identify individuals in a population. For example, with 2–4 injection sites on our geckos (i.e., the near-transparent undersides of knee and elbow joints), a large number of unique color combinations was possible given the availability of five readily distinguishable VIE colors, and the experimenter's own injection-pattern variability. The greater effort and higher cost of elastomer, relative to the other surface-marking methods we tested, are outweighed by the longer retention time of the VIE.

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POINTS OF VIEW

The Evolution of Three Deviations from the Biphasic Anuran Life Cycle: Alternatives to Selection

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The origins of the diversity of breeding modes in anurans beg for more focused hypotheses, but no suggestion for the evolution of any grade of endotrophy (= development without a free-living, feeding tadpole *sensu* Altig and Johnston 1989) has received rigorous testing (e.g., Salthe and Duellman 1973). Direct development occurs in at least nine anuran families (Thibaudeau and Altig 1999), and other grades of endotrophy add to the list of deviations from the classical biphasic anuran life cycle. Selection has been proposed as the process by which these various reproductive modes arose (e.g., Downie 1993; Magnusson and Hero 1991). The prevalence of these breeding patterns in species rich, tropical assemblages has presumably been caused by selection for escaping crowded (i.e., competitors) and hostile (i.e., predators and abiotic factors) aquatic habitats (e.g., Duellman 1978). Yet, hundreds of species reproduce in aquatic sites in many habitats despite experiencing low and sporadic recruitment (e.g., Greenberg and Tanner 2005). Accordingly, we should not assume that any of these reproductive deviations afford vastly superior recruitment over the typical life cycle (e.g., Roberts 1994; Rödel et al. 2002), especially when egg survival is the only criterion that is commonly reported.

In the near absence of prevailing hypotheses that address the evolution of these various developmental modes (see Callery et al. 2001), we discuss an alternative to selection. We argue for a nonhierarchical approach in a system that suggests a hierarchical structure. Adhering to a hierarchical system oversimplifies a complicated process and inhibits finding a viable solution. Many broad questions need to be answered, and only after the collection of pertinent specimens and data can we eventually revisit the larger question of the evolution of divergent reproductive modes. We discuss three reproductive grades as examples that we propose have arisen independently by different genetic mechanisms, usually multiple times: arboreal eggs, nidicolous larvae (= variously modified, nonfeeding tadpoles usually confined to a "nest"), and direct developers (= froglet hatches from egg jellies). With an understanding of developmental biology increasing daily (e.g., Gilbert 2001; Raff 1996; Robert et al. 2001), discussions of competing hypotheses should help direct future studies.

We argue that those taxa that lay arboreal eggs over water and develop normally as tadpoles achieved those capabilities via se-

lective forces that coordinated two primary subjects: initially the calling behaviors of males and subsequently the ovipositional activities of females. If we assume that a male calling from the ground near a breeding site and laying eggs with a female in the adjacent water is the ancestral state, then males calling from elevated sites might be a first step in the evolution of arboreal oviposition. This move by the male was likely stimulated by selection for better spatial and acoustic resolution for mate choice in multispecies choruses. At least three variations in female activities can be recognized in what may be a logical progression: (1) a female goes to a male on an elevated perch and the amplexed pair returns to the water to oviposit (e.g., *Hyla avivoca* and *H. cinerea*; the female is not required to collect cloacal water for egg hydration), (2) a female goes to an elevated male and the amplexed pair returns to the water so that the female can gather cloacal water to hydrate eggs before returning to an elevated site for oviposition (e.g., *Pachymedusa dacnicolor*; Bagnara et al. 1986), and (3) a female goes to an elevated male and oviposits at an arboreal site (e.g., several dendrobatids and leptodactylids). In the third case, the female's actions prior to traveling to the male and/or the characteristics of the eggs must have evolved relative to the other two cases. In the absence of prior changes in eggs or development, we assert that none of these situations is a precursor to direct development. Analyses by Roberts (1994) showed that arboreal eggs evolved independently at least 10 times in Anura, that this mode evolved within lineages having both aquatic and terrestrial oviposition sites, and that it sometimes reverted to the presumed ancestral state. The hypothesis that this mode evolved in response to intense predation in aquatic systems was not supported (Roberts 1994).

We suggest that at least minor changes in egg energetics, egg jelly, and developmental trajectories must precede ovipositional changes for a pathway to lead to a total escape from the aquatic system. Developmental changes indicative of increased yolk density (e.g., Chipman et al. 1999) occur in numerous taxa, but we have little understanding of the relationships among ovum sizes, yolk gradients, or energy contents (Thibaudeau and Altig 1999; see Komoroski and Congdon 2001). Larger eggs result in larger larvae that maintain their size and growth advantages throughout their ontogeny (e.g., Dziminski and Alford 2005), but we have little idea which characteristics of a large egg promote these responses. A proportional increase in energy content is presumed, but this, and variations in other kinds of maternal provisioning, need verification among taxa representing diverse breeding modes.

Is the embryology of direct development more expensive than exotrophic development and is the increase in yolk in large, direct-developing eggs intended for embryological or posthatching development? Physical factors associated with being in air, energy sources and RNA transcripts provided by the mother during vitellogenesis, and provisioning of posthatchlings that are sometimes very small (e.g., hatchling *Sooglossus gardineri* are ca. 1 mm SVL; pers. observ.) are important factors to consider. Knowledge of the kinds and amounts of maternal provisioning of eggs from species that represent a number of reproductive modes are needed before we can start to understand the energetics of development. Changes in breeding mode likely occur only when a number of factors occur collaboratively, if not synergistically. For example, we reject the idea that arboreal foam nests involving nu-merous small eggs could be a precursor to direct development (Bossyut and Milinkovitch 2000). In this case, the eggs are out of water, but none of the other factors we consider required for the transition to direct development is present. This disagreement illustrates that we do not know enough about the probable sequence or many interactions of adults, ova, and development underlying such a transition in reproductive mode.

We suggest that the multiple occurrences of nidicoly represent independent truncations of normal development, but the specific benefits of these developmental modes remain unclear. Although nidicolous species likely share some of the presumed fitness benefits of arboreal eggs or direct development, we suggest that nidicoly has no developmental, genetic, or evolutionary associations with the other two modes. The details of a nidicolous ontogeny surely proceeds by patterns similar to typical larvae, whereas direct development involves a highly modified developmental pattern that does not involve developmental truncations, at least of similar kinds; nidicolous larvae likely are paedomorphic products of more modest regulatory changes (see below) while not violating metamorphic constraints required to recover a frog morphotype. If we knew which characters are affected to what degree and in what sequence or associations (see Thibaudeau and Altig 1999), then we would know the primacy of developmental occurrences, their developmental integration, and thus the relative degree of the truncation.

Direct development is different from the development of exotrophic tadpoles in a biphasic life cycle in many ways beyond the obvious developmental differences and the retention of a subtle, thyroid-based metamorphosis (Callery and Elinson 2000). Such differences include a precocial neural tube anatomy (Schlosser 2003), a different mode of abdominal wall formation (Elinson and Fang 1998), limb development in the absence of an apical ectodermal ridge (Richardson et al. 1998), and at least three types of tail development (i.e., small tails, with small fins, flexed ventrally, some myobatrachids (M. Anstis, pers. comm.); larger tails with large fins, flexed ventrally, some microhylids (pers. observ.); and larger tails with large fins, flexed laterally, some leptodactylids (Townsend and Stewart 1985). Admittedly our perspectives are myopic because most data are based on one species of *Eleutherodactylus*.

The unusual embryology (Elinson and Del Pino 1985), development (Wassersug and Duellman 1984), and unique bell gills of amphignathodontids (*sensu* Frost et al. 2006), although based largely on studies of one species of *Gastrotheca*, represent perhaps another form of endotrophy besides those discussed above. In no other genus is there a scattering of froglet-producing and tadpole-producing species. Wassersug and Duellman's (1984) suggestion that tadpoles are produced by some form of truncation of the froglet-producing program is debatable, but at least the reproductive diversity in this genus suggests that a variety of developmental programs can be switched rather easily, or often, among members of some lineages.

The primary alternative hypothesis for the origin of direct development is: although unknown selective pressures acted on prerequisites (e.g., ovum characteristics), the actual originations of direct development did not involve selection. The presumed switch from exotrophic tadpoles to direct development most likely occurred via major regulatory gene(s) deep within the developmen-

tal cascade, and the wide-ranging occurrences of direct development among families suggests that the genomes of all frogs contain the basic components of this developmental program. The origin of this novel embryogenesis must have been associated with a release from the developmental bias or constraint that governed the biphasic life cycle. There is no need to invoke gradual change via small multiple steps, each selected along the way. Instead there could have been a single, radical developmental change that bypassed the typical larval stage. Concomitant with that change, an independently evolved novel egg phenotype allowed the first direct developer to succeed, and selection would operate after the fact to maintain the novel embryogenesis. The release from the developmental bias can be viewed simply as the removal of barriers to developmental experimentation in contrast to some directional process. From this perspective, we should expect to find the various novel phenotypes that have subsequently evolved.

Did these genetic programs evolve in saltentian (*sensu* Cannatella and Hillis 1993) life histories or are they even older? Direct development occurs in salamanders and caecilians, although the actual ramifications of it vary because of developmental patterns unique to each group. Drastic changes in structural genes were likely not required, thus the end product only allowed those taxa involved to expand into new reproductive niches. Viewing the morphologies of the three developmental deviations described above in a series from least-to-most modified (assuming we had the data to do this), would show the various potentials of developmental genetics but no corresponding phylogenetic affinities among grades. None of the three grades seemingly provides the requisite morphologies from which any of the other two could be derived.

Our proposal was generated from an observation and a presumption. Direct development has evolved numerous times (e.g., Marmayou et al. 2000 for a specific example) with many commonalities and differences across taxa. Conversely, the multiple occurrences of this developmental pattern based on successfully coordinated point mutations seem less plausible than being caused by basal regulatory changes (see above). The alternative, which cannot be resolved because of our paltry database, that the presumed similarities in morphology, behavior, and physiology of direct developers are produced by some unknown number of convergent genetic manipulations, seems equally unlikely because of the complexity of the many developmental changes.

If anuran development is capable of switching from exotrophic to endotrophic development by a yet unknown mechanism, perhaps the reverse occurs. Could the morphological oddities of exotrophic microhylid tadpoles (e.g., Wassersug 1989) be an example of an exotrophic tadpole with endotrophy in its ancestry? Thus, do all tadpoles have the same phylo-developmental history? Such initially outlandish scenarios gain credence in light of discussions (e.g., Chippindale et al. 2004; Mueller et al. 2004) that suggest developmental switches within lineages. Even though these particular cases involve salamanders wherein the direct developers are not nearly as divergent from typical cases as occurs in frogs, the genetic bases for such modifications are at least present in the genome of amphibians.

Other research fields may offer insights into the developmental patterns of direct development and its origins. For example, an exotrophic larva is immunocompetent, but it must reduce its immunocompetence by eradicating certain larval lymphocytes to avoid autoimmune responses when novel proteins appear at metamorphosis (Rollins-Smith 1998; Ruben et al. 1989). Direct development may be a means of avoiding metamorphic antigens without the hazards of immunosuppression. Model-based studies of metamorphic immunosuppression do not include information on direct developers. Also, if direct development involves upregulation of gene expressions, the energetic costs (Wagner 2005) may be an influential factor. Next, Galis et al. (2003) suggested that limb regeneration occurs readily in amphibians but not other tetrapods because the late development of the limbs removes a constraint of being associated with the development of the main body axis. If true, the patterns of limb regeneration (see Alvarado 2000; Brockes et al. 2001) in direct developers, whose limbs develop concurrently with the body axis, may more closely resemble the developmental patterns of reptiles. Last, certain marine invertebrates with varied developmental patterns have been studied in more detail than amphibians. For example, Strathman et al. (2002) noted that embryos that experience parental care develop more slowly than, in their case, free-living, planktonic forms. More informatively, these researchers suggested that slower development may permit compensation for less maternal investment of rate-limiting materials to the eggs and correction of developmental errors. This is the reverse of the common assumption (e.g., Dziminski and Alford 2005) that the large eggs of direct developers are better provisioned, and parental care was suggested as the equalizing factor.

The typically low species diversity among direct-developing lineages suggests that these developmental patterns are not entirely successful. The extant taxa could be the surviving members of larger assemblages in the past, but the fact that ca. 44% of the direct-developing taxa are not monophyletic with other direct-developing lineages suggests that selection did not produce the loss of the aquatic tadpole stage. Selection undoubtedly has maintained these lineages, but we argued above that the required embryological changes were not borne from selective forces per se. Species-rich exceptions may involve undetected developmental improvements over the clades with fewer species, or speciation in these lineages perhaps is not influenced by the success of their developmental modes.

Examples from the rapidly growing evolutionary and genetic literature give us a viewpoint from which to discuss new hypotheses. We do not propose actual mechanisms that may have been instrumental in the originations of any of the three developmental grades discussed here, but it is obvious that we are gaining access to relevant mechanisms that appear to give natural selection much more latitude to operate on a faster time scale. Arthur (2002) proposed the "biased embryo" hypothesis (i.e., the tendency for developmental systems to produce variant trajectories in some directions more readily than others) with four organismal levels of reprogramming that act as partners with selection. Fondon and Garner (2004) proposed that gene-associated tandem repeat expansions and contractions in *Hox*-family genes could promote rapid morphological change. Building on these studies, Ruden et al. (2005) hypothesized that stressors could be the trigger. Dehydration and thus ion balance, gas exchange, immunological factors, and changes in egg provisioning are possible options for stressors in the cases discussed here. The *Bmp*4 gene (Abzhanov et al. 2004; Albertson et al. 2005) is an interesting candidate for developmental adjustments in both direct-developing and typical amphibian

larvae.

Evolutionary and developmental geneticists should be aware that natural experiments in amphibian developmental patterns are awaiting explanations; there are frogs other than *Xenopus* that are strange in more interesting ways.

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RECENT POPULATION CHANGES

The Status of Two Northern Leopard Frog Populations in Western Montana

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Since the 1970s the Northern Leopard Frog (*Rana pipiens*) has experienced significant declines in the western United States and Canada (Clarkson and Rorabough 1989; Corn and Fogelman 1984; Corn et al.1989; Hayes and Jennings 1986; Leonard et al. 1999; Orchard 1992; Roberts 1992; Wagner 1997). In western Montana, Northern Leopard Frogs were not detected at 31 historical sites and 1,324 non-historical sites, about half of which were considered suitable for *R. pipiens*, surveyed between 1997 and 2002 (Werner 2003). During these surveys, two extant, but previously unknown populations, known as the Foy Lakes and Meadow Chain-of-Lakes populations, were found (Fig. 1, Werner 2003). In 2002 to 2005, we initiated new, more intensive surveys of these two populations. Herein, we summarize their recent history (1995-2001), and from 2002–2005 surveys, we address their geographic range, approximate size, and level of reproduction.

Materials and Methods

The Foy Lakes population is located in Flathead County, Montana, 2.2 km W of Kalispell, on a chain of four interconnected lakes (Fig. 1). The area covers about 7 km² and is located mostly on private lands with housing developments around some lakes. The presence of Northern Leopard Frogs at Foy Lakes was first made known to us in 1997. The closest historical record for this frog is at Smith Lake National Wildlife Refuge (NWR), approximately 8 km to the southwest in the same drainage, but the last observation of the frog at the refuge was in 1974. Surveys since 1993 failed to find frogs at the Smith Lake NWR or other nearby

sites (Werner 2003).

The Meadow Chain-of-Lakes population (hereafter, "Chain-of-Lakes") is located 2.5 km S of Eureka in Lincoln County, Montana (Fig. 2). Chain-of-Lakes is situated on a timbered plateau ca. 125 m above the Tobacco River Valley. The area covers ca. 64 km² with numerous interconnecting lakes, ponds and wetlands except during dry years when smaller ponds and interconnecting waterways dry up. Historically, Northern Leopard Frogs were known from several lakes in the Tobacco River valley 10 km to the north, although no frogs were found at those sites in recent surveys (Werner 2003). We first observed Northern Leopard Frogs at Chain-of-Lakes in 1997.

We gathered background information prior to 2002 for the Foy Lakes and Chain-of-Lakes areas from unpublished surveys done by state and federal agencies, by the authors, or by other individuals. Most reports were sporadic surveys made during the spring or summer, usually with an objective to determine species richness, and were conducted by individuals having a wide range of experience. Hence, direct comparisons to the 2002 to 2005 surveys were not possible, but the data are included here because they provide a historical record and point of reference for discussion.

Beginning in 2002, our goal was to survey all marshes, ponds, and lakes within the Foy Lakes and Chain-of-Lakes areas for 3–4
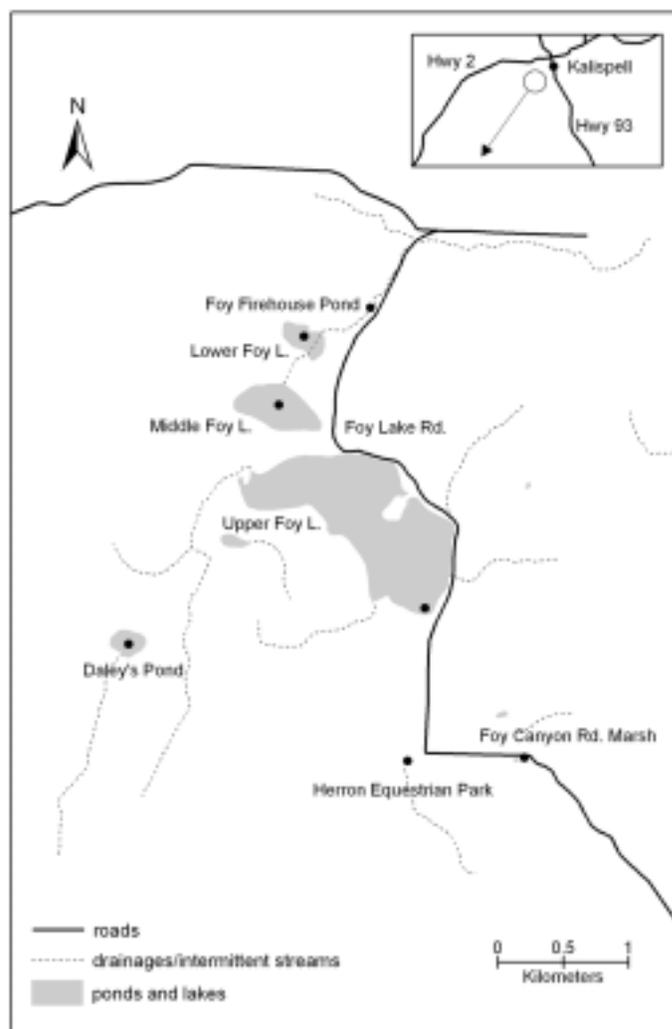

Fig. 1. Foy Lakes survey area in western Montana, USA.