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POINT OF VIEW

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TADPOLES EVOLVED AND FROGS ARE THE DEFAULT

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ABSTRACT: The thesis of this heuristic discussion is that the frog morphotype arose via a regulatory mutation that truncated vertebrae-forming somitogenesis and not via selection on structural genes. This truncation, along with many collaborative events (e.g., other skeletal elements, viscera, jaws, and mouthparts) required to maintain a viable organism, produced the essence of a prototadpole. With the presumed confines of metamorphosis, only something resembling a frog could metamorphose from such a highly paedomorphic larva. Larvae and adults were further altered by other less deep regulatory changes and subsequent selection to produce characters correlated with systematics and ecology.

Key words: Anura; Development; Evolution; Frog; Tadpole

THE INCORPORATION of the major advances in developmental genetics into ecological and evolutionary biology (e.g., Arthur, 2002; Gilbert, 2001) provides an avenue for an exploratory discussion because of how these integrations widen the research arenas. Developmental biologists should be aware that the anuran tadpole, essentially a free-living embryo, is a unique natural experiment waiting to reveal many interesting facets of evolution and development in a biphasic life cycle. A synthesis of the evolution of frogs by a generalist with a larval perspective should produce a new focus. The many queries proposed herein can be attacked from diverse angles ranging from descriptive embryology through molecular genetics, and I leave the formulation of specific hypotheses to the persons who design studies based on various techniques and analyses.

I assumed that a larval stage is the primitive state for anurans, although the primary thesis of this paper would pertain if alternative concepts were true (e.g., Bogart, 1981; Harris, 1999). Tadpole morphological diversity is immense (Altig and McDiarmid, 1999), but there seems to be a tendency to award the reproductive portion of a biphasic life-cycle a greater evolutionary prominence (see M. K. Richardson, 1999). I present a reverse thesis—a resetting of the offset signal of vertebrae-forming somitogenesis to an earlier point was the defining factor among frogs. Somitogenesis operates from early gastrulation through mid-tailbud (Dali et al., 2002), and the method and timing of any alterations will require further research; this truncation also likely resulted in the simplified myomeres of tadpoles. This major developmental event essentially produced a prototadpole, along with many collaborative interactions with other developmental cascades downstream, and a frog morphotype became the metamorphic default of the profoundly paedomorphic (i.e., presenting characteristics in a more embryonic or larval state than its ancestor) larva. A seemingly pervasive metamorphosis cannot alter the embryologically-derived vertebral number. The initial happenings had to be embryological, and thus there

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is no chicken-and-egg conundrum—modified tadpole came first.

The inverse, selection on the adult for a shortened vertebral column and large hind legs for saltatorial locomotion seems much less tenable; one would have to envision heritable-variation in vertebral number and increased fitness for any potential changes. Also, there surely would have been combinations of vertebral number and limb size that would be functionally or ecologically incongruent. One would have to assume that the two activities were developmentally joined very tightly, and the timing differences in vertebral and limb formations suggest that this is not true. Also, a compatible genetic program to produce a selective decrease in vertebral number and reciprocal increase in limb size seems obscure.

Somewhat of an intermediate scenario involving losses and fusions of vertebrae (i.e., embryological events; Trueb, 1973) might be considered. These actions in various taxa surely occurred by lesser, more recent, and less deeply-rooted genetic activities. These changes certainly could reduce the number of vertebrae from 9 to 5 within Anura and perhaps from a state something like *Triadobatrachus* (14 presacral vertebrae; Rage and Roček, 1985), but in the scenario proposed here, *Triadobatrachus* could represent a dead end. The latitude of such a mechanism seems insufficient to arrive at the salientian state from a probable salamander-like lissamphibian ancestor (O'Reilly et al., 2000; also Feller and Hedges, 1998).

In the proposed scenario, something like a tadpole and a frog could have appeared quite rapidly. Such an occurrence would be a crude and more deeply-rooted genetic analog to the speciation event(s) that took place in a meiotic context in the *Hyla versicolor*/*H. chrysoscelis* complex (Ptacek et al., 1994) and *Xenopus* spp. (Kobel, 1996). These chromosomal alterations occurred successfully several times, and there is no reason to think that all lineages survived. Likewise, if a prototadpole were produced as suggested, is it likely that the extant lineages of frogs arose from one such event? If not, how might we detect the various products? Would comparative examinations of the developmental and molecular patterns of somite and myotome formation be informative (e.g., Gatherer and del Pino, 1992; Gemballa and Ebmeyer, 2003; Furlow et al., 1997; Haas, 2003; Wassersug, 1984, 1989)? Variations in centrum shapes among families (Griffiths, 1963) become of interest in this context.

Subsequent selection certainly acted on each stage, probably with little to no effect on the other stage, and increases in the diversity of fundamental (adult: jumping mechanics; larval: mouthpart variations) and superficial (adult and larval: ecological correlates) features of both stages are apparent. The impact of rapid changes in larval developmental processes on evolution of life histories (Wray, 1996), atavisms (e.g., B. K. Hall, 1984; Stiassny, 1992), and monsters (Peters, 1991), all of which have a genetic basis, should be reconsidered. Also, there are unrevealed patterns of lesser complexity associated with Starrett's Rule (in Savage, 1980).

Where in general might the proposed changes have occurred within the anuran genome? One might view amphibian larval evolution from three perspectives with increasingly wider scopes: the evolution of species and their larvae as modified primarily by selection on structural genes, the evolution of anurans and their larvae as modified strongly by changes in regulatory genes, and the evolution of amphibians and their larvae. Strictly as an operational schematic, one can envision the evolution of the anuran life cycle via the actions of three collaborative sets of regulatory and structural genes: a set that produces the larval phenotype (LP), one that produces the adult phenotype (AP), and an overlapping portion (OP) that operates in both stages and during metamorphosis. Five hypotheses from a longer potential list address where in the genome that a major developmental alteration occurred to produce the tadpole-frog bauplan.

(1) Heterochronic events occurred within the genes of the AP. If true, the larval and adult morphotypes remain under different controls, metamorphosis might not be able recover a frog from such a genetically-disassociated tadpole, and the success of such a system seems remote if the latitude of metamorphosis has been similar through time.

(2) Different changes affected the same structures in the same way in the AP and LP simultaneously or collaboratively. The unlikelihood of two such events being

developmentally compatible removes this hypothesis from contention.

(3) Events in either the AP or the LP were transferred to the opposite set via gene duplication or changes in governance of regulatory cascades. Again, the likelihood of the changes being made in a developmentally compatible way seems remote.

(4) The changes affected early development in the LP. Depending on metamorphic latitude and perhaps its variations among lineages and how the metamorphic genes interacted with the LP, there is a possibility that the frog could metamorphically escape the larval confines.

(5) Last, it seems most logical that some part of the OP includes the basal regulatory genes that set up the basic body bauplan during embryology and thus metamorphosis is similarly confined.

To reiterate, I posit that changes in vertebrae-forming somitogenesis produced the paedomorphic prototadpole surprisingly quickly by mutation of basal regulatory genes in the OP and not via selection on structural genes. One can easily argue and expand on the hypotheses concerning the location of the pertinent genes, but it seems obvious that the constraints that vertebral shortening placed on development in the absence of metamorphic changes of vertebral number greatly constrained the resulting metamorph. Talking about the evolution of frogs or tadpoles independently of their total life cycle is misleading, and talking about the evolution of either stage entirely via selection surely is erroneous.

Associated Changes

The shortening of the vertebral column, regardless of its causative mechanisms, profoundly altered larval and adult morphologies. Did its occurrence in a biphasic life history involving metamorphosis add developmental lability that increased its probability of success? Associated changes that kept this drastically-altered creature within the realm of a viable organism involved limb buds and the resulting large hind legs, vent opening, tail morphology, jaw structure and mouthparts, operculum and spiracle formation, and several aspects of the visceral anatomy.

The development of hind legs throughout most of larval life is completed prior to metamorphosis if one defines metamorphosis classically (see below); hind limb buds are larger than the front ones and develop first and a little faster. It is difficult to envision that such appendages could arise via selection on the larva because of their negative influences (e.g., Dudley et al., 1991; and see Wassersug, 1997). One must assume that either the limbs grow allometrically in a basically isometrically-growing larva (Strauss and Altig, 1992) or initial anlagen size profoundly influenced the final product. I suggest that large rear appendages resulted from a change directly associated with changes in vertebral number and not selection for saltatorial locomotion per se. This hypothesis circumvents the suggestions of an aquatic (Griffiths, 1963), terrestrial (Inger, 1962) or riparian (Gans and Parsons, 1966) origin for saltatorial locomotion. Larger than normal hind limb buds or a change in time of initiation or the subsequent growth pattern might have arisen simply by incorporation of part of the considerable local mesoderm that resulted from body axis shortening; more comparative studies of developmental patterns of limbs (e.g., Wake and Shubin, 1998) may provide informative signals. Saltatorial locomotion can then be viewed as a developmental byproduct that allowed an organism with a very short, stiff trunk to remain functional. This new assembly could have influenced ilia elongation that positioned the hind legs at a mechanically feasible position or at a functionally equivalent position relative to the spinal column. Molecular studies of the pelvic elements, especially the ilia, may reveal viable evolutionary scenarios.

Anuran hatchlings are much more embryonic than are salamander hatchlings, and comparisons of limb development of anurans and caudates imply that a tadpole has to develop further (i.e., get to a stage comparable to when a salamander starts leg development) to get to a stage that limb development is possible; Wassersug (1997) posited that the short vertebral column of anurans enhanced innervation to provide proper workings at metamorphosis, but these nerve pathways surely are established much earlier in development. Perhaps we should more often look at anuran evolutionary responses as collective solutions rather than searching for specific selective causes; if a scenario similar to that outlined here were true, then a frog is the result of interactive parts modified by early development and not selection for a given morphotype.

Are there developmental correlations between the degree of paedomorphy and various ontogenetic trajectories—how does the degree of "larvalness" at which an organism enters a given developmental program, especially metamorphosis, influence the rate, duration, sequence, and final product of that program? Are most of the potential effects pre- or post-metamorphic, and what does the ontogenetic distribution of paedomorphic effects suggest about the total ontogeny? For example, manually-produced oral injuries of the tadpoles of *Rana sphenocephala* results in labial teeth being regenerated in both normal and aberrant sites and configurations (D. Drake, unpublished data). Embryological potentials are maintained well into tadpole ontogeny, and the entire disc is competent to form labial teeth (Thibaudeau and Altig, 1988); the postembryological production of cannibal morphotypes (*Spea*; Pfennig, 1990) is another likely example, but perhaps these individuals are in fact not postembryonic. Perhaps staging systems are not properly defined in regards to the actual developmental pattern. The point at which tadpoles cease to present embryological potentials may be the actual signal for the start of metamorphic competence or at least the ability to respond to suggested ecological factors (e.g., Wilbur and Collins, 1973), if one presumes that metamorphosis is not part of embryology. By viewing the plastic responses to predators (see below) as basically embryological, the appearance of actual metamorphic competence may be the stage when these activities no longer occur.

After we factor out the effects of temperature on a basically indeterminate larval growth, larval ontogeny averages quite short, and the variables that influence metamorphosis are debated (e.g., Rose, 2005; Wilbur and Collins, 1973; and see Attwegg and Reyer, 2003 and Wassersug, 1986). Tadpoles likely grow isometrically throughout the tadpole stages (Strauss and Altig, 1992), and over-sized tadpoles maintain the same body proportions as typical individuals (R. Altig, unpublished data). If not, parts of the tadpole morphotype could become out of operational scale either ecologically or metamorphically (e.g., Wassersug, 1997). These insufficiencies might involve the mouthparts, buccopharyngeal structures, digestive organs and enzymes, and surely more importantly, various endocrinological and immunological processes.

Amphibian ontogeny likely occurs over a longer time than commonly realized, and the proper boundaries of the various stages are not clear. The idea (O'Laughlin and Harris, 2000) that a salamander may start to metamorphose as soon as it hatches presents a new perspective to classical views of metamorphosis (also Watkins, 2001). Judged by patterns of limb growth, a tadpole may be in a relatively constant transition to a frog. What we note as metamorphic climax may only be a rush near the end of a continuum to quickly change crucial functions such as feeding, respiratory, nervous, and immunological structures. If so, it seems logical that metamorphic duration would be short (e.g., Wassersug and Sperry, 1977) because the constantly-changing metamorph is not totally functional relative to either the aquatic or terrestrial environments; variations in metamorphic durations of 2.0–7.3 days (Downie et al., 2004), and longer in some stream-inhabiting forms, would seem to be an informative signal concerning developmental and ecological interactions. Are sequences, complexities, and interactions of metamorphic events among taxa caused by or allowed to differ because of the distribution of events throughout ontogeny? For example, calcified teeth appear premetamorphically in *Xenopus* (Shaw, 1979), and Svenson and Haas (2005) noted that some of the jaw elements of *Xenopus* more closely resemble the salamander pattern than in most other tadpoles. These observations suggest that metamorphic changes differ in pervasiveness or occur over a longer period than might be recognized within the classical concept. One must eventually ask what metamorphosis is and realize that its initiation and completion surely are not fixed.

It seems that much of the total ontogeny of anurans has been shifted from the larva to the adult, perhaps because the tadpole is so profoundly larval; Roček and van Dijk (2006) noted such a shift in the timing of bone appearances (see M. K. Richardson, 1999). Although metamorphosis is required to accomplish reproduction, one has to ask if or when the final morphology is expressed. Metamorphic initiation seems to be influenced by an interaction of some part of development and ecological factors, but does this situation demand or allow adult ontogeny to be longer? For example, various bones that appear inordinately late in ontogeny (Smirnov, 1994, 1995, 1997) may signal that a prolonged postmetamorphic ontogeny is either essential or a product of being derived from a pervasively modified larva; sexual maturity is partially divorced from morphological ontogeny. Do we commonly observe the fully developed adult morphology of most frogs? Would systematic opinions based on osteology change if we knew the complete ontogeny?

For example, large and presumably ontogenetically old *Osteocephalus taurinus* gain a casque head (Duellman, 1978), and thus the genome of at least these hylid frogs can make a casque head if given sufficient ontogenetic time. Casque heads develop ontogenetically earlier in *Pternohyla*, *Trachycephalus*, and *Triprion* than in *O. taurinus*. Exostosis occurs in large individuals of some leptodactylids (Wild, 1997). These various types of boneheaded frogs may simply have "old heads"—genetic modules that might be expected to operate late in adult ontogeny (e.g., *Osteocephalus*) have moved forward in development (e.g., *Pternohyla*). Conversely, a taxon with a lightly-ossified skull may offer an inverse perspective on the evolution of ontogeny (but see Haas, 1999). The retention of lateral line systems in partially-metamorphosed pipids as well as frogs (Fritzsch et al., 1987) that seem to be completely metamorphosed signals another ontogenetic shift; Reilly and Altig (1996) noted a prolonged osseous ontogeny in the paedomorphic *Siren intermedia*. Would tracking frogs derived from tadpoles that were forced to either metamorphose earlier than normal or grow exceptionally larger than normal, thus presenting metamorphic and postmetamorphic ontogenies with altered entry morphologies, reveal constraints on postmetamorphic ontogeny? Again one can ask: what is metamorphosis (e.g., Alberch, 1989; Fritzsch, 1990; Reiss, 2002 and citations therein), over what developmental time does it actually occur, how does the ontogenetic input condition affect the outcome, and what are its ultimate limitations?

Are somites that are competent to form vertebrae and thus persist throughout life versus those in the tail that atrophy at metamorphosis of equal developmental status? Are the simplified myomeres in tadpoles tails a paedomorphic trait? Various numbers of postsacral vertebrae (i.e., neural arches; Roček-ova and Roček, 2005) in the body presumably give rise to the urostyle (see Mahendra and Charan, 1972), while the actual tail of a tadpole usually lacks vertebrae. Some megophryid tadpoles have a few to a complete series of simple vertebrae that are only calcified (Griffiths, 1956, 1963) and likely atavistic. Minelli (2003) used the lack of endodermal products and genetic data to argue that a vertebrate tail is an appendage and not part of the body, and if so, one might expect different genetic controls between the tail and body; this assumes that a tadpole tail is homologous to a salamander tail. Factors as far removed from supposed metamorphic ontogeny as skin physiology (e.g., Menon et al., 2000) and wound healing (e.g., Yannas et al., 1996) indicate differences between tadpole bodies and tails.

The structure and formation of the vent are more complex than typically understood (Echeverría, 2002). There are likely two parts, one derived from the proctodeum and another, likely derived from abdominal wall tissue (i.e., the external vent tube) that remains after the yolk reduces in size, that affords the usual association of the tube with the ventral fin. The configurations of the vent may be a signal that the tadpole tail is novel (also see Delsol and Flatin, 1969; Elinson et al., 1999; Izutsu et al., 1993; Utoh et al., 2000). The intestine of a salamander passes low through the pelvic arch, and the longitudinal slit-like opening opens ventrally in the base of the tail. The vent of a tadpole usually is situated posteromedioventrally near the junction of the body wall and the lower margin of the tail muscle. The actual vent is within the classically defined body although postsacral in frogs. This position is quite removed from being directly beneath the plane of the vertebral column as in frogs or from that of salamanders. The tail of male *Ascaphus* lacks vertebrae but is a presumed homolog of a salamander tail based on vestiges of homologous tail-wagging muscles (Van Dijk, 1959). This tail is situated posteromedioventrally on the body well posterior of the sacrum and the longitudinal, slit-like aperture opens in the ventral side of the tail like that of a salamander. It is not a metamorphic vestige of the tadpole's tail. Is the tadpole tail unique or is it merely predictive of a part of a profound paedomorph that is destined to undergo metamorphic atrophy? Molecular comparisons of the skin and tail musculature of tadpoles, which atrophy the entire tail, versus salamanders, which atrophy just the fins, may help answer these questions.

The odd morphology and operations of tadpole jaws (Gradwell, 1968) surely resulted by some concomitant pattern of developmental constraint and arrest related to the alterations of somitogenesis and associated migration and competence of the neural crest (see Falck et al., 2002; Olsson and Hanken, 1996); this morphology represents just one of many possible forms of vertebrate jaws, and the association of the infrarostrals, mentomeckelian, and suprarostrals seems like a sort of "repair" to maintain an operatively morphological coherence. This assembly is likely an embryological condition that persists throughout larval ontogeny, and the metamorphic recovery of classical vertebrate jaws from such an unusual larval configuration supports this idea. Svenson and Haas (2005) hypothesize that some articulations between embryonic jaw elements are new but that the elements are homologs of those in salamanders and suggest ideas on the genetic mechanisms involved. That is, these jaw elements did not appear *de novo* but by concomitant genetic adjustments of the full potential of "jaws" to produce the modified, but surely not a genetical novel, phenotype. The jaw elements of tadpoles are a prime subject to be examined with classical (e.g., Blanco and Sanchiz, 2000) and molecular methods (e.g., Depew et al., 2002). Wassersug's (1975) assertion that anuran tadpoles evolved "to take advantage of the flush of primary productivity in temporary ponds" implies selection, but if the processes outlined herein were true, the concept could be inverted to say that tadpoles found themselves with foraging structures that required that they exploit this food source. Subsequent variations of the oral apparatus arose by selection.

Variations in the growth of the operculum produce the various forms of the spiracle(s) and form a chamber for the regulation and control of respiratory and feeding currents (Gollman and Gollman, 1999; Starrett, 1973). Comparative, fine-grained examinations of the variations in opercular growth would be informative (e.g., J. A. Hall et al., 1997). The initially midventral spiracle of *Otophryne* that then migrates to a sinistral position (Wassersug and Pyburn, 1987) would be particularly informative; Ruibal and Thomas (1988) described the formation of dual, lateral spiracles in the leptodactylid *Lepidobatrachus* that is different from the analogous situations in pipids and rhinophrynids.

The visceral proportions and geography of a tadpole are interestingly unique. The long gut without major modifications for increasing surface area suggests an herbivorous mode of feeding at first glance, but this feature may be an accommodation to weak peristalsis (Naitoh et al., 1990), a small average bore, and actual digestive diet (Schiesari, 2004) or methods (Pryor, 2003). The spiraled arrangement was likely imposed by packaging constraints (Kemp, 1951; Nodzenski et al., 1989) of a long gut within a globose body. There are variations in the final products, and detailed studies of comparative visceral anatomy of an array of stages and taxa are needed.

In contrast to salamanders having their gonads and kidneys positioned anterior to the sacrum, these organs in frogs are near or posterior to the sacrum. It is as if the posterior viscera could not relocate accordingly when the spinal column shortened and that some postsacral part of the body had to be retained. The locations of these organs, the reduction in vertebral number, and the position of the sacrum show that body shortening was not via a simple telescoping action. Interferences with early developmental patterns (e.g., coelom formation, early organ formations) were possible constraints. A supportive strut formed of postsacral elements (i.e., a tail-like structure within the body—urostyle) resulted. One might conjecture that the hind legs occur at a developmentally equivalent point that legs formed prior to the proposed vertebral shortening rather than relative to sacral position; the findings of Neyt et al. (2000) on the evolution of vertebrate appendicular muscles may be a stimulating departure point.

DISCUSSION

The discussion presents further queries that are pertinent to the theme of this paper. Crossfield discussions (e.g., Svoboda and Reenstra, 2002) always benefit both camps, and essays like that by Svenson and Haas (2005) outline interesting questions and sharpen our focus. If written to be reciprocally understandable, summaries and syntheses of modern molecular, endocrinological, and immunological phenomena would be very useful for those who study the morphology, phylogeny and life histories of amphibians.

Experiments involving growth and metamorphic promoters and inhibitors could be used to dissociate events and thus determine which events are developmentally linked or merely occur together. The effects of insults that cannot be metamorphically recovered set the boundaries. Distinguishing between features that are affected by the least endocrine change or occur before what might be considered actual metamorphosis (e.g., Berry et al., 1998) from those that require a larger endocrine change or occur later in ontogeny should define tissue sensitivities and thus the actual sequence of events (e.g., Veldhoen et al., 2002).

Proper choices of research subjects are supremely important. Trueb (1973) emphasized more than 30 years ago that phylogenetic breadth is superior to the aggravating restrictions of the model approach. Metamorphic sensitivities and morphological states presented to the actions of metamorphosis (e.g., calcified teeth: Shaw, 1979; buccal papillae; Wassersug and Heyer, 1988) are developmentally discordant across taxa. Recognizing these discordances would aid metamorphic interpretations as well as the understanding of the evolution of the tadpole stage across lineages.

Other queries involve smaller but tantalizing pieces of information, and the addition of comparative data is always helpful (e.g., J. M. L. Richardson, 2001). Reports of deformed frogs in the field (e.g., Loeffler et al., 2001) show that some fairly obtuse monsters survive; knowledge of the kinds of deformities that cause metamorphic death versus ecological demise would show us the metamorphic compensations for larval perturbations. Abnormal development, as reflected by which elements form and when relative to the normal developmental sequence, can inform us about developmental processes and their connectedness (Kovalenko and Kovalenko, 1996 and citations therein), and perhaps we could identify characteristics with different potentials for either stasis or change. Determination of characters that change from larval isometry to metamorphic allometry may identify features with different fates or potentials. Last, alternative views of the effects of predator- and competitor-induced changes (e.g., Relyea, 2001) may allow categorization of characters that differ in growth or metamorphic and postmetamorphic response patterns. For example, knowing that larval responses affect postmetamorphic phenotypes (Relyea and Hoverman, 2003) suggests a much deeper control than might be expected in an ecological context. Analyses of the postembryonic morphological lability of cannibal *Spea* could be similarly interesting, and other social responses (e.g., metamorphic endocrinology; Hourdry and Guyetant, 1979) require further examinations.

With more evidence, we find that the odd and plastic tadpole and the odd and plastic frog remain firmly bound together developmentally via a strange, varied, and variable ontogeny that perhaps all started with the alteration of a basal developmental event.

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SEXUAL COERCION IN THE SALAMANDER *PLETHODON CINEREUS*: IS IT MERELY A RESULT OF FAMILIARITY?

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Abstract: Previously published studies concerning the social behavior of red-backed salamanders (*Plethodon cinereus*) reported that in the forest (1) some male-female pairs co-inhabit territories even during the summer noncourtship season, and that in laboratory experiments (2) these pairs act as if they are socially monogamous, (3) males aggressively punish female partners that become polyandrous, and (4) females aggressively punish male partners that become polygynous. Past studies suggest that males and females freely choose their pair-partners in the forest and that sexual intimidation functions to keep partners monogamous. However, this inference is based on several underlying assumptions, which we test in the present study. We performed a series of experiments using randomly established pairs to test the assumptions that 'natural' pairs are more than an effect of familiarity between individuals and that extended housing as 'pairs' in the laboratory does not account for pair-like behavior. We found no evidence that members of either sex punished the opposite sex when laboratory–created pairs were housed together for either five or 30 days. Therefore, we conclude that the 'pair-like' behavior of natural pairs represents more than familiarity and that extended housing together does not account for that behavior.

Key words: Intimidation; *Plethodon cinereus*; Sexual coercion; Social monogamy

Darwin's (1871) theory of sexual selection is usually divided into two parts: intrasexual selection (usually male-male competition for mates) and intersexual selection (usually female mate choice). However, Smuts and Smuts (1993) proposed a third form of sexual selection: sexual coercion. Coercion involves males attempting to force females to mate with them by forced copulations, repeated attempts to mate with a female (harrassment), or punishing females that refuse to mate with them (intimidation). Clutton-Brock and Parker

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