (Myers *et al.*, 1991). The basal position of this species suggests that ancestral dendrobatids lived and bred in or along streams, and this is also consistent with the life histories of other closely related outgroups (Vences *et al.*, 2003). Other dendrobatid species typically deposit eggs in the leaf litter, and then transport tadpoles to water in streams or small pools, such as those that form in fallen palm fronds. Derived deposition strategies in the family include the production of nidicolous, endotrophic tadpoles (*e.g.*, Junca *et al.*, 1994; Caldwell and Lima, 2003) and the use of small phytotelmata above the forest floor. The distribution of tadpole deposition sites on the dendrobatid phylogeny indicates a single shift from stream and/or terrestrial pool-breeding to breeding in phytotelmata above the forest floor (Fig. 1). Strictly speaking, pools in fallen palm fronds should be considered phytotelmata. However, in this paper we are contrasting the use of small pools raised above the forest floor to use of terrestrial pools and streams. Hence we will restrict our use of the term phytotemata to small pools that are raised above the forest floor.

A variety of reasons have been suggested for transitions from breeding in permanent pools or streams toward more terrestrial reproductive strategies, such as phytotelmata-breeding (Crump, 1974; Harris, 1999). Predation by fish has been cited as a crucial factor (*e.g.*, Heyer *et al.*, 1975; Kats *et al.*, 1988), as has predation by invertebrates (*e.g.*, Formanowicz and Brodie, 1982). Magnusson and Hero (1991) proposed that egg predation by tadpoles is the most important factor favoring more terrestrial reproductive strategies by frogs in a central Amazonian site, and suggested that this factor is likely to have general importance. Other factors that could be important include parasitism, competition, and abiotic factors such as pool drying.

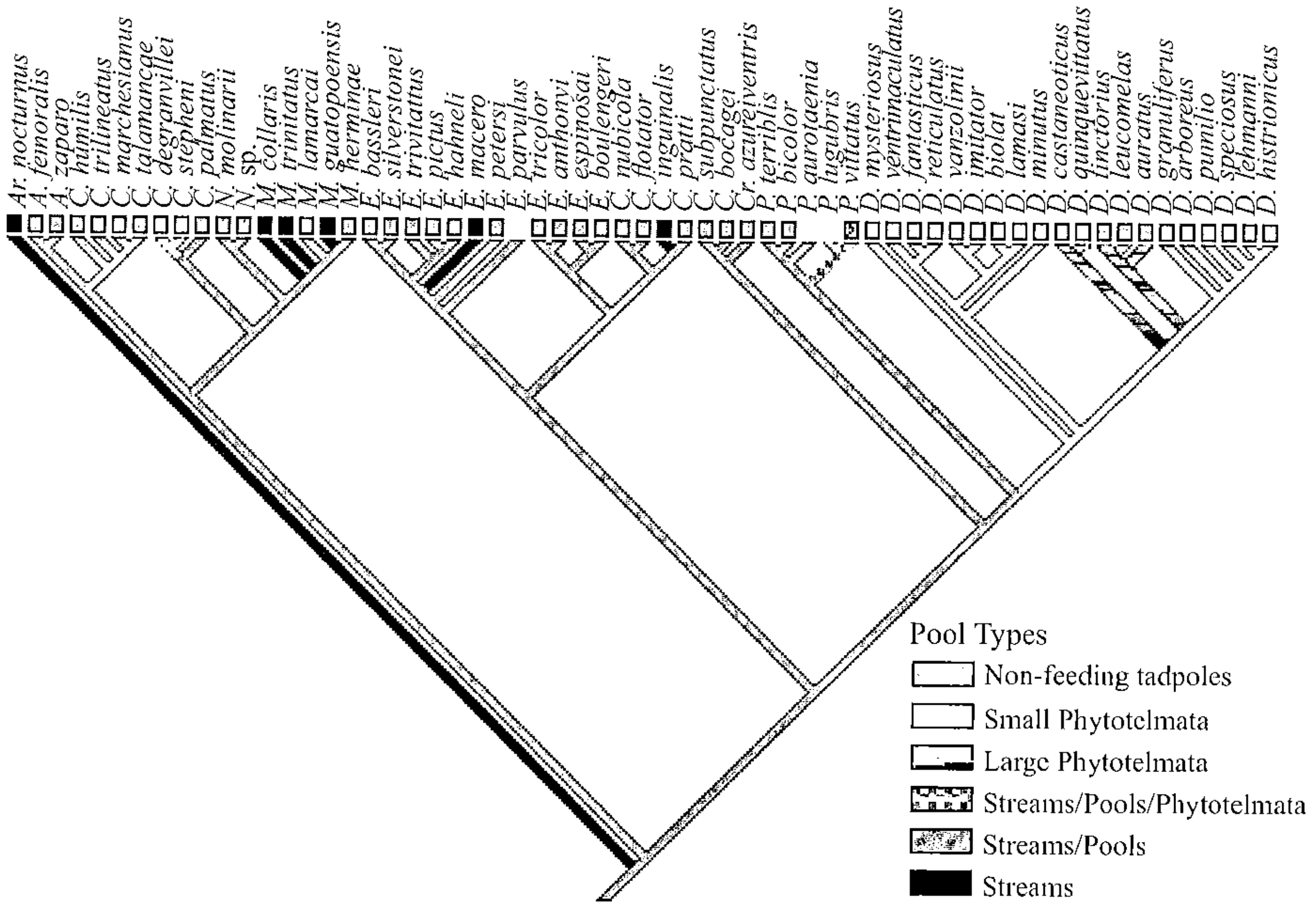

Fig. 1. Phylogenetic tree of dendrobatid frogs, compiled from recent systematic analyses. The nature of the water body utilized for breeding by each species is reconstructed (via squared change parsimony) on the tree. A few minor ambiguities in the reconstruction of breeding location evolution were resolved for the figure (using DELTRAN in MacClade), they do not affect the general conclusions. Data was not available for species without boxes under the species name. Generic abbreviations are as follows: Ar = *Aromobates*, A = *Allobates*, C = *Colostethus*, N = *Nephelobates*, M = *Mannophryne*, E = *Epipedobates*, Cr = *Cryptophyllobates*, P = *Phyllobates*, D = *Dendrobates*. The reconstruction was done with MacClade version 3.1 (Maddison & Maddison, 1993).

Testing the influence of particular factors hypothesized to have affected the evolutionary transition from stream and terrestrial pool breeding to phytotelmata-breeding is challenging because the transition occurred in the distant past. Reconstructing ancestral conditions is difficult, and carrying out evolutionary experiments on long-lived vertebrates is not usually feasible. Nevertheless, there are indirect ways of investigating evolutionary hypotheses. Streams, terrestrial pools and phytotelmata differ from each other in nature and density of predators, competitors and parasites, and in abiotic factors such as size, dissolved oxygen, and temperature. Investigations of the effect of variation in these factors on the growth and survival of larvae, or on habitat choice by adults, across selected species spanning the evolutionary transition of interest can provide insight into which factors are likely to have had significant effects on egg and tadpole deposition strategies over evolutionary history (*e.g.*, Magnusson and Hero, 1994).

Numerous studies have investigated the effects of variation in biotic and abiotic factors on larval growth and survival in temperate ponds, revealing strong effects (*e.g.*, Wilbur, 1987). Many studies of temperate frogs have also investigated how biotic and abiotic factors influence habitat choice by adults. For example, Resetarits and Wilbur (1989) demonstrated the ability of female *Hyla chrysoscelis* to discriminate among oviposition sites (pools) on the basis of both potential predation and competition. Relatively little work on the effect of these factors on larval growth and survival or adult habitat selection has been done on dendrobatids. Below we review relevant research, and discuss how it contributes to our understanding of the evolution of phytotelmata-breeding.

Predation. The intensity of predation in the tropics, where most transitions to phytotelmata-breeding have occurred, is poorly understood and requires further investigation (Gascon, 1995; Harris, 1999). Even basic information on the distributions of potential predators in phytotelmata is limited. Fish are typically absent from small temporary, rain-filled terrestrial pools, as well as phytotelmata, although they do occur in large temporary pools (Wild, 1996). Invertebrate predators such as odonate and mosquito larvae are found across the Neotropics in large phytotelmata such as treeholes, and are known to prey on dendrobatid tadpoles (Fincke, 1992, 1994; K. Summers and C.S. McKeon, personal observations).

Hence, predators do occur in phytotelmata and can affect larval survival. However, surveys at sites in Amazonian Ecuador, southern Peru, and in Panama suggest that these predators rarely colonize small phytotelmata, such as small treeholes, leaf and stem axils of plants, and bromeliad tanks (Summers, 1990, 1999; K. Summers, unpublished data). Other conspicuous invertebrate predators of terrestrial pools, such as dytiscid and hydrophilid beetles, also colonize phytotelmata above ground level rarely if at all (C.S. McKeon and K. Summers unpublished data). These results are consistent with research on predator density in small temperate pools. For example, Roth and Jackson (1987) demonstrated a lower rate of predation on *Hyla cinerea* tadpoles in small pools, due to lower colonization rates by predaceous insects. A low density of predators in phytotelmata may, in part, be due to their generally small size and consequent low nutrient levels.

Inter-specific predation may be rare in phytotelmata, but intra-specific predation (cannibalism) is likely to be common if multiple eggs and tadpoles are placed in a single pool, due to low nutrient levels and small size (Crump, 1992). Cannibalism is common in some species of *Dendrobates*. In *D. auratus*, 4-6 eggs are laid in the leaf litter and attended periodically by the male (Wells, 1978). After several weeks the males carry the tadpoles (usually one at a time) to phytotelmata, typically in tree holes (Dunn, 1941). Males typically carry the tadpoles from a single clutch to different pools, but will take tadpoles from different clutches to the same pool (Summers, 1990). Observations in the field and in the laboratory revealed frequent attacks, particularly by large tadpoles on smaller individuals (Summers, 1990; Caldwell and Araújo, 1998). Experimental manipulations demonstrated that cannibalism is the rule rather than the exception when tadpoles of this species occur together, and typically only a single tadpole survived in a pool (Summers, 1990). In *D. ventrimaculatus*, systematic monitoring of phytotelmata revealed frequent cannibalism of both eggs and tadpoles (eggs are placed just above the pool in this species). Experiments revealed that large tadpoles typically cannibalize smaller tadpoles, and that cannibalism enhances tadpole growth rates (Summers and Amos, 1997; Summers, 1999; Summers and Symula, 2001). Cannibalism also occurs in *D. minutus* (K. Summers, unpublished observations), and *D. castaneoticus* (Caldwell and Araújo, 1998). Although cannibalism may be common in dendrobatids breeding in phytotelmata, it is unlikely to have been an important deterrent to the transition from stream and terrestrial pool-breeding, because cannibalism would only have become a significant factor once the population density of phytotelmata-breeders was high, and because selection imposed by cannibalism is self-limiting (as cannibalism increases mortality, population density, and hence the probability of multiple deposition, is also likely to decline).

Can adult dendrobatids respond adaptively to the presence of predators or cannibals? Research on *D. auratus* in Panama and *D. ventrimaculatus* in Ecuador provides evidence for habitat selection with regard to egg and tadpole deposition. In ecological factors and life history traits in an evolutionary context.

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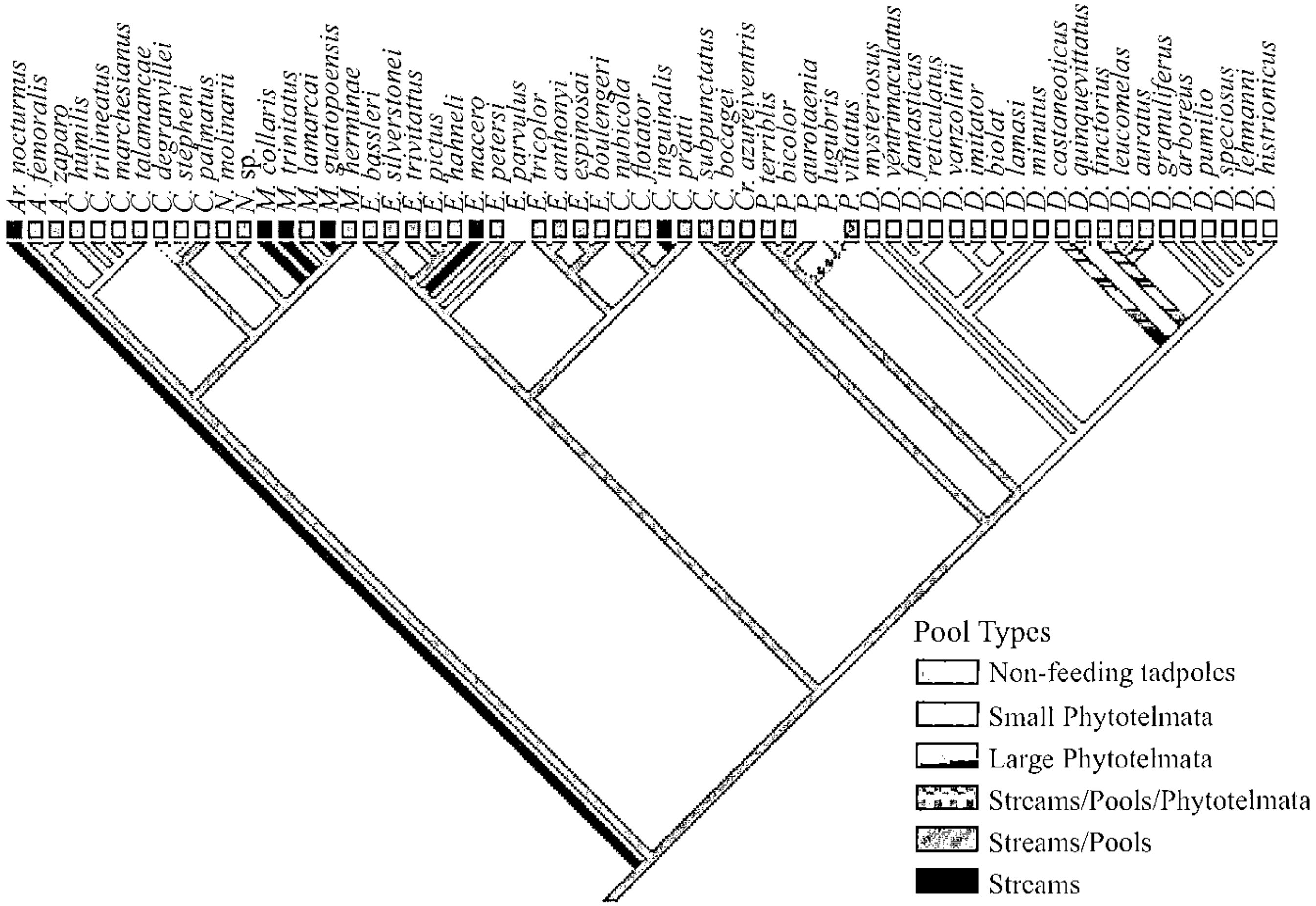

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Can adult dendrobatids respond adaptively to the presence of predators or cannibals? Research on *D. auratus* in Panama and *D. ventrimaculatus* in Ecuador provides evidence for habitat selection with regard to egg and tadpole deposition. In

D. auratus, males carry tadpoles to pools far away from their territories, often depositing them in tree holes in the canopy. Males spend substantial amounts of time investigating pools before carrying tadpoles (Summers, 1989; Summers, 1990; Summers, 1992a), and will also investigate several pools during tadpole transport. Whether males evaluate pools on the basis of potential competitors or predators is unknown. In *D. ventrimaculatus*, systematic monitoring of pools revealed that the rate of egg deposition in *Heliconia* leaf axil pools declines dramatically once a tadpole has been placed in the pool. Experiments utilizing matching paired artificial axil pools to implement choice tests between axils with and without large tadpoles demonstrated that adults avoid both oviposition and tadpole deposition in pools containing tadpoles (Summers, 1999). Hence, *D. ventrimaculatus* adults are capable of evaluating the potential danger of cannibalism, and attempt to avoid it. In contrast, research on *D. castaneoticus* and *D. quinquevittatus* suggests that adults do not attempt to avoid depositing tadpoles in pools with larger tadpoles (Caldwell and Araújo, 1998).

"Basal" dendrobatid species, such as members of the genera *Colostethus*, *Allobates*, and *Epipedobates*, which typically release their tadpoles in small streams and terrestrial pools, are excellent subjects for comparative analyses of larval growth and survival and adult habitat choice. Investigations of habitat choice in these species can reveal which factors were likely to have influenced shifts in habitat use, such as the shift from breeding in terrestrial pools to phytotelmata.

Recent work in southeastern Peru with *Allobates femoralis* (C.S. McKeon and K. Summers, unpublished data) experimentally tested the tadpole deposition strategy of this frog in response to small terrestrial pools of different sizes and predator assemblages. In blocked, fully crossed tests, *A. femoralis* strongly preferred larger pools with caged belostomatids and consequent lowered levels of naturally colonizing dytiscid beetles (voracious tadpole predators), to small pools with and without belostomatids, and large pools with normal levels of beetle predators. These results indicate an important role for predation in pool choice in *A. femoralis*, and suggest that it may have played a significant part in the transition to phytotelmata-breeding. Further experiments on the effect of dytiscids on larval growth and mortality are certainly warranted for this system.

Parasitism. Kiesecker and Skelly (2000) have demonstrated the role of parasites in oviposition site selection in temperate treefrogs. The prevalence of parasites has not been investigated with regard to differences between streams, terrestrial pools and phytotelmata in the tropics. Intuitively it seems likely that parasites would be more common in streams and terrestrial pools, and could have been a factor favoring the transition to phytotelmata-breeding. This hypothesis awaits investigation.

Competition. Competition is another factor that may have favored the transition from stream or terrestrial pool-breeding to phytotelmata-breeding. Competition (both inter-specific and intra-specific) is a common phenomenon among tadpoles in temperate pools, and both exploitative and interference competition have been demonstrated in field and laboratory experiments (Alford, 1999). Evidence for competition has also been found in tropical systems (*e.g.*, Heyer *et al.*, 1975; Inger *et al.*, 1986).

The streams and terrestrial pools utilized as tadpole deposition sites by members of *Epipedobates*, *Colostethus* and related genera are typically used by several different species of dendrobatids, and by other species of frogs as well (*e.g.*, Wild, 1996). In contrast, the number of species of frogs (dendrobatid or otherwise) using phytotelmata in a single area is typically low (*e.g.*, Summers, 1999). This trend has not been assessed quantitatively, but it is supported by general observations in a number of published studies, and by our own unpublished observations. If the tadpoles of frogs breeding in phytotelmata typically experienced less competition than those breeding in terrestrial pools or streams, this would favor a transition. The benefits (in terms of reduced competition) of breeding in phytotelmata are obviously frequency-dependent. As more species breed in particular phytotelmata, the more inter-specific competition is likely to occur. The effect may be particularly acute given the low nutrient levels associated with phytotelmata (Crump, 1992). This is intriguing, given the phylogenetic evidence presented above that the evolution of phytotelmata-breeding has been conservative. Once this ecological niche (phytotelmata) had been exploited by one evolutionary lineage, this may have largely prevented the independent evolution of similar strategies by other lineages due to competition. Comparative analysis of the levels of inter-specific and intra-specific competition experienced by tadpoles of both stream and terrestrial pool-breeding and phytotelmata-breeding dendrobatids is needed.

Some work has been done on intra-specific competition among dendrobatid tadpoles in phytotelmata. For example, field observations indicated that deposition of multiple tadpoles in single pools is common in *D. auratus* on Taboga Island, Panama (Summers, 1990). Experiments manipulating tadpole densities in phytotelmata used by *D. auratus* indicated that both exploitative and interference competition among tadpoles for resources negatively influenced growth rates (Summers, 1990). This could be seen as evidence against the hypothesis that competition drove a transition from streams or terrestrial pools to phytotelmata, but it should be noted that these levels of competition probably developed only after the ancestors of *D. auratus* had been breeding in phytotelmata for many generations. Presumably, levels of both intra-specific and inter-specific competition would be low in the early stages of the transition to phytotelmata-breeding.

Abiotic Factors: Pool Drying. Abiotic environmental factors also affect reproductive strategies. For example, many amphibian larvae face the threat of desiccation from pool drying. In *Pseudacris* treefrogs, there is an association between rates of growth and development and the probability of pond drying, such that *P. triseriata*, which breeds in temporary ponds and faces a high threat of desiccation, reaches metamorphosis more quickly than *P. crucifer*, which breeds mainly in permanent ponds (Skelly, 1996). It is conceivable that differential risks of pool drying could have favored a transition from breeding in streams or terrestrial pools to breeding in phytotelmata, but there is little information available on the relative frequency with which phytotelmata dry out relative to streams or terrestrial pools.

A more basic question concerns whether or not dendrobatid tadpoles can respond adaptively to pool drying. Wilbur and Collins (1973) proposed a model integrating environmental influences on growth and development of anuran larvae. The model predicts that tadpoles will adjust their development to environmental factors affecting growth rate and pool duration. For example, they predicted that anuran larvae would respond to pool drying by accelerating their rate of development relative to growth, sacrificing large size at metamorphosis in order to leave the pond before it dries. Since their seminal paper, a variety of researchers have investigated how environmental factors influence growth and developmental trajectories in anuran larvae (*e.g.*, Wilbur, 1987; Tejedo, 1994). The results of these studies have been generally consistent with the Wilbur and Collins model (Alford, 1999).

A relatively small number of studies have focused on developmental plasticity in tropical systems (*e.g.*, Crump, 1989; Warkentin, 1995), and no one has worked on developmental plasticity in dendrobatids. There is ample evidence that seasonal patterns of rainfall and water-availability influence adult breeding patterns in the Neotropics (*e.g.*, Aichinger, 1987). Furthermore, small phytotelmata are subject to desiccation (*e.g.*, Summers, 1999). This suggests that studies of plasticity in response to pool drying regimes might be rewarding in dendrobatids. Here we present results from a study of the Amazonian poison frog, *D. ventrimaculatus* that suggest an adaptive association between pool drying and morphological changes during development.

Monitoring of pools (see Appendix 1) revealed that most *Heliconia* axils pools lost water over time, eventually drying out and collapsing. Typically, this was a slow, gradual process, but small leaks can cause more rapid water loss. Most tadpoles were deposited in pools soon after their formation (Summers, 1999), and reached metamorphosis before the pools dried out and collapsed. However, some tadpoles were trapped in axils that had lost most of their water before they reached metamorphosis. They remained alive, but were unable to swim or (presumably) feed.

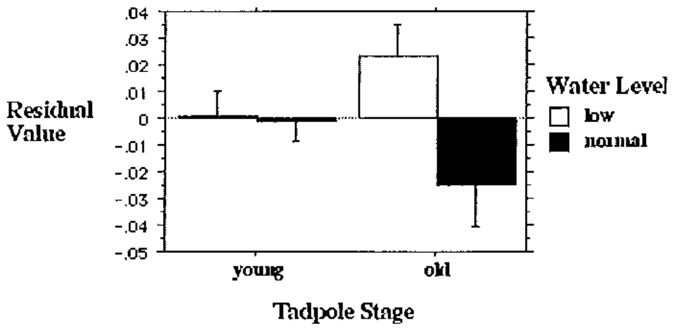

Fig. 2. Interaction plot of a Two-Way ANOVA on the residuals from the regression of tadpole weight on SVL. Factors are tadpole stage category (young = stage 25-35, old = stage 35-45) and pool water level category (low = less than 20 ml, normal = 20 ml or above). Error bars show one standard error.

Tadpole weight was strongly related to both body length and total length (Linear Regression, for log body length on log weight: $N = 37$, $R^2 = 0.81$, $t = 17.34$, $F = 150.74$, $P < 0.0001$; for log total length on log weight: $N = 37$, $R^2 = 0.75$, $t = 45.89$, $F = 103.22$, $P < 0.0001$). An ANOVA on the residuals of the regression of log body length on log weight by stage category and final pool volume category (see Appendix 1) showed a significant main effect of pool volume, and a significant interaction effect of stage by volume (Fig. 2, $N = 37$, $df = 1$, $F = 4.94$ (volume), 0.002 (stage) and 4.22 (stage by volume); $P < 0.05$ (volume), $P = 0.96$ (stage), $P < 0.05$ (stage by volume)). This was not an effect of pool size, as there was no significant effect of pool size on the residuals of weight on log body length (Welch's Test, a one-way ANOVA robust to unequal variances), $N = 42$, $P = 0.228$). This was also not an effect of differences in the average stage of tadpoles taken from low and normal pools, as these were not significantly different within stage categories (t-test, $N = 17$, $t = 0.261$, $P = 0.798$, for late stage tadpoles).

These results indicate that late stage tadpoles in dry or almost dry pools tended to have a large body length for their weight. This could imply that late stage tadpoles in drying pools are accelerating development in order to reach metamorphosis before they desiccate. Alternatively, it could simply mean that these tadpoles are starving, and hence losing weight relative to their size. However, this latter hypothesis predicts that the same relationship seen for body length should hold for total length as well. This was not the case; there was a significant effect of pool volume on the residuals of log weight on log total length, but no significant effect of tadpole stage, nor any significant interaction between volume and stage (ANOVA, $N = 37$, $df = 1$, $F = 9.29$ (volume), 2.08 (stage) and 0.117 (stage by volume); $P < 0.005$ (volume), 0.159 (stage) and 0.734 (stage by volume)).

Although sample sizes are small, the evidence indicates that late stage *D. ventrimaculatus* tadpoles respond to pool drying by increasing their body length relative to body weight. This suggests that these tadpoles respond adaptively to pool drying by accelerating development (resorbing tail tissue). This hypothesis could be tested experimentally by randomly assigning late stage tadpoles from a single clutch to full or (nearly) empty pools (see Fincke, 1994). The larger issue of whether differential rates or probabilities of pool drying between terrestrial pools and phytotelmata have favored the transition to phytotelmata-breeding will have to await more

D. auratus, males carry tadpoles to pools far away from their territories, often depositing them in tree holes in the canopy. Males spend substantial amounts of time investigating pools before carrying tadpoles (Summers, 1989; Summers, 1990; Summers, 1992a), and will also investigate several pools during tadpole transport. Whether males evaluate pools on the basis of potential competitors or predators is unknown. In *D. ventrimaculatus*, systematic monitoring of pools revealed that the rate of egg deposition in *Heliconia* leaf axil pools declines dramatically once a tadpole has been placed in the pool. Experiments utilizing matching paired artificial axil pools to implement choice tests between axils with and without large tadpoles demonstrated that adults avoid both oviposition and tadpole deposition in pools containing tadpoles (Summers, 1999). Hence, *D. ventrimaculatus* adults are capable of evaluating the potential danger of cannibalism, and attempt to avoid it. In contrast, research on *D. castaneoticus* and *D. quinquevittatus* suggests that adults do not attempt to avoid depositing tadpoles in pools with larger tadpoles (Caldwell and Araújo, 1998).

"Basal" dendrobatid species, such as members of the genera *Colostethus*, *Allobates*, and *Epipedobates*, which typically release their tadpoles in small streams and terrestrial pools, are excellent subjects for comparative analyses of larval growth and survival and adult habitat choice. Investigations of habitat choice in these species can reveal which factors were likely to have influenced shifts in habitat use, such as the shift from breeding in terrestrial pools to phytotelmata.

Recent work in southeastern Peru with *Allobates femoralis* (C.S. McKeon and K. Summers, unpublished data) experimentally tested the tadpole deposition strategy of this frog in response to small terrestrial pools of different sizes and predator assemblages. In blocked, fully crossed tests, *A. femoralis* strongly preferred larger pools with caged belostomatids and consequent lowered levels of naturally colonizing dytiscid beetles (voracious tadpole predators), to small pools with and without belostomatids, and large pools with normal levels of beetle predators. These results indicate an important role for predation in pool choice in *A. femoralis*, and suggest that it may have played a significant part in the transition to phytotelmata-breeding. Further experiments on the effect of dytiscids on larval growth and mortality are certainly warranted for this system.

Parasitism. Kiesecker and Skelly (2000) have demonstrated the role of parasites in oviposition site selection in temperate treefrogs. The prevalence of parasites has not been investigated with regard to differences between streams, terrestrial pools and phytotelmata in the tropics. Intuitively it seems likely that parasites would be more common in streams and terrestrial pools, and could have been a factor favoring the transition to phytotelmata-breeding. This hypothesis awaits investigation.

Competition. Competition is another factor that may have favored the transition from stream or terrestrial pool-breeding to phytotelmata-breeding. Competition (both inter-specific and intra-specific) is a common phenomenon among tadpoles in temperate pools, and both exploitative and interference competition have been demonstrated in field and laboratory experiments (Alford, 1999). Evidence for competition has also been found in tropical systems (*e.g.*, Heyer *et al.*, 1975; Inger *et al.*, 1986).

The streams and terrestrial pools utilized as tadpole deposition sites by members of *Epipedobates*, *Colostethus* and related genera are typically used by several different species of dendrobatids, and by other species of frogs as well (*e.g.*, Wild, 1996). In contrast, the number of species of frogs (dendrobatid or otherwise) using phytotelmata in a single area is typically low (*e.g.*, Summers, 1999). This trend has not been assessed quantitatively, but it is supported by general observations in a number of published studies, and by our own unpublished observations. If the tadpoles of frogs breeding in phytotelmata typically experienced less competition than those breeding in terrestrial pools or streams, this would favor a transition. The benefits (in terms of reduced competition) of breeding in phytotelmata are obviously frequency-dependent. As more species breed in particular phytotelmata, the more inter-specific competition is likely to occur. The effect may be particularly acute given the low nutrient levels associated with phytotelmata (Crump, 1992). This is intriguing, given the phylogenetic evidence presented above that the evolution of phytotelmata-breeding has been conservative. Once this ecological niche (phytotelmata) had been exploited by one evolutionary lineage, this may have largely prevented the independent evolution of similar strategies by other lineages due to competition. Comparative analysis of the levels of inter-specific and intra-specific competition experienced by tadpoles of both stream and terrestrial pool-breeding and phytotelmata-breeding dendrobatids is needed.

Some work has been done on intra-specific competition among dendrobatid tadpoles in phytotelmata. For example, field observations indicated that deposition of multiple tadpoles in single pools is common in *D. auratus* on Taboga Island, Panama (Summers, 1990). Experiments manipulating tadpole densities in phytotelmata used by *D. auratus* indicated that both exploitative and interference competition among tadpoles for resources negatively influenced growth rates (Summers, 1990). This could be seen as evidence against the hypothesis that competition drove a transition from streams or terrestrial pools to phytotelmata, but it should be noted that these levels of competition probably developed only after the ancestors of *D. auratus* had been breeding in phytotelmata for many generations. Presumably, levels of both intra-specific and inter-specific competition would be low in the early stages of the transition to phytotelmata-breeding.

Abiotic Factors: Pool Drying. Abiotic environmental factors also affect reproductive strategies. For example, many amphibian larvae face the threat of desiccation from pool drying. In *Pseudacris* treefrogs, there is an association between rates of growth and development and the probability of pond drying,

such that *P. triseriata*, which breeds in temporary ponds and faces a high threat of desiccation, reaches metamorphosis more quickly than *P. crucifer*, which breeds mainly in permanent ponds (Skelly, 1996). It is conceivable that differential risks of pool drying could have favored a transition from breeding in streams or terrestrial pools to breeding in phytotelmata, but there is little information available on the relative frequency with which phytotelmata dry out relative to streams or terrestrial pools.

A more basic question concerns whether or not dendrobatid tadpoles can respond adaptively to pool drying. Wilbur and Collins (1973) proposed a model integrating environmental influences on growth and development of anuran larvae. The model predicts that tadpoles will adjust their development to environmental factors affecting growth rate and pool duration. For example, they predicted that anuran larvae would respond to pool drying by accelerating their rate of development relative to growth, sacrificing large size at metamorphosis in order to leave the pond before it dries. Since their seminal paper, a variety of researchers have investigated how environmental factors influence growth and developmental trajectories in anuran larvae (*e.g.*, Wilbur, 1987; Tejedo, 1994). The results of these studies have been generally consistent with the Wilbur and Collins model (Alford, 1999).

A relatively small number of studies have focused on developmental plasticity in tropical systems (*e.g.*, Crump, 1989; Warkentin, 1995), and no one has worked on developmental plasticity in dendrobatids. There is ample evidence that seasonal patterns of rainfall and water-availability influence adult breeding patterns in the Neotropics (*e.g.*, Aichinger, 1987). Furthermore, small phytotelmata are subject to desiccation (*e.g.*, Summers, 1999). This suggests that studies of plasticity in response to pool drying regimes might be rewarding in dendrobatids. Here we present results from a study of the Amazonian poison frog, *D. ventrimaculatus* that suggest an adaptive association between pool drying and morphological changes during development.

Monitoring of pools (see Appendix 1) revealed that most *Heliconia* axils pools lost water over time, eventually drying out and collapsing. Typically, this was a slow, gradual process, but small leaks can cause more rapid water loss. Most tadpoles were deposited in pools soon after their formation (Summers, 1999), and reached metamorphosis before the pools dried out and collapsed. However, some tadpoles were trapped in axils that had lost most of their water before they reached metamorphosis. They remained alive, but were unable to swim or (presumably) feed.

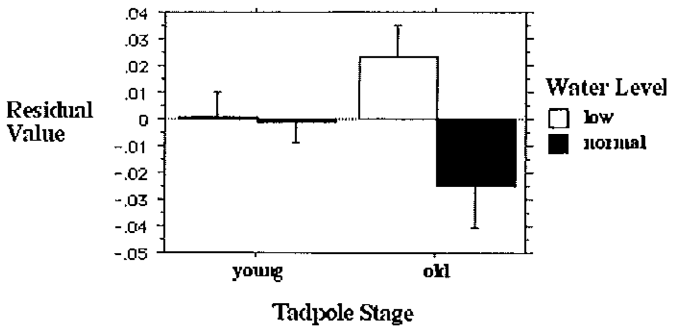

Fig. 2. Interaction plot of a Two-Way ANOVA on the residuals from the regression of tadpole weight on SVL. Factors are tadpole stage category (young = stage 25-35, old = stage 35-45) and pool water level category (low = less than 20 ml, normal = 20 ml or above). Error bars show one standard error.

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The Evolution of Complex Parental Care. The factors causing the transition to phytotelmata-breeding are (as yet) poorly understood, but there is considerable evidence that the transition had profound impacts on many aspects of dendrobatid life history. Parental care strategies, in particular, have been affected by the transition to phytotelmata-breeding, and these changes have in turn affected other reproductive strategies, such as courtship and competition for mates.

Most species of dendrobatids have male parental care, with periodiceggattendanceandtadpoletransport.Inthe*Dendrobates histrionicus* clade, female parental care predominates. In some species in this group (*e.g. D. pumilio*) the male periodically tends the eggs (Weygoldt, 1980), but the female transports them to phytotelmata. Females return regularly to the pools and provide trophic eggs for the tadpoles (Weygoldt, 1980; Brust, 1993). In other species (*e.g. D. histrionicus*) females perform all parental care duties (Weygoldt, 1987). However, even in species with biparental care (*e.g. D. pumilio*), the amount of time and effort that males put into parental care is small relative to that of females (Pröhl and Hödl, 1999). This has important implications for sexual selection (see below). In another clade of dendrobatids in Amazonia (*D. vanzolinii* and probably its close relatives), males and females form lasting pair bonds, and cooperate in parental care (Caldwell, 1997; Caldwell & Oliviera 1999). Males carry the tadpoles, and females provide trophic eggs for them periodically. Hence, in these species there is a more equitable distribution of parental effort between the sexes.

The most parsimonious reconstruction of male care on the poison frog phylogeny shows male care as primitive (Fig. 3), with female care evolving independently two times in the toxic dendrobatids: to biparental care in some Amazonian frogs (*Dendrobates vanzolinii* and close relatives), and asymmetric biparental and then uniparental female care in the *D. histrionicus* clade in northern South America and Central America.

The reasons for the transition to trophic feeding behavior (in either clade) are unknown. One possibility is that selection pressures such as those discussed above (*e.g.* predation and inter-specific competition) favored the exploitation of small pools, but the low availability of nutrients favored the evolution of provisioning. Females may have been favored to carry out this behavior because they can readily produce eggs, and hence more efficiently feed tadpoles (Summers and Earn, 1999). Alternatively, uniparental female care may have been driven by an interaction between sexual selection and a cost of polygyny to females (Summers and Earn, 1999; Weygoldt, 1987). This hypothesis is discussed in more detail below.

Parental Investment and Sexual Selection. The relationship between parental investment and sexual selection is central to our understanding of mating systems (Trivers, 1972). Females invest more than males in parental effort in most species (Andersson, 1994). This appears to be the case in members of the *D. pumilio* group (see above). High female parental effort correlates with intense male-male competition and female selectivity (Pröhl and Hödl, 1999). Comparative research on populations living in different areas indicates that the intensity of sexual selection is influenced by the availability and distribution of phytotelmata (Pröhl, 2002).

In species with male parental care, male mating effort can affect the quality of paternal care, which in turn can reduce female fitness (Andersson, 1994). Sexual conflict occurs when males pursue polygyny, reducing the quality of parental care they provide (Summers, 1992b). This imposes a cost on some or all of a male's mates, leading to female-female aggression and mate guarding by females. This cost can accrue via the effects of male parental care on larval interactions. Evidence for this hypothesis, which connects larval ecology, parental care, and sexual selection, has rarely been documented in the field (Fincke, 1992).

Previous research has demonstrated sexual conflict in two species: *D. auratus* and *D. leucomelas,* two species with male parental care that utilize medium sized phytotelmata (Summers, 1989; Summers, 1990; Summers, 1992a,b). Males in both species are territorial, and attempt to attract and mate with all females they encounter in their territories. Some females associate with particular males for prolonged periods and try to prevent other females from mating with them (Summers, 1989, 1992a). Intrasexual aggression is frequent and intense in both sexes (Summers, 1989, 1992a). In *D. auratus*, some females suffer a cost (reduced offspring growth rates and increased offspring mortality) when their mates care for the offspring of other females (because males will deposit offspring from different clutches in the same pool). Experimental manipulation of tadpole densities in artificially constructed phytotelmata (in calabash husks and in tree holes) demonstrated significant effects of increasing tadpole numbers on both growth and mortality (Summers, 1990). Hence, in *D. auratus*, there appears to be a connection between male parental care, phytotelmata-breeding and sexual conflict (Summers, 1992b).

Sexual Conflict and Parental Care. Despite substantial research on the effect of parental investment on mating systems and sexual selection (see above), little attention has been paid to the idea that sexual selection may in turn influence parental care evolution. The poison frogs provide an excellent system in which to investigate the influence of a cost of polygyny on the evolution of female care from male care.

Weygoldt (1987) proposed that a high cost of polygyny to female reproductive success drove the transition from male care to female care in an ancestor of the *D. histrionicus* clade, which he hypothesized to be derived from the *D. ventrimaculatus* clade. He argued that there is a high cost of polygyny in the *D. ventrimaculatus* clade, and that this high cost of polygyny existed in the ancestor of the *D. histrionicus* clade.

Recent research provides evidence that there is a high cost of polygyny in a population of *D. ventrimaculatus* in Amazonian Ecuador (Summers and Amos, 1997; Summers, 1999; Summers and Symula, 2001). Males undertake the parental care, and they also use small phytotelmata, typically in the stem axils of *Heliconia* plants. Eggs are deposited just above the waterline in the phytotelmata, where they develop. Some tadpoles are transported by the males, while others go into the pool below. In spite of the fact that adults attempt to avoid placing eggs or tadpoles in pools with tadpoles (see above), pools with eggs frequently have tadpoles in them (Summers and Amos, 1997; Summers, 1999). This usually occurs because males deposit tadpoles in pools that have eggs already. Although eggs are placed above the waterline, increases in water levels caused by rainfall cause them to come into contact with the water, where tadpoles can reach them. Eggs are frequently cannibalized, and experiments in manipulated *Heliconia* axil pools have demonstrated that cannibalism enhances the growth rate of cannibals (Summers, 1999).

In some cases, this is a form of reproductive parasitism, in that the reproductive effort of one individual (in the form of eggs) is consumed by the offspring of another individual. The frequency and nature of such reproductive parasitism depends on the relatedness of the eggs and the cannibals. If they are full siblings, then cannibalism is similar to trophic egg feeding. If they are half-siblings, then cannibalism is a form of reproductive parasitism. Because polygny is common and males control the transport of tadpoles (Summers and Amos, 1997), the most likely scenario is that the egg and the cannibal are paternal half-sibs. In this case, one of the males' mates (the mother of the tadpole) would experience a benefit from polygyny, and the other (the mother of the egg) would experience a cost. Finally, if the egg and the cannibal are unrelated, then one adult pair (the parents of the tadpole) would be practicing a form of reproductive parasitism on another pair (the parents of the egg).

Genetic analyses using microsatellite markers indicate that eggs and tadpoles deposited in the same pool are a mixture of full-sibs, half-sibs and non-relatives (Summers and Amos, 1997). Tadpoles will cannibalize both relatives and non-relatives (Summers and Symula, 2001). Hence, reproductive parasitism is occurring in some instances of cannibalism. This begs the question of whether such parasitism is intentional on the part of males that engage in it. It is possible that constraints on pool availability make it inevitable that deposition of multiple eggs and tadpoles in a pool will occur, resulting in cannibalism. On the other hand, it is possible that males actively seek out opportunities to parasitize the eggs of a mate or of another pair. This would be equivalent to forms of "brood parasitism" seen in birds and social insects. The resolution of this issue awaits further investigation.

Although the research described above provides some support for Weygoldt's first argument (a high cost of polygyny in the *D. ventrimaculatus* clade), mapping the evolution of parental care on the phylogeny of the poison frogs contradicts Weygoldt's hypothesis that female care in the *D. histrionicus* clade derived from an ancestral member of the *D. ventrimaculatus* clade (Figure 3): biparental care in the *D. ventrimaculatus* clade and female care in the *D. histrionicus* clade evolved independently. Nevertheless, the evolution of female care in the *D. histrionicus* lineage could still have occurred in the manner suggested by Weygoldt (1987). Summers and Earn (1999) carried out a game theoretical analysis to investigate the assumptions and implications of the hypothesis that a high cost of polygyny drove the evolution of female parental care. Simple models demonstrate that the evolution of a pure female care strategy due to a cost of polygyny is not feasible. The reason for this is that the cost of polygyny necessarily declines as the frequency of female care increases in the population, reducing selection for female care. However, Summers and Earn (1999) showed that the cost of polygyny can interact in a reciprocally catalytic manner with the cost of lost mating opportunities to males. As female care increases in frequency, the cost of lost mating opportunities also increases (that is, the reproductive returns on male mating effort increase as the number of females performing care increases). In turn, increased mating effort comes at the expense of male parental effort. The coevolutionary dynamic between the cost of polygyny to females and the cost of lost mating opportunities to males can drive female care to fixation in the population (Summers and Earn, 1999).

Life History Tradeoffs in Growth and Development. The transition to phytotelmata-breeding affected many aspects of dendrobatid life history beyond parental care and mating strategies. For example, clutch size and egg size differ according to both pool type (phytotelmata versus terrestrial pools and streams) and parental care type (male versus female). Here we examine egg and clutch size in stream and terrestrial pool-breeders relative to phytotelmata-breeders from a comparative perspective. Ideally, we would approach these issues using modern comparative methods (Felsenstein, 1985; Harvey and Pagel, 1991). Unfortunately, the evolution of phytotelmata-breeding was conservative (Fig. 1), so variation is confounded by phylogenetic similarity. Here we present simple statistical analyses without taking phylogenetic relationships into account. Given the small sample sizes, we used nonparametric tests to be conservative. We also mapped characters onto the phylogenetic tree of the dendrobatids, using parsimony. These analyses can suggest potentially interesting relationships between life history characteristics. However, proper comparative analyses will have to be carried out on a larger phylogenetic scale (broad enough to include substantial convergent evolution), in order to test the validity of these relationships.

In contrast to some previous studies (*e.g.*, Salthe and Duellman, 1973), there was no significant relationship between egg and clutch size across species (Spearman Rank Correlation, N = 30, Rho = 0.020, P = 0.913). There was data on pool drying (for both types of pools) in the field. Comparative studies of developmental plasticity in a variety of dendrobatid species would also be useful in this regard.

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In some cases, this is a form of reproductive parasitism, in that the reproductive effort of one individual (in the form of eggs) is consumed by the offspring of another individual. The frequency and nature of such reproductive parasitism depends on the relatedness of the eggs and the cannibals. If they are full siblings, then cannibalism is similar to trophic egg feeding. If they are half-siblings, then cannibalism is a form of reproductive parasitism. Because polygny is common and males control the transport of tadpoles (Summers and Amos, 1997), the most likely scenario is that the egg and the cannibal are paternal half-sibs. In this case, one of the males' mates (the mother of the tadpole) would experience a benefit from polygyny, and the other (the mother of the egg) would experience a cost. Finally, if the egg and the cannibal are unrelated, then one adult pair (the parents of the tadpole) would be practicing a form of reproductive parasitism on another pair (the parents of the egg).

Genetic analyses using microsatellite markers indicate that eggs and tadpoles deposited in the same pool are a mixture of full-sibs, half-sibs and non-relatives (Summers and Amos, 1997). Tadpoles will cannibalize both relatives and non-relatives (Summers and Symula, 2001). Hence, reproductive parasitism is occurring in some instances of cannibalism. This begs the question of whether such parasitism is intentional on the part of males that engage in it. It is possible that constraints on pool availability make it inevitable that deposition of multiple eggs and tadpoles in a pool will occur, resulting in cannibalism. On the other hand, it is possible that males actively seek out opportunities to parasitize the eggs of a mate or of another pair. This would be equivalent to forms of "brood parasitism" seen in birds and social insects. The resolution of this issue awaits further investigation.

Although the research described above provides some support for Weygoldt's first argument (a high cost of polygyny in the *D. ventrimaculatus* clade), mapping the evolution of parental care on the phylogeny of the poison frogs contradicts Weygoldt's hypothesis that female care in the *D. histrionicus* clade derived from an ancestral member of the *D. ventrimaculatus* clade (Figure 3): biparental care in the *D. ventrimaculatus* clade and female care in the *D. histrionicus* clade evolved independently. Nevertheless, the evolution of female care in the *D. histrionicus* lineage could still have occurred in the manner suggested by Weygoldt (1987). Summers and Earn (1999) carried out a game theoretical analysis to investigate the assumptions and implications of the hypothesis that a high cost of polygyny drove the evolution of female parental care. Simple models demonstrate that the evolution of a pure female care strategy due to a cost of polygyny is not feasible. The reason for this is that the cost of polygyny necessarily declines as the frequency of female care increases in the population, reducing selection for female care. However, Summers and Earn (1999) showed that the cost of polygyny can interact in a reciprocally catalytic manner with the cost of lost mating opportunities to males. As female care increases in frequency, the cost of lost mating opportunities also increases (that is, the reproductive returns on male mating effort increase as the number of females performing care increases). In turn, increased mating effort comes at the expense of male parental effort. The coevolutionary dynamic between the cost of polygyny to females and the cost of lost mating opportunities to males can drive female care to fixation in the population (Summers and Earn, 1999).

Life History Tradeoffs in Growth and Development. The transition to phytotelmata-breeding affected many aspects of dendrobatid life history beyond parental care and mating strategies. For example, clutch size and egg size differ according to both pool type (phytotelmata versus terrestrial pools and streams) and parental care type (male versus female). Here we examine egg and clutch size in stream and terrestrial pool-breeders relative to phytotelmata-breeders from a comparative perspective. Ideally, we would approach these issues using modern comparative methods (Felsenstein, 1985; Harvey and Pagel, 1991). Unfortunately, the evolution of phytotelmata-breeding was conservative (Fig. 1), so variation is confounded by phylogenetic similarity. Here we present simple statistical analyses without taking phylogenetic relationships into account. Given the small sample sizes, we used nonparametric tests to be conservative. We also mapped characters onto the phylogenetic tree of the dendrobatids, using parsimony. These analyses can suggest potentially interesting relationships between life history characteristics. However, proper comparative analyses will have to be carried out on a larger phylogenetic scale (broad enough to include substantial convergent evolution), in order to test the validity of these relationships.

In contrast to some previous studies (*e.g.*, Salthe and Duellman, 1973), there was no significant relationship between egg and clutch size across species (Spearman Rank Correlation, N = 30, Rho = 0.020, P = 0.913). There was

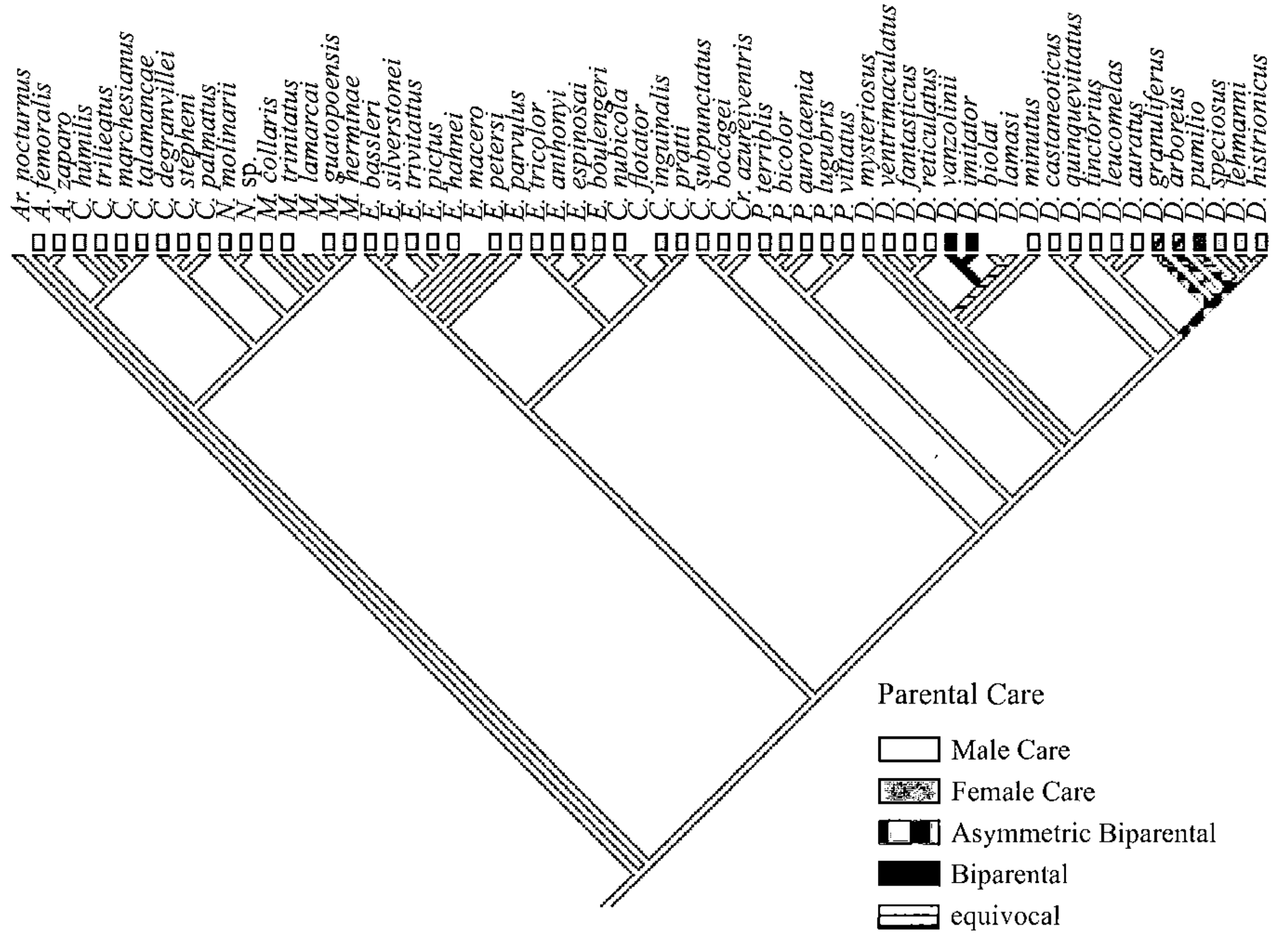


Fig. 3. The evolution of parental care, mapped onto the tree described for Fig. 1. Tree construction and abbreviations as in Fig. 1.

also no relationship between average female size and egg size (Spearman Rank Correlation, N = 29, Rho = 0.288, P = 0.128), or tadpole size (Spearman Rank Correlation, N = 23, Rho = 0.069, P = 0.747). There was, however, a significant relationship between clutch size and female size (SVL), as has been found in other taxa (Spearman Rank Correlation, N = 40, Rho = 0.549, P = 0.001). Using maximum female size yielded similar results. The direction of causality is not clear. Selection on clutch size may drive change in female size, or selection on female size in other contexts may secondarily influence the evolution of clutch size.

Clutch size declined with the transition from stream and terrestrial pool breeding to phytotelmata-breeding, and this appeared to be independent of the effect of female size on clutch size (Figure 4). Both factors could be examined simultaneously with a two-way ANOVA, but the variances of mean clutch sizes for stream and terrestrial pool breeders relative to phytotelmata-breeders were not homogeneous, violating an assumption of parametric ANOVA. Hence, we used separate Mann-Whitney U tests for species with small (< 25 mm SVL) and large (≥ 25mm SVL) average female SVL. There was a significant decline in clutch size for each size category considered separately (Small size category: phytotelmata-breeders: N = 10, X = 3.84, SE = 0.48; stream/pool breeders: N = 9, X = 13.01, SE = 1.80; Mann-Whitney U = 5.00, P = 0.001; Large size category: phytotelmata-breeders: N = 5 = 7.66, SE = 1.91; stream/pool breeders: N = 15, X = 23.19, SE = 2.33; Mann-Whitney U = 3.00, P = 0.003). Figure 5 maps clutch size on the dendrobatid phylogenetic tree, illustrating the trend.

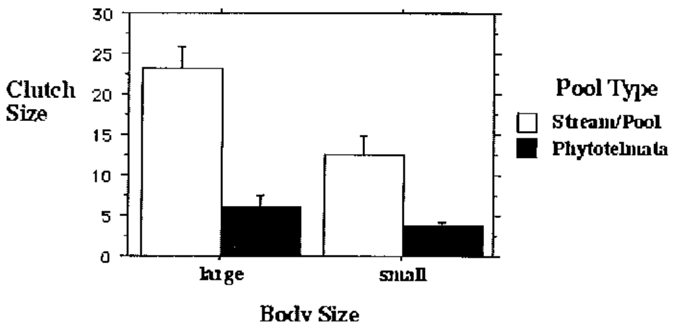


Fig. 4. Bar chart comparing clutch size in phytotelmata and stream/pool breeding species, split by the average size of adults in the species (large = greater than or equal to 25 mm SVL, small = less than 25 mm SVL). Error bars represent one standard error.

The reason for this trend is not known, and there are several possible explanations. For species with female parental care, the higher effort that locating and transporting individual larvae to phytotelmata (and feeding them) requires may cause a smaller allocation to embryo production as a result of a trade-off. This explanation is less likely to apply to species with male care, but females may adjust clutch sizes to provide a steady stream rather than large pulses of offspring for males to care for. This could reduce mortality by allowing males time to care for one set of offspring before another reaches maturity. A male caring for large numbers of offspring reaching maturity simultaneously (in a large clutch) may not be able to transport them all before they suffer from desiccation or predation. It is also possible that selection for larger egg size in phytotelmata-breeding species with male care (see below) led indirectly to smaller clutch size due to inherent tradeoffs between egg and clutch size. We need to learn more about rates of clutch production in stream and terrestrial pool-breeders relative to phytotelmata-breeders in order to resolve the factors influencing clutch size.

There was no difference between phytotelmata-breeders and stream/pool breeders in egg size (phytotelmata: N = 11, X = 2.15, SE = 0.26; stream/pool: N = 17, X = 2.31, SE = 0.16, Mann-Whitney U = 81.50, P = 0.54), or in tadpole size (phytotelmata: N = 9, = 13.04, SE = 1.10; stream/pool: N = 11, X = 11.67, SE = 0.53, Mann-Whitney U = 34.50, P = 0.260). There is, however, a significant difference in egg size between species with male and female parental care (Fig. 6a, male care: N = 22, X = 2.43, SE = 0.15; female care: N = 4, X = 1.57, SE = 0.22, Mann-Whitney U = 13.00, P = 0.028). There is also a significant difference in tadpole size with regard to parental

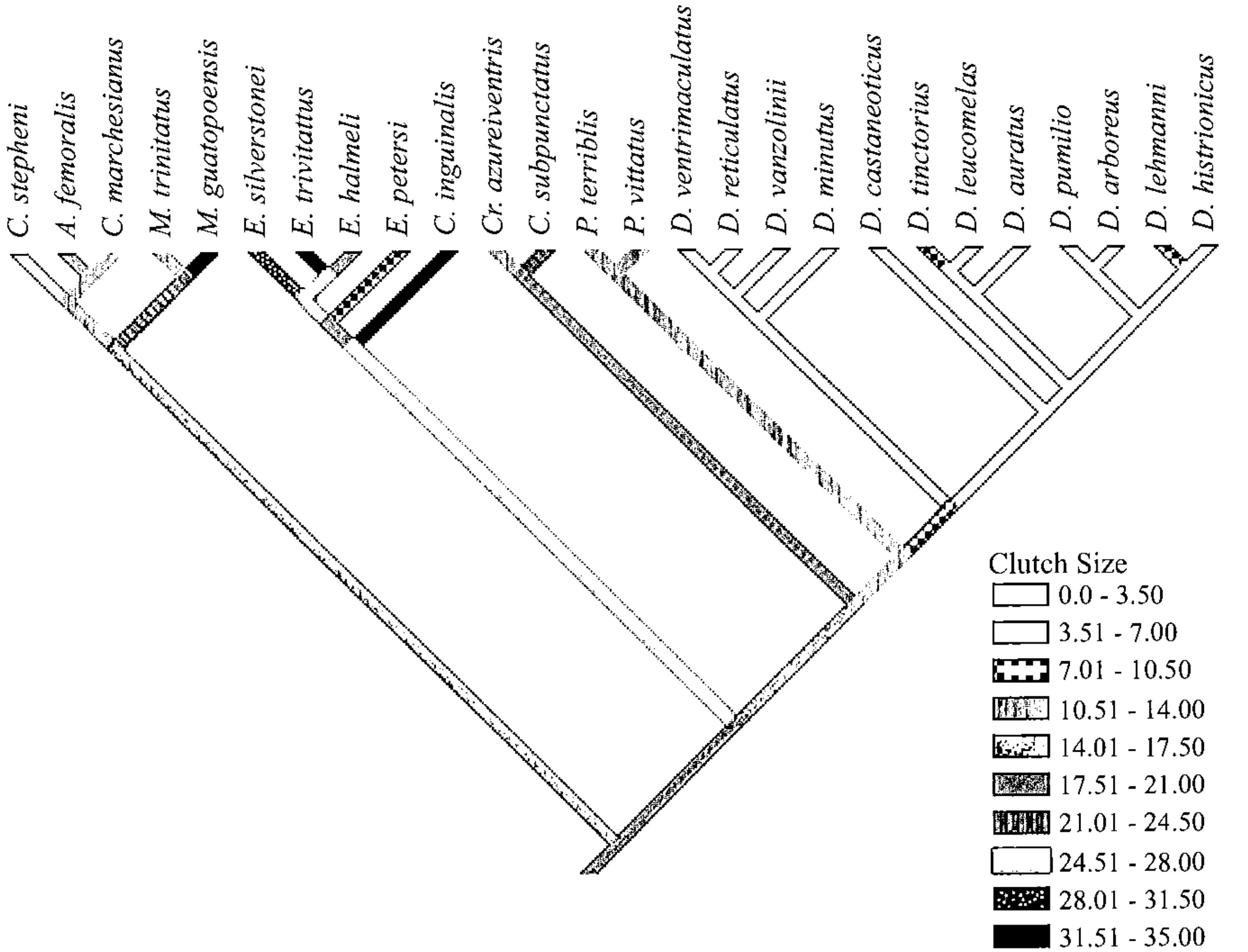
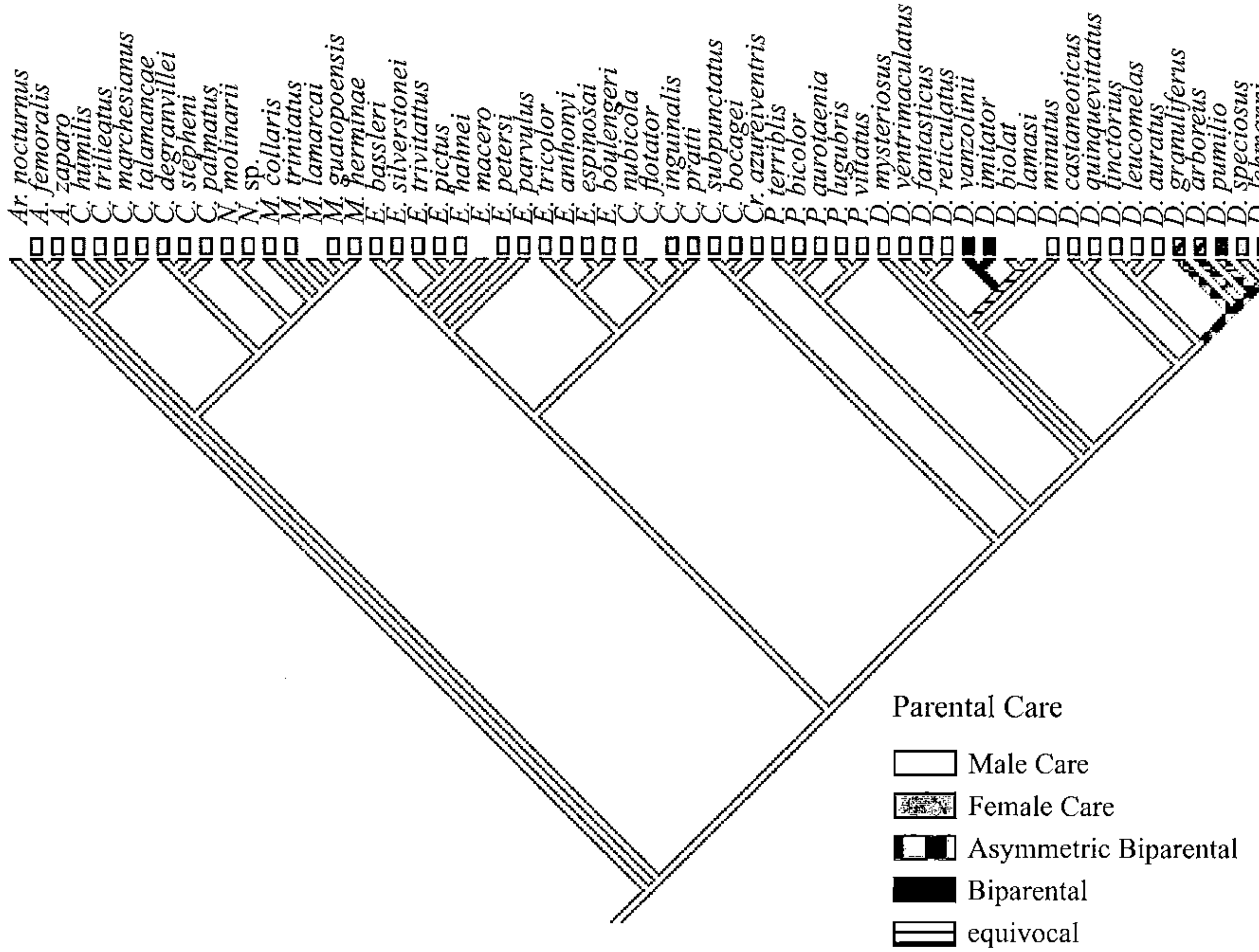


Fig. 5. The most parsimonious reconstruction (using squared change parsimony) of clutch size on the phylogenetic tree of dendrobatid frogs. Species for which data was not available have been trimmed from the tree. Tree construction and abbreviations as in Fig. 1.



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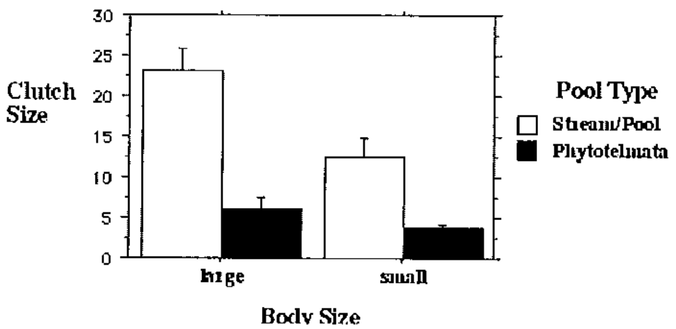

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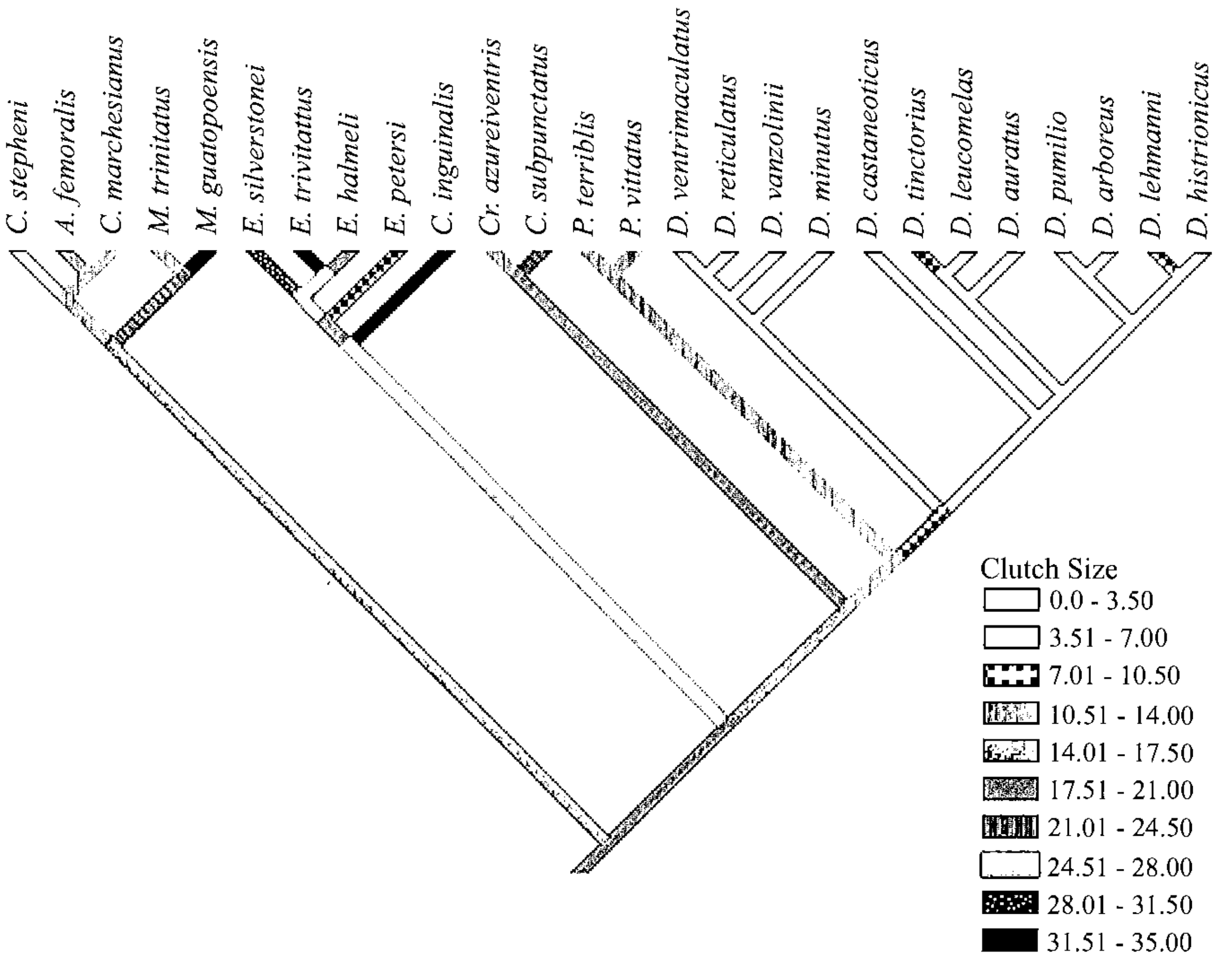

Fig. 5. The most parsimonious reconstruction (using squared change parsimony) of clutch size on the phylogenetic tree of dendrobatid frogs. Species for which data was not available have been trimmed from the tree. Tree construction and abbreviations as in Fig. 1.

care (Fig. 6b, male care: N = 18, X = 12.79, SE = 0.57; female care: N = 3, X = 9.67, SE = 0.83, Mann-Whitney U = 4.00, P = 0.021). Figure 7 and 8 map egg and tadpole size, respectively, on the phylogenetic tree of dendrobatids.

Why does this difference exist? Two factors seem likely to be important. First, in species with female parental care, females feed the tadpoles regularly over the course of the tadpole stage (Weygoldt, 1987). Hence, females do not have to provide a large amount of yolk to eggs in order to minimize the offspring's risk of starvation. In species where trophic eggs are not provided, extra yolk may be critical in allowing tadpoles to avoid starvation early in their development in small, nutrient poor phytotelmata. Second, tadpoles placed together in small phytotelmata may face high a high risk of cannibalism from larger conspecifics (Summers, 1990; Caldwell and Araújo, 1998). Species with female care generally deposit only a single tadpole in a pool, so that the risks of cannibalism are reduced (Brust, 1990). In species where cannibalism is common, it may pay females to produce relatively large offspring, to decrease their risk of being eaten (and increase their chances of being cannibals).

The first hypothesis predicts only that species with male parental care will have larger egg and tadpole size than species with female care, which is the case (see above). The second hypothesis further predicts that species in which cannibalism is frequent will tend to have larger eggs and tadpoles, even within the species with male parental care. In general, species with male care that utilize phytotelmata seem to have the highest levels of cannibalism (Zimmermann and Zimmermann, 1984; Weygoldt, 1987; Summers, 1990, 1999; Summers and Amos, 1997; Caldwell and Araújo, 1998). Hence, the hypothesis predicts that among species with male care, species that breed in phytotelmata should have larger egg and tadpole size.

For egg size, there is a trend in the direction predicted by the second hypothesis, but it is not significant (Fig. 6a, phytotelmata: N = 5, X = 2.76, SE = 0.40; stream/pool: N = 15, X = 2.36, SE = 0.16; Mann-Whitney U = 25.5, P = 0.30). However, there is a significant difference in size for Gosner Stage 25 tadpoles (Fig. 6b, phytotelmata: N = 5, X = 15.43, SE = 0.99; stream/pool: N = 11, X = 11.67, SE = 0.53; Mann-Whitney U = 5.50, P = 0.013). This result is not confounded by body size, because there was no significant difference in body size between phytotelmata-breeders and stream/ pool breeders with male care. Given the relative inaccuracy of frog egg measurements (Crump, 1974), it is likely that the difference in tadpole size reflects a real difference in investment between phytotelmata and stream and terrestrial pool-breeding dendrobatids with male care.

Earlier in this paper we argued that inter-specific predation may have driven the transition from terrestrial pool-breeding to phytotelmata-breeding. It may seem contradictory to now argue that cannibalism imposes stronger selection on phytotelmata-breeding dendrobatids, favoring larger egg size. However, the argument concerning the effect of inter-specific predation focused on the ancestral period of the transition, at which point cannibalism would have been non-existent. The fact that cannibalism may now create stronger selection on egg and clutch size than inter-specific predation is not relevant to the former argument. Furthermore, there is a key difference between inter-specific predation and intra-specific predation (cannibalism), in that for most inter-specific predators (such as damselfly larvae), small differences in the size of the tadpole at deposition are not likely to save the tadpole from predation. In contrast, small differences in the size of the tadpole at deposition may well save a tadpole from being cannibalized by another tadpole that is only slightly larger.

In summary, egg, tadpole and clutch size seem to have been affected by the transition to phytotelmata-breeding. Egg and tadpole size have declined in phytotelmata-breeding species with female care, but tadpole size has increased in phytotelmata-breeding species with male care, possibly because of high levels of cannibalism. Clutch size has declined, possibly in response to the intensive effort required to locate suitable phytotelmata and transport each offspring to separate phytotelmata. Whether smaller clutch size reflects a lower overall investment, or simply a different distribution of

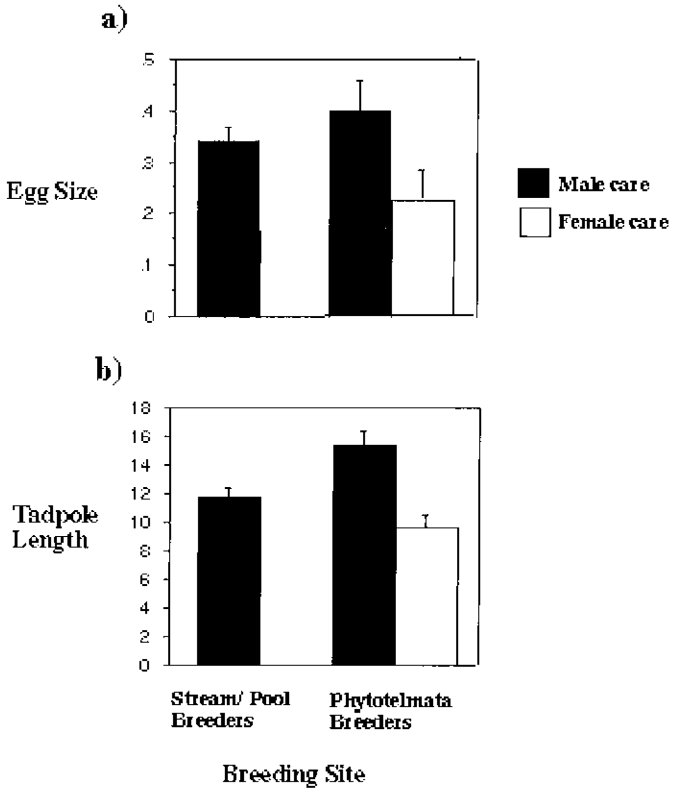

Fig. 6. a) Bar chart showing average egg size in stream and terrestrial pool-breeding dendrobatids, and phytotelmata-breeding dendrobatids, divided up by parental care type (male and female). b) Bar chart showing average tadpole length in stream and terrestrial pool-breeding dendrobatids, and phytotelmata-breeding dendrobatids, divided up by parental care type (male and female). Error bars show one standard error for each chart.

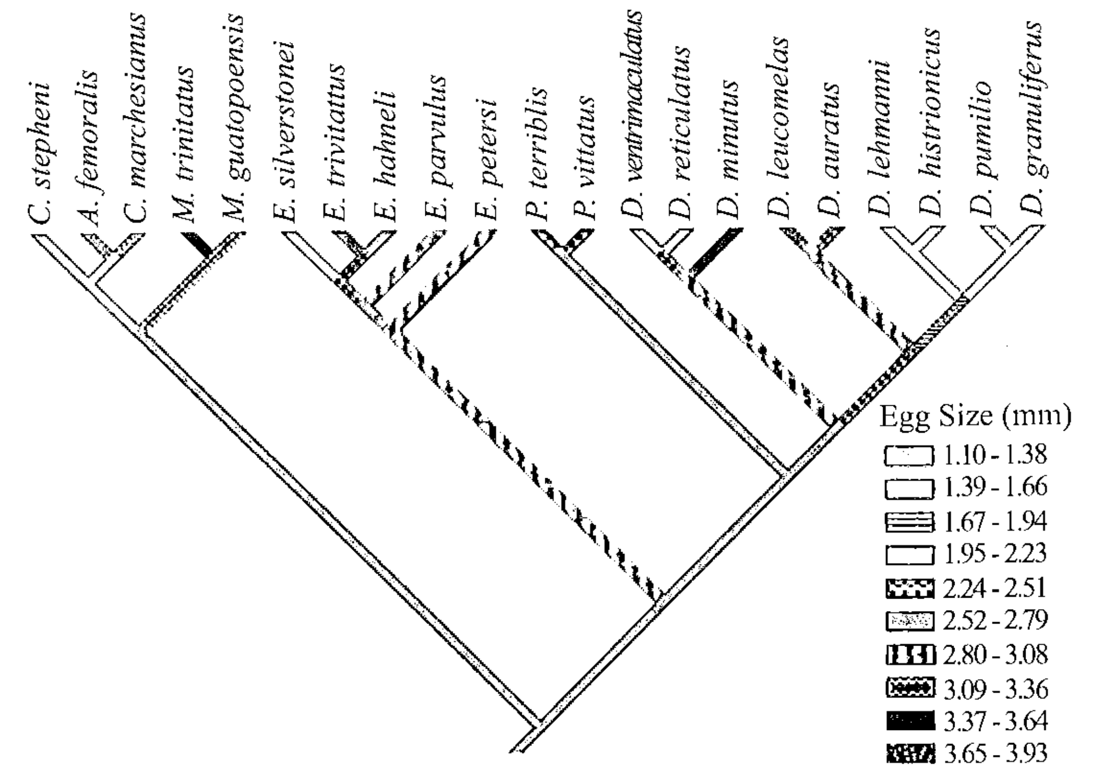

Fig. 7. The most parsimonious reconstruction (using squared change parsimony) of egg size on the phylogenetic tree of dendrobatid frogs. Species for which data was not available have been trimmed from the tree. Tree construction and abbreviations as in Fig. 1.

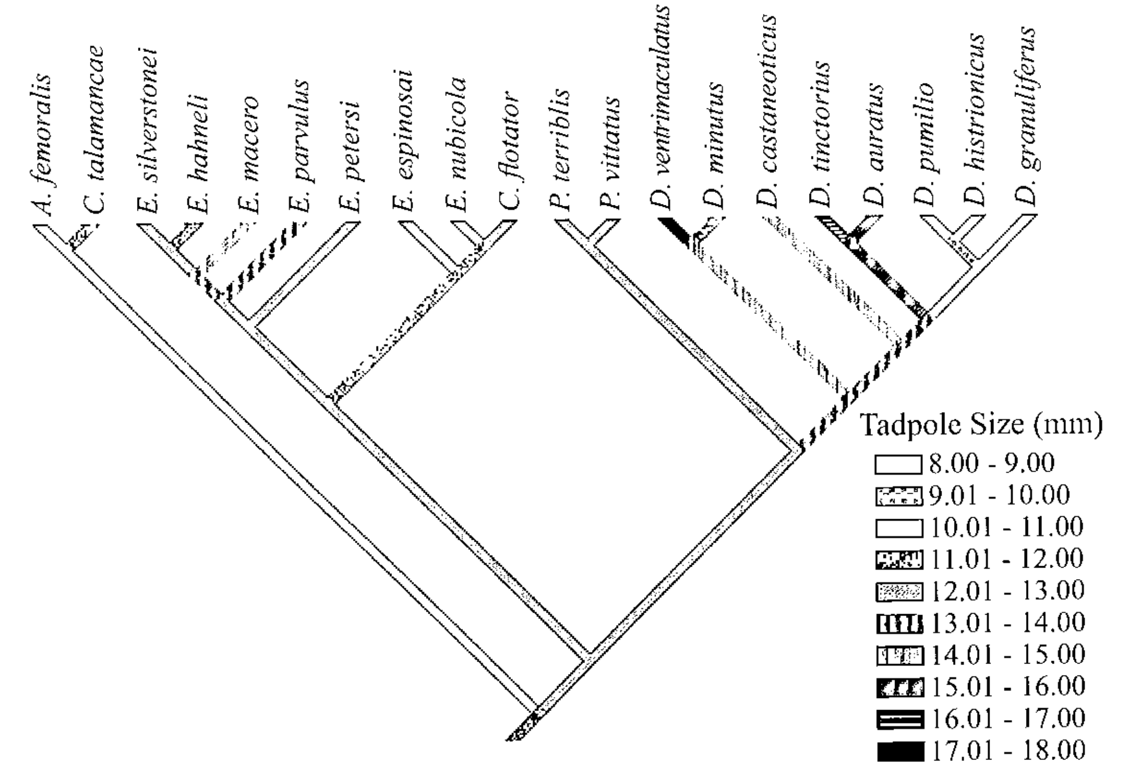

Fig. 8. The most parsimonious reconstruction (using squared change parsimony) of total tadpole length (stage 25 tadpoles) on the phylogenetic tree of dendrobatid frogs. Species for which data was not available have been trimmed from the tree. Tree construction and abbreviations as in Fig. 1.

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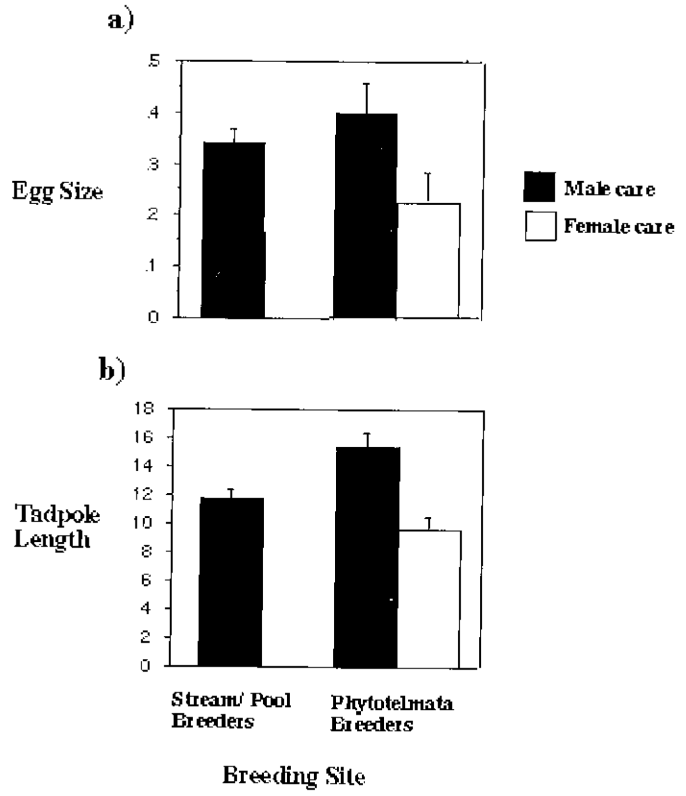

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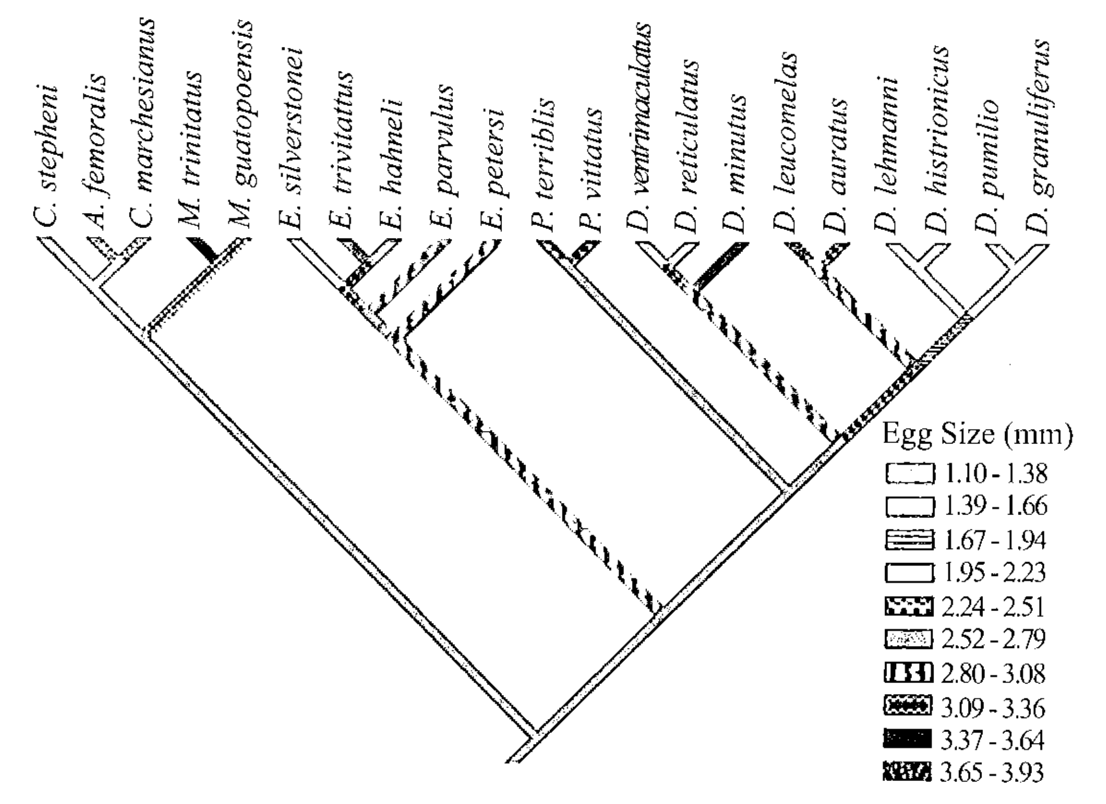
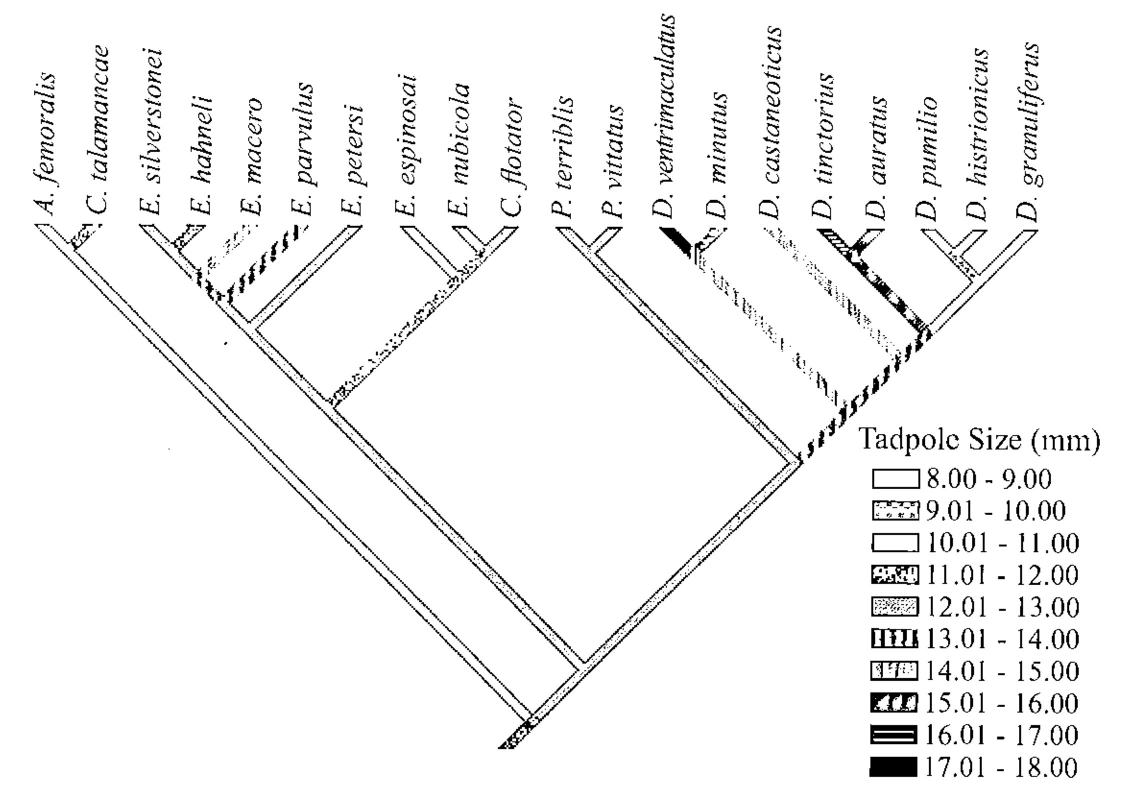


Fig. 7. The most parsimonious reconstruction (using squared change parsimony) of egg size on the phylogenetic tree of dendrobatid frogs. Species for which data was not available have been trimmed from the tree. Tree construction and abbreviations as in Fig. 1.



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clutches over time, is not known. Resolving this question will require more complete data on the reproductive schedules of dendrobatids in the field, information that is currently available for very few species.

Larval Ecology, Population Density, and Community Structure. As mentioned above, inter-specific competition among larvae appears to be rare in phytotelmata-breeding dendrobatids. It is not clear why this is the case, although specialization on different types of phytotelmata is a possibility. If such specialization occurs, then the availability of different types of phytotelmata could influence the abundance of particular species. Whether or not the availability of any type of phytotelmata affects population density in dendrobatids has rarely been investigated. Donnelly (1989*a,b*) established experimental and control plots in cacao groves at the La Selva Biological Station in Costa Rica, and manipulated the abundance of leaf litter and bromeliads in a two-factor factorial design. This experiment demonstrated a positive effect of phytotelmata (bromeliad) abundance on the population densities of both males and females in this population. However, this effect was due to increased immigration and decreased emigration of adults, rather than enhanced recruitment.

The degree to which tadpole growth and survival affects adult dendrobatid abundance and community structure has not been investigated. Here we present data that is consistent with a role for larval ecology on the relative abundance of two species of poison frogs that co-occur at the Nusagandi Biological Reserve in San Blas Province, Panama. Casual observations at this reserve reveal that *D. minutus* is very abundant. In contrast, *D. auratus* is rarely seen and hence appears uncommon. In order to confirm this initial impression, Summers (2002) used visual encounter surveys (Heyer *et al.*, 1994) to assess the relative abundance of leaf litter anurans on three different plots in the reserve. These surveys revealed that *D. minutus* is substantially more abundant than any other leaf litter species occurring in the area. The relative abundance of *D. minutus* was 0.36, compared to a second highest relative abundance of 0.14 for *Colostethus nubicola* (Summers, 2002). In contrast, *D. auratus* was present, but sufficiently uncommon that it was not detected during the surveys.

An obvious question arises as to why *D. minutus* is so much more common than *D. auratus*, particularly given their close phylogenetic relationship and similar ecological niche. Many things can influence relative abundance, but predation and diet are two of the most commonly invoked factors. Predation is unlikely to explain the difference in abundance. *Dendrobates auratus* is highly toxic, whereas *D. minutus* is relatively non-toxic (Daly *et al.*, 1987). Diet also seems unlikely to play a major role. Toft (1980) investigated the diet of these species (among others) in an area very close to the Nusagandi Reserve. Her research demonstrated that these two species have similar diets, and that their prey occur in abundance.

Another possibility is that larval ecology has an important influence on adult population densities. Larval interactions between these species involving competition or predation could certainly influence adult population size. Differential availability of phytotelmata suitable for each species could also affect recruitment. Surveys carried out to locate phytotelmata for ecological experiments suggested that small bromeliads were substantially more abundant in the area than larger phytotelmata such as treeholes. We investigated the potential effects of larval interactions and pool availability with experimental manipulations (see Appendix 1).

Tadpoles of the two species collected during this study differed significantly in size: *D. auratus* tadpoles averaged 15.9 mm in total length, compared to 12.6 mm for *D. minutus* tadpoles at the same stage (stage 25). This is consistent with differences between the species in adult body size: adult *D. auratus* averaged 32.3 mm SVL, whereas adult *D. minutus* averaged 13.1 mm.

Three experimental treatments relevant to competition and predation between *D. auratus* and *D. minutus* tadpoles were carried out. Tadpoles were matched for size to minimize size and weight discrepancies between the different species. There was no significant size difference between the tadpoles at the start of the experiment. In spite of this size matching, in each case the *D. auratus* tadpole cannibalized the *D. minutus* tadpole within a week.

In order to evaluate whether *D. minutus* tadpoles were better able to survive and grow in small phytotelmata than *D. auratus*, experiments on the growth rates of single *D. minutus* and single *D. auratus* in small phytotelmata were carried out. *Dendrobates minutus* tadpoles were placed in smaller phytotelmata than the *D. auratus* tadpoles, to make the test conservative. There were significant differences between the growth rates of *D. auratus* and *D. minutus* for SVL (Fig. 9a; t-test: *D. minutus*: N = 10, X = 0.49; *D. auratus*: N = 4, X = -0.73; t = -3.22, P = 0.007) and head width (Fig. 9b; *D. minutus*: N = 10, X = 0.69; *D. auratus*: N = 4, X = -0.26; t = -2.39, P = 0.034), but not for total length. These results suggest that *D. minutus* tadpoles are able to grow in the readily available small phytotelmata, whereas *D. auratus* tadpoles are not. Since the *D. auratus* tadpoles shrank instead of growing in the small pools, it is unlikely that they would survive.

In summary, *D. auratus* tadpoles predate *D. minutus* tadpoles when they occur in the same phytotelmata. Nevertheless, *D. auratus* do not utilize the small phytotelmata used by *D. minutus*. This is probably because there are insufficient nutrients available for *D. auratus* tadpoles to grow and survive in those pools. This may have a significant effect on the abundance of adult *D. minutus* relative to *D. auratus* at this site.

Conclusions. We have explored the evolutionary ecology of phytotelmata-breeding by dendrobatids from many different angles. It should be apparent that many of the factors we have discussed, such as pool size, predation, competition, cannibalism, nutrient availability, patterns of parental care, mating strategies, reproductive parasitism, egg and clutch size, population density and community structure are intimately connected through a complex web of interactions. As a visual summary, we illustrate some of these connections in Fig 10, which shows interactions between the factors we have discussed.

The ecological factors driving the transition from terrestrial pool-breeding to phytotelmata-breeding remain obscure, but progress in understanding what factors were likely to have been important can be made by investigating the effects of selected factors on extant species. The presence of a relatively contiguous range of reproductive mode within the extant Dendrobatidae allows for experimental testing of larval growth and survival, and adult habitat choice, in species utilizing breeding strategies that span the transition between terrestrial pools and phytotelmata. We have carried out preliminary research that is relevant to this issue. Experiments transplanting tadpoles of terrestrial-pool breeders to phytotelmata to investigate growth and survival effects may also prove useful.

The synthesis of multiple avenues of research will allow us to better evaluate particular hypotheses concerning the transition from terrestrial pool to phytotelmata-breeding. For example, if we find that predation by invertebrate predators is the most important factor influencing larval survival and adult habitat choice in dendrobatids that currently utilize terrestrial pools, and if transplantation experiments reveal a pronounced survival advantage to larvae in phytotelmata, these results would support the hypothesis that predation was an important factor driving the transition to phytotelmata-breeding.

Many promising lines of ecological inquiry remain unexplored, and greater systematic resolution of the group will continue to add context to future work. Ultimately, the reproductive use of phytotelmata has bearing on most elements of the biology of the family Dendrobatidae. As such, an understanding of the evolution of this trait, and the ecological forces that drove the transition from the forest floor to arboreal phytotelmata, may be our most useful key to gain insight into this fascinating group.

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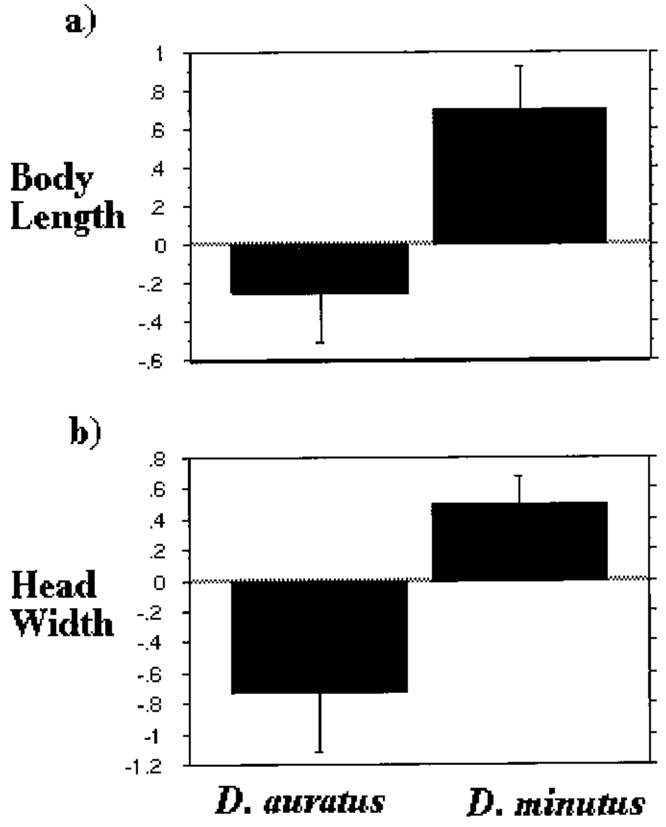

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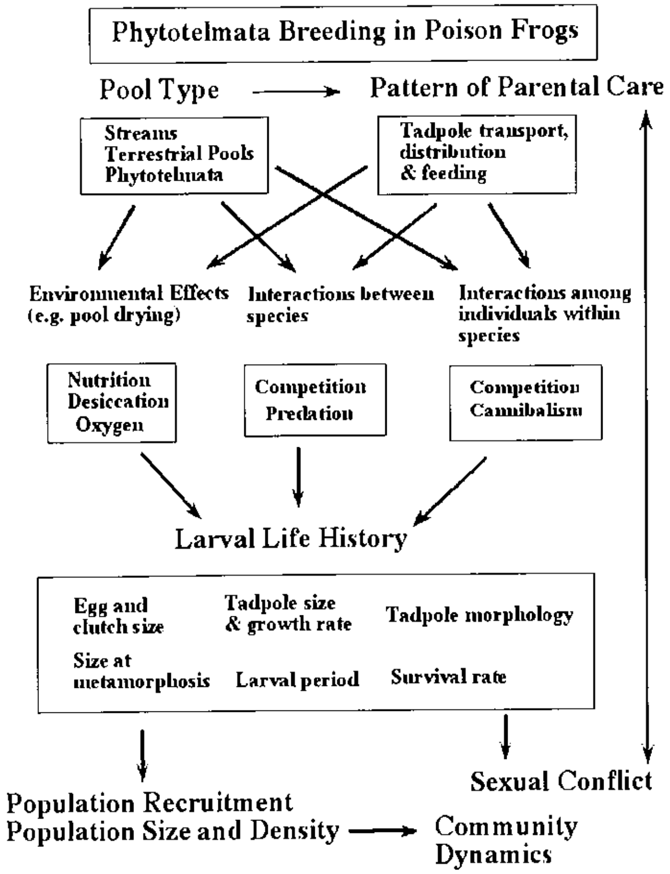

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clutches over time, is not known. Resolving this question will require more complete data on the reproductive schedules of dendrobatids in the field, information that is currently available for very few species.

Larval Ecology, Population Density, and Community Structure. As mentioned above, inter-specific competition among larvae appears to be rare in phytotelmata-breeding dendrobatids. It is not clear why this is the case, although specialization on different types of phytotelmata is a possibility. If such specialization occurs, then the availability of different types of phytotelmata could influence the abundance of particular species. Whether or not the availability of any type of phytotelmata affects population density in dendrobatids has rarely been investigated. Donnelly (1989*a,b*) established experimental and control plots in cacao groves at the La Selva Biological Station in Costa Rica, and manipulated the abundance of leaf litter and bromeliads in a two-factor factorial design. This experiment demonstrated a positive effect of phytotelmata (bromeliad) abundance on the population densities of both males and females in this population. However, this effect was due to increased immigration and decreased emigration of adults, rather than enhanced recruitment.

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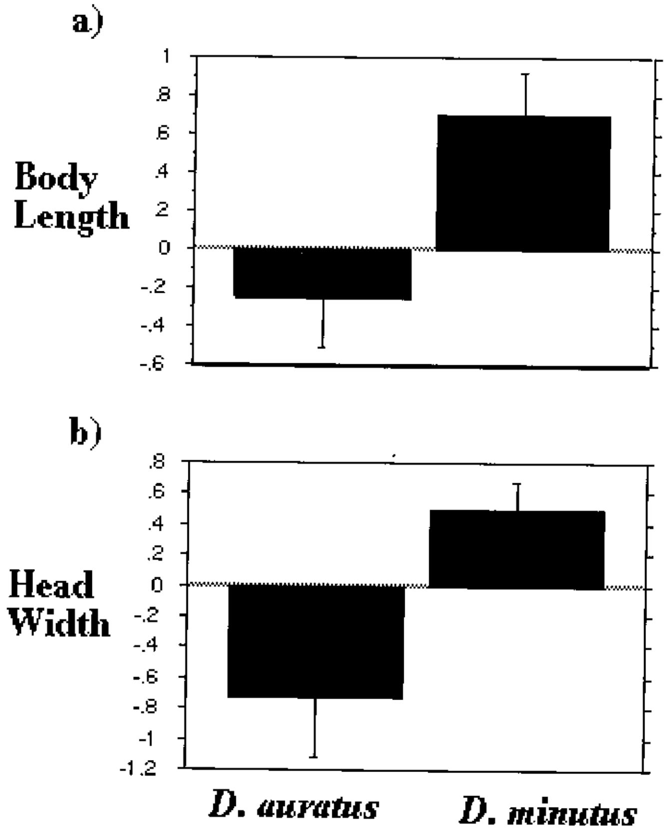

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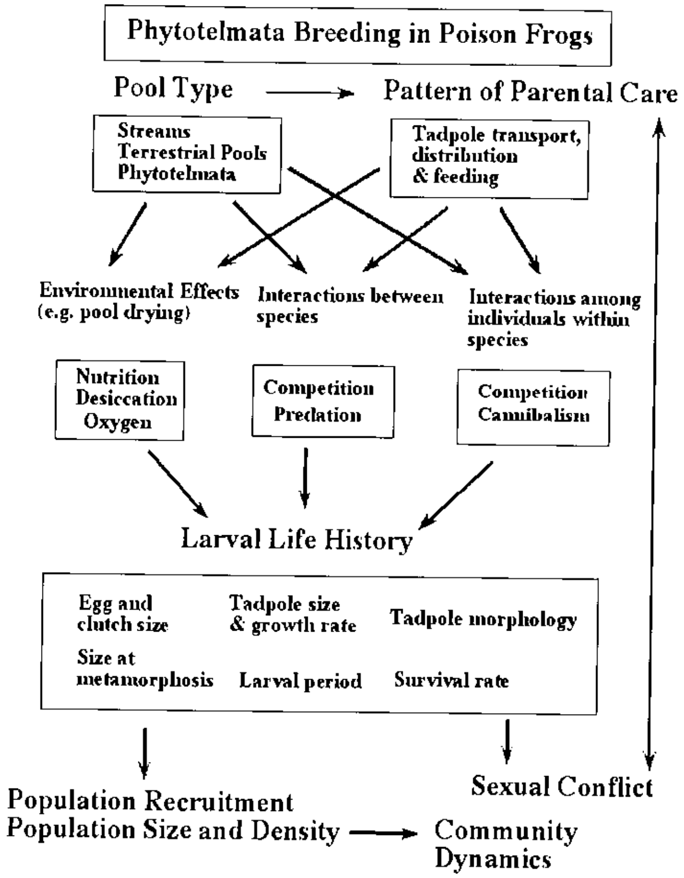

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Appendix 1: Field Methods

Dendrobates ventrimaculatus

Dendrobates ventrimaculatus was studied during June through August, 1997, in lowland rainforest near Pompeya, Ecuador. This species utilizes *Heliconia stricta* axils for both egg and tadpole deposition. Several hundred axil pools were monitored for several months (Summers, 1999). A 40 x 85 m grid was established in an area of high *Heliconia* density, marked with plastic flagging. Pools that contained eggs or tadpoles were monitored every other day for two months. A total of 241 breeding pools (containing eggs, embryos, tadpoles, or adults) were marked and monitored. A qualitative estimate of initial pool size (based on perceived similarity to pools for which volume had been measured by removal of all water) was made for each pool: Small (less than 20 ml), Medium/ Small (20-50 ml), Medium (50-100 ml), Medium/ Large (150-200 ml), Large (>200 ml). The final volume of 43 pools from which tadpoles were collected was measured by removing the water with a pipet. Pools were assigned to two final volume categories for an analysis of tadpole morphology: normal (20 ml or above), and low (less than 20 ml).

Tadpoles in pools with very low water levels (less than 20 ml) were collected approximately two weeks after the low water levels had been detected. Hence, tadpoles in these pools had several weeks to respond developmentally to pool drying. Tadpoles were also collected from pools that were not dry, for comparative purposes. Tadpoles were transported to the village of Limoncocha, where they were weighed on an electronic scale (Ohaus Model 300), measured (SVL and total length) and staged (Gosner, 1960). A total of 61 tadpoles were collected. Almost all (60) were weighed and staged. Most tadpoles were measured for SVL (58) and total length (52). Some were not measured due to damage, particularly to the tail. For the purpose of analysis, tadpoles were divided into two stage categories: Early (from stage 25 to 34), and Late (from stage 35 to 45).

Dendrobates minutus and *Dendrobates auratus*

Dendrobates minutus and *D. auratus* were studied at the Nusagandi Biological Reserve, in the Comarca of San Blas, Republic of Panama. Observations and experiments were carried out in three areas along the Ina Igar trail, in primary moist tropical forest.

Methods used for species abundance surveys were described by Summers (2002). Tadpole experiments were carried out in bromeliads collected from the field. Bromeliads were emptied of all detritus, tadpoles and insect larvae, filled with a small amount of detritus and water, and planted in plastic cups. Experiments were carried out on a sheltered porch at the Nusagandi Field Station and in fenced enclosures in the field. *Dendrobates minutus* tadpoles were collected from bromeliads in the field. *Dendrobates auratus* tadpoles were not found in bromeliads, but were collected by placing jars of water near areas where *D. auratus* adults were seen. Tadpoles were staged using Gosner's (1960) staging tables. Tadpoles were weighed on an electronic balance (Ohaus Model 300), and three morphological features were measured: total length, body length, and body width. The number of replicates per experiment was kept low to minimize the pain and trauma due to cannibalism or starvation. Statistical analyses were performed with Statview (Abacus, 1996).

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Dendrobates minutus and *Dendrobates auratus*

Dendrobates minutus and *D. auratus* were studied at the Nusagandi Biological Reserve, in the Comarca of San Blas, Republic of Panama. Observations and experiments were carried out in three areas along the Ina Igar trail, in primary moist tropical forest.

Methods used for species abundance surveys were described by Summers (2002). Tadpole experiments were carried out in bromeliads collected from the field. Bromeliads were emptied of all detritus, tadpoles and insect larvae, filled with a small amount of detritus and water, and planted in plastic cups. Experiments were carried out on a sheltered porch at the Nusagandi Field Station and in fenced enclosures in the field. *Dendrobates minutus* tadpoles were collected from bromeliads in the field. *Dendrobates auratus* tadpoles were not found in bromeliads, but were collected by placing jars of water near areas where *D. auratus* adults were seen. Tadpoles were staged using Gosner's (1960) staging tables. Tadpoles were weighed on an electronic balance (Ohaus Model 300), and three morphological features were measured: total length, body length, and body width. The number of replicates per experiment was kept low to minimize the pain and trauma due to cannibalism or starvation. Statistical analyses were performed with Statview (Abacus, 1996).

Appendix 2: Egg and Clutch Size Data

Genus	Species	Avg. Egg	Avg. Clutch	Avg. Tad	Avg. SVL	Avg. F	Max. F	Breeding Site	PC
Allobates	*femoralis*	1.80	17.50			27.00		Stream/ Pool	Male
Allobates	*femoralis*	2.00	22.70	7.40		26.00	29.00	Stream/ Pool	Male
Allobates	*femoralis*			10.50	26.60	27.30	33.50	Stream/ Pool	Male
Allobates	*zaparo*				27.90	28.00	30.50	Stream/ Pool	Male
Aromobates	*nocturnus*			68.10	53.02	57.49	61.60	Stream	
Colostethus	*bromelicola*	1.70	4.00	14.50	16.03	17.35	17.20	Small Phyto	
Colostethus	*caerulodactylus*	1.18	19.20		15.80	16.10	16.80	Stream/ Pool	Male
Colostethus	*degranvillei*				18.26	19.67		Direct Devel.	
Colostethus	*flotator*			12.50	16.10	16.60	18.00	Stream/ Pool	Male
Colostethus	*guatopoensis*	3.00	34.00	16.00	35.00	37.00	43.50	Stream	Male
Colostethus	*inguinalis*		35.00		26.00	27.00	31.00	Stream	Female
Colostethus	*marchesianus*	2.00	15.50		16.50	17.00	18.00	Stream/ Pool	Male
Colostethus	*marchesianus*	1.50	14.00		16.50	17.00	18.00	Stream/ Pool	Male
Colostethus	*marchesianus*	1.00	9.20					Stream/ Pool	Male
Colostethus	*nubicola*			11.00	18.00	18.60	23.00	Stream/ Pool	Male
Colostethus	*palmatus*				32.15	33.57		Stream/ Pool	Male
Colostethus	*pratti*				19.35	20.03		Stream/ Pool	Female
Colostethus	*sauli*	1.50	11.00		24.25	24.01	28.00	Stream/ Pool	Male
Colostethus	*stepheni*	2.00	3.80				18.00	Direct Devel.	Male
Colostethus	*subpunctatus*		21.90		20.55	22.44		Stream/ Pool	Male
Colostethus	*talamancae*			12.00	21.75	23.90	25.00	Stream/ Pool	Male
Colostethus	*trilineatus*				16.77	17.09	19.30	Stream/ Pool	Male
Colostethus	*trinitatus*	3.50	12.00		24.35	25.60	29.00	Stream/ Pool	Male
Colostethus	*vertebralis*	3.00	8.50	11.70	17.47	18.50	20.20	Stream/ Pool	Male
Dendrobates	*arboreus*		5.00		21.00	21.26	22.20	Small Phyto	Female
Dendrobates	*auratus*	2.35	4.31	15.95	32.80	33.90	42.00	Large Phyto	Male
Dendrobates	*biolat*				15.25	16.00	17.00	Small Phyto	Bipar
Dendrobates	*castaneoticus*		2.40	14.94	20.60	21.90	22.70	Large Phyto	Male
Dendrobates	*fantasticus*				19.50	20.50	23.00	Small Phyto	Male
Dendrobates	*granuliferus*	2.16	4.54	10.50	20.70	20.80	22.00	Small Phyto	Female
Dendrobates	*histrionicus*	1.50	3.50	10.50	33.20	33.10	38.00	Small Phyto	Female
Dendrobates	*lamasi*				18.75	20.50	21.00	Small Phyto	
Dendrobates	*lehmanni*	1.50	9.50			32.80		Small Phyto	Female
Dendrobates	*leucomelas*	3.93	7.00		33.80	34.80	37.50	Large Phyto	Male
Dendrobates	*minutus*	3.50	2.00	12.00	13.35	13.50		Small Phyto	Male
Dendrobates	*mysteriosus*				27.00	27.00	29.30	Small Phyto	Male
Dendrobates	*pumilio*	1.10	6.00	8.00		20.70		Small Phyto	Female
Dendrobates	*reticulatus*	2.00	2.50		14.75	15.50	17.00	Small Phyto	Male
Dendrobates	*tinctorius*			16.25	27.20	46.50	50.00	Large Phyto	Male
Dendrobates	*vanzolinii*		5.20		17.80	18.60	19.90	Small Phyto	Bipar
Dendrobates	*variabilis*				17.43		19.00	Small Phyto	Male
Dendrobates	*ventrimaculatus*	2.00	2.93	18.00		15.42		Small Phyto	Male
Dendrobates	*ventrimaculatus*				16.00	16.50	18.00	Small Phyto	Male
Dendrobates	*ventrimaculatus*				17.10	17.30	21.50	Small Phyto	Male
Epipedobates	*anthonyi*				19.20	20.00	21.00	Stream/ Pool	Male
Epipedobates	*azureiventris*		15.00		22.85	24.70	28.00	Stream/ Pool	Male
Epipedobates	*bassleri*		26.00		37.30	37.50	42.00	Stream/ Pool	Male

Avg. Egg = average egg diameter (mm), Avg. Clutch = average clutch size, Avg. Tad = average tadpole length (mm), Avg. SVL = average adult snout-vent length (mm), Avg. F = average female snout-vent length (mm), Max. F = maximum female snout-vent length (mm), PC = parental care type, Direct Develop. = Direct Development, Small/Large Phyto. = Small or Large Phytotelm

Appendix 2: Egg and Clutch Size Data

Genus	Species	Avg. Egg	Avg. Clutch	Avg. Tad	Avg. SVL	Avg. F	Max. F	Breeding Site	PC
Epipedobates	*bolivianus*				24.80	25.80	26.00	Stream/ Pool	Male
Epipedobates	*boulengeri*				17.70	18.50	21.00	Stream/ Pool	Male
Epipedobates	*espinosai*			11.00	16.90			Stream/ Pool	Male
Epipedobates	*hahneli*	2.30	22.00		19.75	20.50	22.00	Stream/ Pool	Male
Epipedobates	*hanheli*		18.00	11.50		24.40		Stream/ Pool	Male
Epipedobates	*macero*			14.10	27.20	28.59		Stream/ Pool	Male
Epipedobates	*parvulus*	3.00	8.90	13.20		21.10	23.00	Stream/ Pool	Male
Epipedobates	*parvulus*				20.50	21.20	24.00	Stream/ Pool	Male
Epipedobates	*petersi*	3.00	10.00			29.00		Stream/ Pool	Male
Epipedobates	*petersi*			12.50	26.60	28.00	31.00	Stream/ Pool	Male
Epipedobates	*pictus*	2.00	18.00			22.10	24.00	Stream/ Pool	Male
Epipedobates	*pictus*				23.80	24.40	31.50	Stream/ Pool	Male
Epipedobates	*pulchripectus*				24.50	26.00	27.00	Stream/ Pool	Male
Epipedobates	*silverstonei*	2.00	30.00	12.42	39.00	41.83	42.80	Stream/ Pool	Male
Epipedobates	*tricolor*		20.00		23.70	24.40	26.50	Stream/ Pool	Male
Epipedobates	*trivittatus*	3.00	38.00			45.00		Stream/ Pool	Male
Epipedobates	*trivittatus*		27.00	20.50	39.80	43.60	49.50	Stream/ Pool	Male
Mannophryne	*collaris*				23.82	25.43		Stream	Male
Mannophryne	*herminae*		12.70	13.60	21.98	22.99		Stream	Male
Phyllobates	*aurotaenia*			10.48	27.70	30.40	34.00		Male
Phyllobates	*bicolor*				38.20	39.80	42.00	Stream/ Pool	Male
Phyllobates	*lugubris*			10.39	20.50	22.20	23.50		Male
Phyllobates	*terriblis*	2.50	14.00	11.65	42.00	43.23	47.00	Stream/ Pool	Male
Phyllobates	*vittatus*	2.50	14.00	12.70	25.70	27.70	29.00	Stream/Pool/Phyto	Male

Avg. Egg = average egg diameter (mm), Avg. Clutch = average clutch size, Avg. Tad = average tadpole length (mm), Avg. SVL = average adult snout-vent length (mm), Avg. F = average female snout-vent length (mm), Max. F = maximum female snout-vent length (mm), PC = parental care type, Direct Develop. = Direct Development, Small/Large Phyto. = Small or Large Phytotelm

References:
Brust, 1993; Caldwell and Araújo, 1998; Caldwell and Oliveira, 1999; Caldwell and Myers, 1990; Coloma, 1995; Crump, 1974; Dixon and Rivero-Blanco, 1985; Donnelly et al., 1990; Duellman and Trueb, 1986; Dunn, 1941; Edwards, 1974; Grant and Rodriguez, 2001; Heselhaus, 1992; Ibanez and Smith, 1995; Junca et al., 1994; Kneller and Henle, 1985; Lima and Caldwell, 2001; Lima et al., 2001; Limerick, 1980; Meyer, 1992, 1993; Myers and Daly, 1979; Myers et al., 1978; Myers et al., 1984; Myers et al., 1991; Rodriguez and Myers, 1993; Rodriguez and Duellman, 1994; Roithmair, 1992; Savage, 2002; Schulte, 1999; Silverstone, 1975, 1976; Stebbins and Hendrickson, 1959; Wells, 1980; Weygoldt, 1980; Zimmerman and Zimmerman, 1984.

Appendix 2: Egg and Clutch Size Data

Genus	Species	Avg. Egg	Avg. Clutch	Avg. Tad	Avg. SVL	Avg. F	Max. F	Breeding Site	PC
Allobates	*femoralis*	1.80	17.50			27.00		Stream/ Pool	Male
Allobates	*femoralis*	2.00	22.70	7.40		26.00	29.00	Stream/ Pool	Male
Allobates	*femoralis*			10.50	26.60	27.30	33.50	Stream/ Pool	Male
Allobates	*zaparo*				27.90	28.00	30.50	Stream/ Pool	Male
Aromobates	*nocturnus*			68.10	53.02	57.49	61.60	Stream	
Colostethus	*bromelicola*	1.70	4.00	14.50	16.03	17.35	17.20	Small Phyto	
Colostethus	*caerulodactylus*	1.18	19.20		15.80	16.10	16.80	Stream/ Pool	Male
Colostethus	*degranvillei*				18.26	19.67		Direct Devel.	
Colostethus	*flotator*			12.50	16.10	16.60	18.00	Stream/ Pool	Male
Colostethus	*guatopoensis*	3.00	34.00	16.00	35.00	37.00	43.50	Stream	Male
Colostethus	*inguinalis*		35.00		26.00	27.00	31.00	Stream	Female
Colostethus	*marchesianus*	2.00	15.50		16.50	17.00	18.00	Stream/ Pool	Male
Colostethus	*marchesianus*	1.50	14.00		16.50	17.00	18.00	Stream/ Pool	Male
Colostethus	*marchesianus*	1.00	9.20					Stream/ Pool	Male
Colostethus	*nubicola*			11.00	18.00	18.60	23.00	Stream/ Pool	Male
Colostethus	*palmatus*				32.15	33.57		Stream/ Pool	Male
Colostethus	*pratti*				19.35	20.03		Stream/ Pool	Female
Colostethus	*sauli*	1.50	11.00		24.25	24.01	28.00	Stream/ Pool	Male
Colostethus	*stepheni*	2.00	3.80				18.00	Direct Devel.	Male
Colostethus	*subpunctatus*		21.90		20.55	22.44		Stream/ Pool	Male
Colostethus	*talamancae*			12.00	21.75	23.90	25.00	Stream/ Pool	Male
Colostethus	*trilineatus*				16.77	17.09	19.30	Stream/ Pool	Male
Colostethus	*trinitatus*	3.50	12.00		24.35	25.60	29.00	Stream/ Pool	Male
Colostethus	*vertebralis*	3.00	8.50	11.70	17.47	18.50	20.20	Stream/ Pool	Male
Dendrobates	*arboreus*		5.00		21.00	21.26	22.20	Small Phyto	Female
Dendrobates	*auratus*	2.35	4.31	15.95	32.80	33.90	42.00	Large Phyto	Male
Dendrobates	*biolat*				15.25	16.00	17.00	Small Phyto	Bipar
Dendrobates	*castaneoticus*		2.40	14.94	20.60	21.90	22.70	Large Phyto	Male
Dendrobates	*fantasticus*				19.50	20.50	23.00	Small Phyto	Male
Dendrobates	*granuliferus*	2.16	4.54	10.50	20.70	20.80	22.00	Small Phyto	Female
Dendrobates	*histrionicus*	1.50	3.50	10.50	33.20	33.10	38.00	Small Phyto	Female
Dendrobates	*lamasi*				18.75	20.50	21.00	Small Phyto	
Dendrobates	*lehmanni*	1.50	9.50			32.80		Small Phyto	Female
Dendrobates	*leucomelas*	3.93	7.00		33.80	34.80	37.50	Large Phyto	Male
Dendrobates	*minutus*	3.50	2.00	12.00	13.35	13.50		Small Phyto	Male
Dendrobates	*mysteriosus*				27.00	27.00	29.30	Small Phyto	Male
Dendrobates	*pumilio*	1.10	6.00	8.00		20.70		Small Phyto	Female
Dendrobates	*reticulatus*	2.00	2.50		14.75	15.50	17.00	Small Phyto	Male
Dendrobates	*tinctorius*			16.25	27.20	46.50	50.00	Large Phyto	Male
Dendrobates	*vanzolinii*		5.20		17.80	18.60	19.90	Small Phyto	Bipar
Dendrobates	*variabilis*				17.43		19.00	Small Phyto	Male
Dendrobates	*ventrimaculatus*	2.00	2.93	18.00		15.42		Small Phyto	Male
Dendrobates	*ventrimaculatus*				16.00	16.50	18.00	Small Phyto	Male
Dendrobates	*ventrimaculatus*				17.10	17.30	21.50	Small Phyto	Male
Epipedobates	*anthonyi*				19.20	20.00	21.00	Stream/ Pool	Male
Epipedobates	*azureiventris*		15.00		22.85	24.70	28.00	Stream/ Pool	Male
Epipedobates	*bassleri*		26.00		37.30	37.50	42.00	Stream/ Pool	Male

Avg. Egg = average egg diameter (mm), Avg. Clutch = average clutch size, Avg. Tad = average tadpole length (mm), Avg. SVL = average adult snout-vent length (mm), Avg. F = average female snout-vent length (mm), Max. F = maximum female snout-vent length (mm), PC = parental care type, Direct Develop. = Direct Development, Small/Large Phyto. = Small or Large Phytotelm

Appendix 2: Egg and Clutch Size Data

Genus	Species	Avg. Egg	Avg. Clutch	Avg. Tad	Avg. SVL	Avg. F	Max. F	Breeding Site	PC
Epipedobates	*bolivianus*				24.80	25.80	26.00	Stream/ Pool	Male
Epipedobates	*boulengeri*				17.70	18.50	21.00	Stream/ Pool	Male
Epipedobates	*espinosai*			11.00	16.90			Stream/ Pool	Male
Epipedobates	*hahneli*	2.30	22.00		19.75	20.50	22.00	Stream/ Pool	Male
Epipedobates	*hanheli*		18.00	11.50		24.40		Stream/ Pool	Male
Epipedobates	*macero*			14.10	27.20	28.59		Stream/ Pool	Male
Epipedobates	*parvulus*	3.00	8.90	13.20		21.10	23.00	Stream/ Pool	Male
Epipedobates	*parvulus*				20.50	21.20	24.00	Stream/ Pool	Male
Epipedobates	*petersi*	3.00	10.00			29.00		Stream/ Pool	Male
Epipedobates	*petersi*			12.50	26.60	28.00	31.00	Stream/ Pool	Male
Epipedobates	*pictus*	2.00	18.00			22.10	24.00	Stream/ Pool	Male
Epipedobates	*pictus*				23.80	24.40	31.50	Stream/ Pool	Male
Epipedobates	*pulchripectus*				24.50	26.00	27.00	Stream/ Pool	Male
Epipedobates	*silverstonei*	2.00	30.00	12.42	39.00	41.83	42.80	Stream/ Pool	Male
Epipedobates	*tricolor*		20.00		23.70	24.40	26.50	Stream/ Pool	Male
Epipedobates	*trivittatus*	3.00	38.00			45.00		Stream/ Pool	Male
Epipedobates	*trivittatus*		27.00	20.50	39.80	43.60	49.50	Stream/ Pool	Male
Mannophryne	*collaris*				23.82	25.43		Stream	Male
Mannophryne	*herminae*		12.70	13.60	21.98	22.99		Stream	Male
Phyllobates	*aurotaenia*			10.48	27.70	30.40	34.00		Male
Phyllobates	*bicolor*				38.20	39.80	42.00	Stream/ Pool	Male
Phyllobates	*lugubris*			10.39	20.50	22.20	23.50		Male
Phyllobates	*terriblis*	2.50	14.00	11.65	42.00	43.23	47.00	Stream/ Pool	Male
Phyllobates	*vittatus*	2.50	14.00	12.70	25.70	27.70	29.00	Stream/Pool/Phyto	Male

Avg. Egg = average egg diameter (mm), Avg. Clutch = average clutch size, Avg. Tad = average tadpole length (mm), Avg. SVL = average adult snout-vent length (mm), Avg. F = average female snout-vent length (mm), Max. F = maximum female snout-vent length (mm), PC = parental care type, Direct Develop. = Direct Development, Small/Large Phyto. = Small or Large Phytotelm

References:
Brust, 1993; Caldwell and Araújo, 1998; Caldwell and Oliveira, 1999; Caldwell and Myers, 1990; Coloma, 1995; Crump, 1974; Dixon and Rivero-Blanco, 1985; Donnelly et al., 1990; Duellman and Trueb, 1986; Dunn, 1941; Edwards, 1974; Grant and Rodriguez, 2001; Heselhaus, 1992; Ibanez and Smith, 1995; Junca et al., 1994; Kneller and Henle, 1985; Lima and Caldwell, 2001; Lima et al., 2001; Limerick, 1980; Meyer, 1992, 1993; Myers and Daly, 1979; Myers et al., 1978; Myers et al., 1984; Myers et al., 1991; Rodriguez and Myers, 1993; Rodriguez and Duellman, 1994; Roithmair, 1992; Savage, 2002; Schulte, 1999; Silverstone, 1975, 1976; Stebbins and Hendrickson, 1959; Wells, 1980; Weygoldt, 1980; Zimmerman and Zimmerman, 1984.