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Female Choice and Mating System Structure

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I. INTRODUCTION

MUCH of the social behaviour of amphibians, like that of most other ectothermic vertebrates, is centered on reproductive activities. Unlike many birds and mammals, adult amphibians usually interact only rarely with conspecifics, typically during a temporally well-defined breeding season. Perhaps as a consequence, until relatively recently, amphibians were largely overlooked as subjects for evolutionary studies of social behaviour. Over the past two decades, however, there has been an explosion of interest in the social, and especially reproductive, behaviour of amphibians (Wells 1977a; Arak 1983; Ryan 1985, 1991; Sullivan 1989a; Verrell 1989a; Halliday 1990). This increased attention can be traced to a number of causes.

From a theoretical perspective, clarification of the importance of selection acting at the level of individuals (rather than populations or species) during the 1960s caused many evolutionary biologists to reconsider explanations accounting for sexual dimorphism and intraspecific variation in reproductive behaviour (Williams 1966; Campbell 1972). Similarly, interest in relationships between environmental variables and behaviour of individuals led many workers to examine the ecological context of reproductive behaviour (e.g., see reviews in Emlen and Oring 1977; Rubenstein and Wrangham 1986; Clutton-Brock 1988). In a different vein, efforts to link quantitative genetics theory to field studies of microevolutionary change facilitated investigations of the forces of selection operating under natural conditions (e.g., Arnold and Wade 1984a,b; Endler 1986; Harvey and Bradbury 1991; Brodie and Garland 1993). These methods have allowed workers to estimate the forces of selection, both sexual and natural, on particular traits in the field.

From an empirical perspective, in spite of any initial misconceptions regarding their suitability as subjects for studies of social behaviour, amphibians have served admirably for a great many investigations of sexual selection and mating system structure. Many anurans and some urodeles are relatively easy to observe and manipulate experimentally, either in the field or laboratory. The temporally and spatially restricted breeding activities of many species provide excellent opportunities for observations and experiments (Wells 1977a; Arak 1983; Sullivan 1989a). Mating success, a critical component of fitness in the context of sexual selection, often can be estimated, at least in anurans. Important behavioural components of male-male competition and female choice can be examined readily given the relatively simple sensory system modalities involved in mate location and courtship behaviour. Although adequate demonstrations of female choice among the vertebrates are relatively few (Halliday 1983; Bradbury and Andersson 1987), anuran amphibians have provided some of the best examples (see reviews in Searcy and Andersson 1986; Gerhardt 1988; Ryan 1991).

In this chapter female choice and mating system structure in amphibians are examined. Theoretical issues surrounding female choice are reviewed, and the empirical evidence and conceptual implications derived from studies of amphibians are summarized. The chapter is concluded with a review of mating system structure theory, and contributions from work with amphibians. The goal is to assess the most significant contributions of studies on amphibians to theories of sexual selection and mating systems, rather than present an exhaustive review of all such studies in the Amphibia. In addition, a number of aspects of sexual selection primarily concerned with male-male competition and species recognition are left aside since these issues are examined elsewhere in this volume. Unfortunately, given the absence of observations on the reproductive behaviour of apodans, the review is restricted to the representatives of the two other amphibian orders, Anura and Urodela.

II. FEMALE CHOICE

A. Historical Developments

The most striking differences among individuals of the same species are dimorphisms between the sexes (Fig. 1). Relative to females, males typically are adorned more and are more conspicuous in their morphology and behaviour. Often the most obvious and diagnostic differences between species are sex-limited traits of males; many a naturalist attempting field

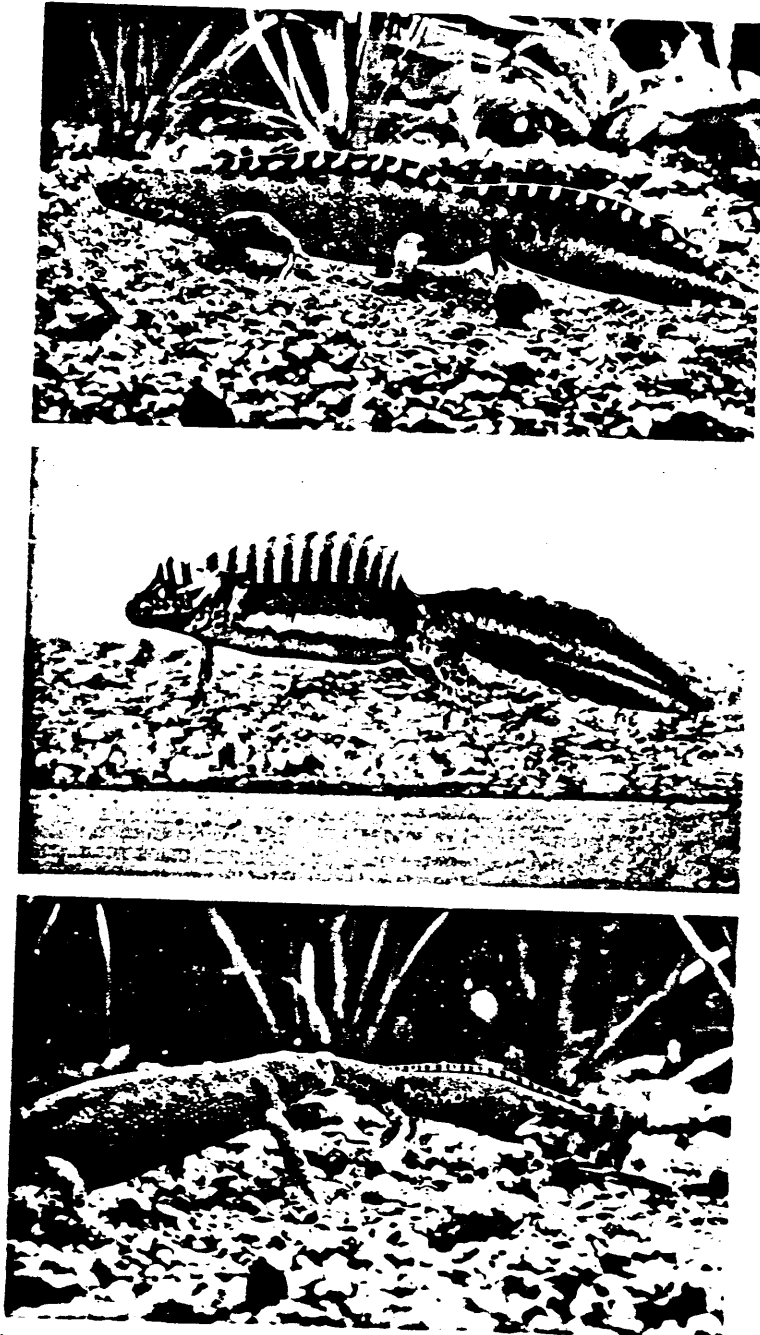


Fig. 1. Male adornments (crests/sails/fins) in various European newts. Upper: Male *Triturus marmoratus*. Center: Male *Triturus vittatus*. Lower: Courting pair of *Triturus alpestris* (male on right). Photographs courtesy of Tim Halliday.

identification of a bird or fish winces at the task of classifying a nondescript female. These traits share certain features: they are usually extreme in sexually mature males and often absent in females (i.e., they are sexually dimorphic); they are associated with, but not required for, sexual behaviour (i.e., they are secondary, not primary sexual characters); finally, they often decrease survivorship. How these traits evolve is the subject of sexual selection theory.

The history of sexual selection theory has been reviewed in varying degrees over the last two decades (Campbell 1972; West-Eberhard 1979, 1983; Thornhill 1980; Ryan 1985). For a recent, detailed treatment of the history of the theory the reader is referred to Cronin (1992), with the caveat that there is some disagreement with her discussion of the current scientific status of the theory (Ryan 1992).

Darwin (1859, 1871) recognized that his theory of natural selection, which emphasized adaptations for survival, could not explain adequately secondary sexual characters that rarely contribute to longevity and often decrease it. He suggested that traits that did not provide an advantage in the struggle for existence might be sexually selected if they provided an advantage in reproductive competition among conspecifics. Sexual selection, Darwin proposed, could favour traits that enhance a male's ability to compete with other males for access to females, or increase a male's attractiveness to females. The hypothesis of sexual selection acting through male competition was readily accepted, but the notion that females actually had important input into the mating decision was dismissed by many in Victorian England, including such staunch Darwinians as Alfred Wallace and Thomas Huxley.

Today, the essence of Darwin's sexual selection theory has been accepted. There is a general consensus that sexual selection can promote the evolution of traits that reduce survivorship of males, and there is ample evidence that this force of selection can operate through both male competition and female mating preferences (Bradbury and Andersson 1987; Harvey and Bradbury 1991). Sexual selection is one of the most active fields in evolutionary biology, however, because there are many areas of disagreement and controversy. For example, there is some debate as to whether sexual selection should be considered an alternative to, or a subset of, natural selection (e.g., Mayr 1972; Endler 1986; Williams 1992). Also, the dichotomy Darwin drew between male competition and female choice often can be blurred, as females may incite competition among males (e.g., Cox and LeBoeuf 1977) and these mechanisms can exert quite different forms of selection on the same trait (Moore 1990).

The evolution of female mating preferences is one of the most controversial areas of sexual selection. An initial criticism of Darwin was that he seemed to endow females with an aesthetic appreciation of beauty that seemed to imply some underlying anthropomorphism. At that time there was little evidence that females attended to variation in male traits when choosing a mate. Furthermore, Darwin did not suggest any selective advantage to female choice. Female appreciation of beautiful males was a given; in that sense, sexual selection by female choice was a quite "non-Darwinian" hypothesis (Cronin 1992; Enquist and Arak 1993). Now, however, there is ample evidence that female mating decisions can be influenced by variation in male traits, but there is little agreement as to why females show these preferences. This is the topic of the following section.

Kirkpatrick and Ryan (1991) recently reviewed the current status of hypotheses for the evolution of female mating preferences, and Ryan (1991) discussed some of the contributions of studies of anuran amphibians to sexual selection. The present review will parallel those discussions. First, the various hypotheses for the evolution of female mating preferences are outlined. Then, evidence drawn from studies of amphibians that support or reject these hypotheses is discussed. Last, research areas for which amphibians may be good model systems as well as research areas in which amphibians are less likely to provide important insights are identified.

B. Evolution of Female Mating Preferences

The problem addressed here is: Why should the mating preferences of a female be influenced by variation in male traits? In many cases the answer is clear. If mate choice influences immediate reproductive success, then natural selection should favour females

exhibiting preferences that maximize this important parameter of fitness. In many cases, however, males contribute little to the female besides sperm and there might be minimal variation among males in their ability to fertilize all the eggs of a female (but see Dewsbury 1982). Thus, there is no variance in female reproductive success derived from mate choice. In such situations, which are common on bird leks, it is not clear how selection can induce the evolution of mating preferences if there is no variation in reproductive success associated with a preference. This conundrum has been termed: "the paradox of the lek" (Borgia 1979).

Characters can evolve in several ways, selection being only one example, genetic drift being another. There also are different modes by which a character can evolve under selection. If a character is favoured by selection because of its contribution to fitness, then it can be viewed as a target of selection evolving under direct selection. Different characters can be related, however, and these may evolve in a correlated fashion, referred to by Maynard Smith (1978) and others as "hitchhiking". If a character evolves because it is correlated with another character that is the target of selection, then the former is said to evolve under indirect selection. Kirkpatrick and Ryan (1991) classified hypotheses for the evolution of female mating preferences into categories of either direct or indirect selection. Despite some gray areas, that classification scheme is adopted here. Precisely how to measure fitness best is controversial; followed here is the recommendation of Arnold and Wade (1984a,b; see also Arnold 1983) that accounting must not cross generations as this confuses selection and inheritance, thereby confounding sexual and natural selection. The operating principle is that if a preference evolves because it has an immediate effect on female reproductive output, which by convention is restricted to the summing of her offspring, then this is an example of direct selection. If a preference evolves because it is correlated with other traits that enhance the mating success of her offspring or the fecundity of her granddaughters, it would be an example of indirect selection.

1. Direct Selection

A. SPECIES RECOGNITION

Many female mating preferences are readily explained; the most obvious, perhaps, are species-specific. Hybrid matings often are deleterious because eggs are not fertilized, do not develop properly, or hybrids have reduced survivorship or fertility, or are less attractive to potential mates. There has been considerable controversy as to how selection favours preferences for conspecific mates. Whether selection favours females that avoid heterospecifics, as stated in the hypotheses of reproductive character displacement and reinforcement (Littlejohn 1981; Butlin 1987; Howard 1993), or whether it favours common mate recognition systems regardless of the influence of heterospecifics (Lambert and Paterson 1984; Paterson 1985), it will favour mating preferences that result in conspecific matings. It should be noted, however, that such a form of selection still could generate sexual selection within a species; for example, it might favour conspecific males that produce sexual signals that are the least similar to those of heterospecifics. Species recognition and sexual selection are not mutually exclusive phenomena (Ryan and Rand 1993a, b).

In urodeles, species differences can be substantial both for morphological (Raxworthy 1990) and behavioural (Halliday 1977a) components of mate-recognition systems. These observations are consistent with the notion that differences among species in secondary sexual characters and the exact form of courtship behaviour allow effective recognition of conspecifics. Furthermore, discrimination tests have revealed that individuals usually prefer conspecific over heterospecific signals (e.g., Himstedt 1979). But, there is no direct evidence to support the hypothesis that selection against interspecific mating has given rise to species differences in urodeles (see Arnold *et al.* 1993, for a review of recent work with plethodontid salamanders). Indeed, available evidence indicates that such differences may evolve largely, if not solely, during the time that populations are allopatric. For example, in the genus *Desmognathus* levels of sexual incompatibility among geographically-isolated but conspecific populations may be as high as, or even higher than, levels seen among sympatric species (Maksymovitch and Verrell 1993).

Of course, there can be no direct selection against mismatching for geographically-isolated populations. The data available for salamanders are consistent with a model in which recognition systems become differentiated before previously isolated populations come into secondary contact. Random processes such as drift, founder effects, local adaptation and sexual selection may be responsible for divergence of sexual signals and preferences (Emlen 1989).

B. DIRECT SELECTION AND RESOURCES

There are several additional means by which preferences among conspecific males evolve under direct selection. If males provide resources, such as food, shelter, protection or parental care, that have an immediate effect on female fecundity, then selection will favour those preferences that maximize the female's reproductive success. These are situations where direct selection does not occur on a lek where males provide only sperm and thus have not been considered controversial.

Direct selection even can act on mating preferences in a lek (Kirkpatrick and Ryan 1991, Reynolds and Gross 1990). There are several possibilities: if sperm is limiting, some males might be able to fertilize more eggs than other males. There can be search costs associated with mate choice; under such conditions selection should favour preferences that reduce search costs and might result in females choosing the most conspicuous, easily-located males. Females also should avoid males that might transmit parasites or venereal diseases (Hamilton 1990).

C. DIRECT SELECTION AND SENSORY EXPLOITATION

Direct selection can influence mating preferences in a more subtle manner than is associated with selection of conspecifics or adequate quantities of sperm. Females use their sensory systems in choosing males, and neuro-physiological biases in sensory systems can affect a female's perception of male traits and perhaps mating preferences as well. For a trait, for example, if a male bird evolves an epaulet that is visible only in the ultraviolet, then this character could be favoured by selection only if females perceive colours in that range.

Females also use their sensory systems for biologically important tasks other than mate choice, such as prey detection and predator avoidance. For these tasks as well, biases in sensory systems will affect their performance. Thus, properties of the sensory system should evolve under a variety of selective forces which might favour different sensory properties. The resulting sensory system might not be a solution that is optimal for each task, but one that is a compromise among many tasks. Hence, mating preferences might be strongly influenced by selection in contexts other than conspecific mate choice. One simple example would be a species in which foraging favours perception of certain colours; as a result females might then favour males that evolve these colours because they are more easily perceived. Similarly, if selection favours females that avoid heterospecific males with slow pulse rates in their calls, they also might prefer males with faster pulse rates among conspecifics. This hypothesis was developed in more detail by Ryan (1990) and Ryan and Rand (1990, 1993). Similar ideas also were discussed by Endler (1992) and Dawkins and Guilford (1991).

One way to uncover patterns of sensory exploitation is to demonstrate that there are preexisting preferences in females for certain male traits. This requires that one can test for preferences that do not occur in conspecific males but are exhibited by males in other, related species, and also that a phylogenetic analysis will allow one to reconstruct with some confidence the sequence of female preference-male trait evolution.

2. Indirect Selection

Much of the controversy surrounding the evolution of female preferences has centered on two competing hypotheses: (1) Fisher's theory of runaway sexual selection and (2) various hypotheses for selection of good genes (viability models). Cronin (1992) contrasted these hypotheses as being "arbitrary" and "utilitarian", respectively. They are similar in that female

preferences are not under direct selection but evolve because they are correlated with other traits. Thus, trait and preference coevolve, a different historical pattern than predicted by the sensory exploitation model (where preference precedes trait).

A. INDIRECT SELECTION AND RUNAWAY SEXUAL SELECTION

Fisher (1958) was among the first to seek an explanation for why females should exhibit certain mating preferences. Briefly, he suggested that preferences and preferred traits initially might evolve in a population due to a natural selection advantage accrued by females mating with certain males. Others have pointed out that the same result could occur through stochastic processes such as drift (Lande 1981; Kirkpatrick 1982). Once the trait and preference reach some threshold frequency, alleles for each will become genetically correlated through linkage disequilibrium as a result of assortative mating; males and females possess genes for both preferences and traits but only females express the preference and only males express the trait. The male trait will increase in the population because it is preferred by females, and the preference will increase as a correlated response to evolution of the trait. Through this process of "self-reinforcing choice" (Maynard Smith 1978), both trait and preference can evolve rapidly. The mathematical details of the dynamics of the runaway process are complex and sometimes controversial. Arnold (1983) provided a readable summary without mathematical detail.

B. INDIRECT SELECTION AND GOOD GENES

Zahavi (1975, 1977) first championed the idea of selection of good genes through his handicap model. He suggested that male displays are costly, and that a male's ability to bear such costs indicates his genetic quality to females. It is important to note that in good genes hypotheses, "quality" does not refer to the male's attractiveness but to other components of fitness, such as survival ability.

The good genes hypothesis has been controversial since it was first proposed because early population genetic models were unable to verify the suggested outcomes of the process (e.g., Maynard Smith 1978; Kirkpatrick 1986). Recently, however, simulation studies have shown that good genes models can operate (Pomiankowski 1988; Grafen 1990a,b). Interestingly, preferences for good genes can evolve under indirect selection. This can be illustrated using the hypothesis proposed by Hamilton and Zuk (1982), positing that bright bird plumage evolved as an indication of genetic resistance to parasites. In this situation, parasites have an adverse effect on plumage colour and males that are genetically resistant to parasites should thus have brighter plumage; plumage colour itself need not be heritable. If some females begin to prefer brighter males, then assortative mating should result in a genetic correlation between genes for parasite resistance and preference for brighter males. If so, then natural selection will promote an increase in the frequency of the parasite-resistance gene and the preference gene will evolve as an indirect response.

The parasite-good genes hypothesis is only one example of how preferences for good genes might evolve. It could operate when a female preference gene becomes correlated with any other gene that is favoured by natural selection if the presence of that gene is somehow revealed by a male's phenotype.

C. TESTING MODELS OF INDIRECT SELECTION

In spite of considerable effort, it has proven difficult to assess the relative importance of the runaway and good genes hypotheses for the evolution of female preferences (see reviews by Bradbury and Andersson 1987; Balmford and Read 1991; Kirkpatrick and Ryan 1991; Sullivan 1991). Part of the dilemma is that it is difficult to derive predictions allowing confident falsification of one hypothesis and support for the other. Another problem is the difficulty of separating causes from effects in evaluation of the relationships between male traits, good genes, and preferences (Kirkpatrick and Ryan 1991; Sullivan 1991).

It is conceivable, perhaps even probable, that the evolution of female choice in a particular taxon might be influenced by more than one of these mechanisms, including forms of both indirect and direct selection. For example, sensory biases might have much to do with how

preferences originate. Given some level of heritable variation in preferences, subsequent coevolution of male traits and preferences will occur as predicted by Fisherian runaway evolution models. Continued evolutionary change might be consistent with a good genes hypothesis by either cause (i.e., males exhibit correlated variation in genetic quality) or effect (i.e., males evolve higher viability as the preferred trait becomes exaggerated). As a consequence, it is now widely appreciated that these hypotheses are not necessarily mutually exclusive. Future studies should be directed toward an elucidation of the relative importance of these forces in the origin, elaboration, and maintenance of male traits and female preferences.

III. EMPIRICAL CONTRIBUTIONS FROM THE AMPHIBIA: ANURA

A. Demonstrating Female Choice

As indicated previously, Darwin's suggestion that female mate choice contributes to variation in male mating success was roundly criticized when first proposed because, among other reasons, there was no evidence that females attended to differences in secondary sexual characters among males (e.g., Huxley 1938). This concern was related to two different aspects of female choice that sometimes have been confounded: (1) Do females have preferences? (2) Do these preferences generate sexual selection on males?

A preference results from the interaction between biases in the sensory system and stimuli that impinge on that system, while a choice is the behavioural act of discrimination based on a preference. It is important to note this distinction between preference and choice. Preferences always result from sensory biases, whether these biases reside in the sense organs, the central nervous system, or some less well-defined area of cognition. Thus, we can only uncover preferences for stimuli that females encounter, either in nature or ones that we concoct and present experimentally.

The other aspect of female choice deals with selection in an evolutionary context. Searcy and Andersson (1986) proposed two criteria necessary to demonstrate that female mate choice generates sexual selection. First, there must be a correlation between male mating success and male characters; second, females must effectively exhibit preferences for these traits in a manner not confounded by male competition; this is best examined experimentally.

Females could have preferences, but these preferences need not generate sexual selection. However, that lack of selection may not diminish interest in the existence of female preferences, as illustrated by the following three examples taken from studies of anurans.

Call dominant frequency is correlated with male body size in the spring peeper, *Pseudacris* (= *Hyla*) *crucifer*, and females prefer calls of lower frequency (Forester and Czarnowsky 1985). These frogs also exhibit alternative mating strategies in which larger males call while smaller males abandon calling and attempt to intercept females *en route* to calling males. In their population, male size and male mating success were not significantly related (Forester and Lykens 1986), suggesting that female preference for low frequency (and large size) does not generate variance in male mating success. However, it seems possible that it is the female preference for lower frequencies and larger males that might be responsible for smaller males abandoning calling (Forester and Lykens 1986). In many species, including a number of anurans, males that are less attractive to females adopt satellite mating behaviours (e.g., Howard 1978a; Dominey 1984; Ryan *et al.* 1990). It might be true that spring peeper females currently do not generate selection on male traits, but it might also be a mistake to discount the role of female choice in the evolution of the mating system. Similar arguments for size-based satellite strategies in anurans also have been made by a number of researchers, including Bourne (1992) in his study of lekking in the neotropical hylid *Ololygon rubra*, and Sullivan (1982a) and Krupa (1989) in their studies of the Great Plains toad, *Bufo cognatus*.

A different sort of example comes from studies of the túngara frog, *Physalaemus pustulosus*. In this species, males add to their whine-like calls elements termed "chucks" that increase their attractiveness to females (Fig. 2). Females prefer whines to which chucks have been added over the same calls without chucks (Rand and Ryan 1981). Chucks are neither necessary nor sufficient for species recognition, and seem to function only in enhancing the attractiveness

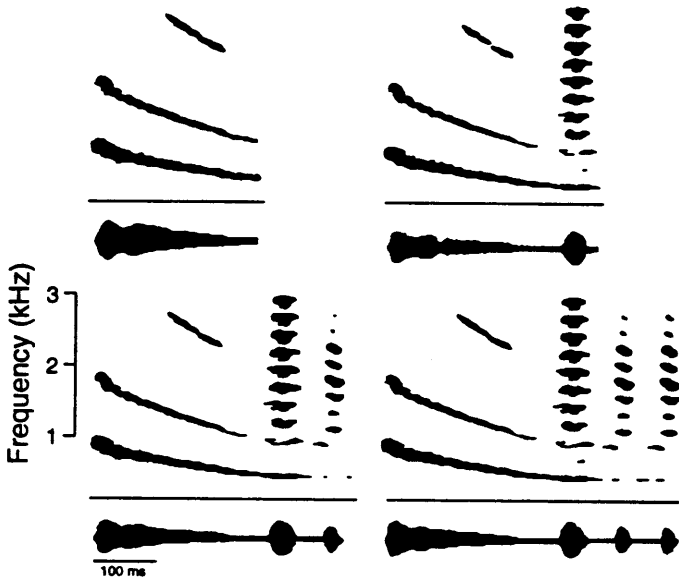


Fig. 2. Calls of male túngara frogs (*Physalaemus pustulosus*). All calls contain a whine which can be produced alone or followed by 1–3 chucks (top left, no chucks; top right, 1 chuck; lower left, 2 chucks; lower right, 3 chucks).

of males to conspecific females (Ryan 1983a; Ryan and Rand 1993a). It seems likely that the chuck evolved under the influence of sexual selection, especially when it is considered that males increase their risk of predation by frog-eating bats (*Trachops cirrhosus*) when they add chucks to their calls (Ryan *et al.* 1982). It seems equally clear, however, that female choice does not generate sexual selection on this male trait. All males appear to add chucks to their calls when in choruses, and thus there is no variance in the presence/absence of chucks on which female choice can act — if there is no variance in the trait there can be no selection. This is an example in which female choice probably played an important role in the earlier evolution of the male trait, and this information would be lost if only those studies in which female choice currently generates selection were considered important.

As a final example, several cases will be considered in which females exert preferences for traits not expressed by conspecific males. Such data suggest that females might have preexisting preferences for male traits, and that males evolve characteristics that exploit those preferences (sensory exploitation of Ryan 1990). This phenomenon, if true, offers some important insights into how traits and preferences evolve. But again, these studies offer no evidence that female choice currently is exerting selection on male traits — of course, this is not possible if the traits do not exist in conspecifics! Some empirical evidence, both for the existence of female preferences distinct from any influence on male mating success, as well as cases demonstrating how female mate choice influences variation in male mating success will be considered.

1. Female Preference for Male Call Characters

Anuran mate recognition has been a good model for investigating female preferences for several reasons: (1) the advertisement call is the primary recognition signal, (2) it is easily recorded and quantified, (3) it can be synthesized for phonotaxis experiments, (4) the phonotactic behaviour of reproductively active females provides a reliable bioassay for trait preference, and (5) much is understood about the neural basis underlying call preferences (Ryan 1991).

A series of studies, initiated by Blair and his students (e.g., Blair 1958; Littlejohn and Michaud 1959; Littlejohn 1981; Gerhardt 1988), showed that different species of frogs exhibit different advertisement calls, and that females exhibit preferences for the conspecific call over the heterospecific call (see reviews by Gerhardt 1988 and Gerhardt and Schwartz 1995). Although species recognition sometimes is considered distinct from sexual selection, Ryan and Rand (1993c) illustrate how these phenomena are not mutually exclusive. At a minimum, these studies of species-specific call preferences reveal that females attend to variation in calls among males in their community, at least at the species level.

Although the anuran advertisement call is species-specific, there is little doubt that calls vary substantially among conspecific males, both within and among populations (e.g., Ryan and Wilczynski 1991), and in many cases females exhibit preferences among conspecific calls. Gerhardt (1988) and Ryan and Keddy-Hector (1992) reviewed female preferences based on advertisement calls in anurans, and based on acoustic and visual traits across a diversity of taxa, respectively. There is substantial evidence that females exhibit preferences based on call intensity, repetition rate, duration, and complexity (Table 1).

Table 1. Studies of female choice in anurans in which variation in male call traits (i.e., consistency in call behaviour), relationships with mating success, and female preferences were examined experimentally for a single population under natural conditions. "No frequency preference" indicates that females did not exhibit a preference for low frequency calls. DF = dominant frequency of advertisement call; intensity = sound pressure level.

Taxon	Male Trait(s)	Mating Success (MS)	Female Preference(s)	Source
BUFONIDAE				
<i>Bufo americanus</i>	call rate, duration, DF	no relationships, but small sample	females prefer high call effort; no preference for low DF	1
<i>Bufo calamita</i>	call rate, intensity, DF	male size, low DF, call rate and intensity all correlated with MS	females prefer high call rate, intensity; no preference for low DF	2
<i>Bufo rangieri</i>	call rate, duration, DF	call rate correlated with MS	females prefer high call rate; no preference for low DF or long duration	3
<i>Bufo valliceps</i>	call rate, duration, DF	no relationships	females prefer high call effort but not low DF	4
<i>Bufo woodhousii</i>	call rate, DF	call rate correlated with MS	females prefer high call rate but not low DF	5
HYLIDAE				
<i>Hyla chrysocelis</i>	DF	male size (DF?) correlated with MS in some seasons	females prefer high call rate and low DF	6
<i>Hyla cinerea</i>	DF	no relationships	females prefer high call rate; weak preferences for intermediate DF	7
<i>Hyla versicolor</i>	call rate, duration, DF, pulse rate	no relationships	females prefer high call efforts	8
<i>Pseudacris crucifer</i>	DF	no relationships	females prefer intermediate to low DF	9
LEPTODACTYLIDAE				
<i>Eleutherodactylus coqui</i>	call rate	call rate correlated with MS	females prefer high call rate but not low DF	10
<i>Physalaemus pustulosus</i>	DF	male size (DF?) correlated with MS	females prefer low DF	11
MYOBATRACHIDAE				
<i>Uperoleia laevigata</i>	DF	male size (DF?) correlated with MS	females prefer DF indicating male of "right" size	12
HYPEROLIDAE				
<i>Hyperolius marmoratus</i>	call rate, DF	call rate but not size correlated with MS	females prefer high call rates and low DF	13

1 = Sullivan (1992); 2 = Arak (1988); 3 = Cherry (1993); 4 = Wagner and Sullivan, unpublished; 5 = Sullivan (1983); 6 = Morris (1989), Morris and Yoon (1989); 7 = Gerhardt *et al.* (1987); 8 = Sullivan and Hinshaw (1992); 9 = Forester and Lykens (1986); 10 = Lopez and Narins (1991); 11 = Ryan (1985); 12 = Robertson (1986, 1990); 13 = reviewed by Passmore *et al.* (1992).

In many of these species, preferences are for calls that deviate from the mean in the direction of having greater quantity, such as faster, longer, more intense calls. There also can be stabilizing selection on call characters; that is, females may prefer the mean condition rather than traits at either extreme. The form of selection (directional versus stabilizing) resulting from the preference can vary among call parameters. For example, Gerhardt (1991) showed that pulse rate is under stabilizing selection while call duration is under directional selection in gray trees frogs, *Hyla versicolor*. In túngara frogs, the chuck can be altered experimentally in a variety of ways without diminishing its attractiveness to females, while the whine, which is important in species recognition, has a much stricter range of permissible variation if it is to elicit female phonotaxis.

2. Female Preference Generating Sexual Selection

As discussed above, merely demonstrating preferences is not sufficient for showing that female choice based on such preferences currently generates sexual selection. To demonstrate that choice generates selection, the criteria of Searcy and Andersson (1986) should be followed, and in the order proposed: (1) there should be a correlation between mating success and the male trait, and (2) female preference for the trait should be demonstrated experimentally.

Given the relatively large number of studies demonstrating female call preferences, there are few studies that can argue strongly for sexual selection resulting from such preferences in natural populations (Table 1). Sullivan (1983) found that male Woodhouse's toads (*Bufo woodhousii*) exhibit consistent differences in call rate, and that those with high call rates achieve higher mating success under natural conditions. He also documented female preferences for high call rates under experimentally controlled conditions.

In a study of the túngara frog, *Physalaemus pustulosus*, Ryan (1980, 1983b, 1985) showed that females move through choruses and choose mates with little interference from males, that larger males have greater mating success (whether quantified on a seasonal or nightly basis), and that larger males produce calls, specifically the whine, of lower frequencies. These findings suggest that females might prefer larger males because they prefer lower frequency calls, an hypothesis supported by a series of phonotaxis experiments (Ryan 1980, 1983b, 1985). Recently, Ryan *et al.* (1990) suggested the neural basis for such a preference; acoustic tuning of one of the female's auditory organs, the basilar papilla, is slightly biased toward conspecific calls with frequencies lower than average. Ryan and Rand (1993a) presented further behavioural tests that offer statistically weak ($P = 0.10$) support for that neural mechanism.

A similar relationship between auditory tuning and call preference appears to exist in cricket frogs, *Acris crepitans*. The basilar papilla of females is tuned to frequencies below the dominant frequency of the average call for their "home" population, and females show a corresponding behavioural preference for call frequencies lower than average; in some cases this generates preferences for frequencies that characterize other populations (Ryan *et al.* 1992). Variation in male mating success in nature is related to variation in call frequency in *Uperolia laevigata* (= *rugosa*) (Robertson 1986). In this case, females prefer frequencies leading to mating with a male of a certain size relative to their own size.

3. Constraints on Preferences Generating Selection

If there are female preferences for call traits within the range commonly expressed by conspecific males, it is surprising there are not more studies showing a direct correlation between call preferences and male mating success.

The most important constraint on female preferences is the method of mate acquisition employed by males (discussed below). Females have ample opportunity to choose mates when males remain stationary at calling sites and are not actively searching. The mating system of the túngara frog, discussed above, is perhaps an extreme example of this. In many other species, however, males actively search for females, clasping any object remotely resembling a

female frog; male wood frogs (*Rana sylvatica*) are well known for their lack of mate discrimination (Howard 1980). In such species, females might have strong preferences which play no role in sexual selection because they can not be expressed; that is, the preferences might not result in choice. Likewise, in many toads (*Bufo*) males actively struggle for possession of females: 30–40% of matings can involve the displacement of the original male in amplexus (Davies and Halliday 1979; Verrell and McCabe 1986; Cherry 1992).

Another constraint on preferences generating choice could be a negative correlation among traits in their attractiveness. Phonotaxis experiments usually are designed to experimentally isolate the influence of a single trait on female preference. However, calls consist of a constellation of traits (e.g., spectral and temporal characters), and it is not always clear how individual parameters interact to influence overall call attractiveness.

A specific example of interaction of call parameters is intensity-dependent attractiveness. In phonotaxis experiments the attractiveness of one stimulus of a stimulus-pair can be negated or even reversed if the alternative stimulus is increased in intensity (e.g., Arak 1988; Gerhardt 1988, 1991; Ryan and Rand 1990). In nature, there might be variation among males in call intensity, but most of the variance among calls perceived by the receiver may be due to the distance between the signallers and the receiver. Thus, depending on the specific search pattern employed by females and the spatial distribution of males, intensity-dependent factors could introduce a large stochastic component to female mate choice.

Signal intensity in relation to female search patterns and the evolution of female choice was critical to the concepts of passive and active choice developed by Parker (1983). On one level, this hypothesis suggests that if females mate with one male rather than another, this act alone can not be considered active choice; the female may not have been exposed to signals emitted by unselected males. This is true, and an important caution when trying to ascribe the cause of differential male mating success to female choice. A more extreme application of this active/passive dichotomy posits that if females choose mates "passively" on the basis of intensity-dependent cues, it can be assumed that such behaviour requires no special explanation, and by extension, that females do not obtain genetic benefits from the chosen male (allowing rejection of the good genes hypotheses). This applies, it is argued, even if intensity-dependence is a sensory bias that females use in recognizing mates. Sullivan (1989b) and Ryan (1990) discussed the problems with this interpretation, such as the inappropriateness of confusing proximate and ultimate levels of analysis. Additionally, it has proven difficult to operationalize and evaluate these supposed alternative mechanisms (Searcy and Andersson 1986). Overall, the active/passive dichotomy seems to have contributed little to an understanding of the evolution of female choice and of male secondary sexual characters.

There is good evidence that the array of calling males influences the extent to which females choose, although the reason this happens is not clear. In most phonotaxis experiments females are given a choice between a pair of stimuli. Gerhardt (1982, 1988) suggested this is an unrealistically simple choice for females exposed to multiple male choruses, and he showed that in four-speaker experiments choices exhibited in simpler experiments become extinguished (see also Dyson and Passmore 1992a).

A detailed series of studies of the African painted reed frog, *Hyperolius marmoratus*, demonstrate how variation in chorus structure can influence the opportunity for female choice. Females of this species exhibit phonotactic preferences for lower frequency calls, and as with many frogs, call frequency is negatively correlated with body size (Dyson and Passmore 1992a,b). By artificially manipulating chorus size in a greenhouse, Telford *et al.* (1989) showed that females choose larger males in small choruses but not in large ones (also see Dyson and Passmore (1992b) for effects on male aggression), and in four-speaker playback experiments, Dyson and Passmore (1992a,b) showed that the placement of speakers also influenced female choice; they were more likely to exhibit preferences if speakers were equidistant.

Another factor that can constrain mating preferences is within-male variation in call characters. Many studies have concentrated on dominant frequency as a target of sexual selection because spectral characters are thought to be much less variable within a male than

are temporal ones (e.g., Gerhardt 1991; Ryan and Wilczynski 1991). However, in at least two species, *Leptodactylus albilabris* (Lopez *et al.* 1988) and *Acris crepitans* (Wagner 1989a), males may alter call dominant frequency in response to social stimuli. A reason for this difference is the much more pronounced effect of temperature on temporal characters (Zweifel 1968; Wagner 1989b), although this does not negate the possibility of females choosing males based on temporal factors and still generating sexual selection. For example, Sullivan (1992) showed that call duration varies with temperature in *Bufo americanus*. Despite this environmentally-induced variation, males exhibit statistically significant repeatabilities in call duration and call rate among nights. Thus, the female phonotactic preference that Sullivan showed for higher calling effort (rate \times duration) could possibly result in sexual selection for those traits, although field data on mating success are inadequate to evaluate this hypothesis properly for the population he studied (see Howard 1988 for more extensive observations on a different population).

There are some caveats in interpreting studies showing that preferences might not result in choice. One is the statistical issue of falsely accepting the null hypothesis and thus committing a Type II error. There are many reasons the null hypothesis might not be rejected, such as poor experimental design or small sample size. For example, using a sample size of 10 females in discrimination trials with gray treefrogs (*Hyla versicolor*), Sullivan and Hinshaw (1992) confidently rejected the null hypothesis of no preference for a particular call variable since all ten females selected the same call type. However, when five females selected one call type and five selected another, acceptance of the null hypothesis with such a low sample size was problematic. Gerhardt (1992) discussed this problem in interpreting results of phonotaxis experiments, and suggested abandoning classical statistics, which are biased toward committing a Type II error, in favour of Bayesian statistical inference, which shows no biases between Type I and Type II errors. This suggestion merits serious consideration.

Another difficulty that could influence results is identification of the sample of males from which females choose. This point was emphasized by Morris (1989) who showed that female gray treefrogs (*H. chrysocelis*) approach small clusters of males, and from this sample their preference for lower frequency calls results in them choosing larger males as mates. If data were collected at the scale of the entire chorus, however, this choice would be obscured. As just discussed, Telford *et al.* (1989) showed that female reed frogs did not exhibit choice in some situations but did in others. It is an empirical argument as to how effective selection would be if it were restricted to some years, to some parts of years, or to some populations or even parts of populations. Significantly, in the examples discussed above chorus complexity (either in choruses of real males or speakers) influenced choices made by females but not the traits they preferred.

Finally, Gerhardt (1982) argued that two-choice experiments are unrealistic relative to natural choruses; this problem might plague all phonotaxis experiments. For example, túngara frog females spend considerable amounts of time in the pond sitting in front of first one male, then another, before finally choosing a mate, sometimes returning to a male they "sampled" earlier (see Fig. 3.11 in Ryan 1985). Ryan and Rand (1990) showed that some female preferences are intensity-dependent, but their observations also show that females might not actually base their mate choice on this parameter, since a female may move away from one male whose call is much more intense than that of the one to whom she moves next. Phonotaxis experiments do not account adequately for female sampling behaviour.

Phonotaxis experiments probably are prone to over-interpretation, and a more modest role for them in sexual selection studies is suggested. They should be used to test hypotheses generated by field data, as in the spirit of Searcy and Andersson (1986). The study of the túngara frog is a good example. First, it was shown that larger males had greater mating success and were more likely to be chosen by females. Next, it was shown that these males produced lower frequency calls. These data were then used to generate the hypothesis that females had a preference for lower frequencies that caused them to choose larger males. A phonotaxis experiment was used to test this hypothesis. This appears to be a more productive sequence of research than first using phonotaxis experiments to reveal preferences and then extrapolating to interpretations about how choice influences male mating success.

Another use of phonotaxis experiments that appears productive is the uncovering of "hidden preferences". There appear to be cases in which females have preferences for traits not expressed by conspecific males (see below). This is important information for sexual selection theory even though it need not engender interpretations about how preferences result in choice-generating selection in current populations.

B. Female Choice and Direct Selection

One hypothesis for the evolution of female mating preferences is that such preferences enhance a female's reproductive success and thus are favoured by natural selection. Many studies have attempted to document this type of immediate effect on females in order to test the direct-selection hypothesis. These studies of anuran mating systems will be reviewed with the caveat that documenting a current effect is not sufficient to demonstrate that the effect generated the selection responsible for earlier evolution of the preference (e.g., Williams 1966). It also must be remembered that certain characters, such as preferences, might characterize monophyletic groups and thus need not have evolved independently in each species studied; thus, the number of studies supporting a hypothesis might not be a true sample of the number of times any character has independently evolved (e.g., Brooks and McLennan 1991).

1. Species-Specific Advertisement Call Preferences

For at least the past three decades it has been clear that female frogs are attracted to conspecific advertisement calls in preference to heterospecific calls. Furthermore, in many cases mismating among species drastically reduces a female's reproductive output, so there appears to be a direct selective advantage to female choice for mates of the same species. This issue of species recognition is covered in detail by Gerhardt and Schwartz (1995).

2. Preference for Males with Superior Resources

In some species of frogs, males call from and defend areas that females use for oviposition. A defended site may have an important impact on survivorship of eggs and larvae; thus, natural selection should favour the abilities of females to ascertain variation in quality of oviposition sites. Such an effect seems to explain mate choice in the bullfrog *Rana catesbeiana*. In a series of studies, Howard (1978a,b) showed that females preferentially mate with larger males, and that egg survivorship is higher on territories of preferred males, due primarily to reduced egg predation by leeches as well as to these areas having a temperature more amenable to embryonic development. Howard did not ascertain whether female choice is based on characteristics of the male or of the territory he defended. Nevertheless, the choice influences female reproductive success.

Paternal care is one situation in which males potentially could have an immediate impact on survivorship of offspring. Although not as common in anurans as in salamanders, parental care has evolved independently several times (Crump 1995). There is not much evidence, however, that females choose better fathers as mates. One such case is suggested by circumstantial evidence in the gladiator frog, *Hyla rosenbergi* (Kluge 1981). Males guard mud nests into which females deposit their eggs which then float on the water's surface. If eggs are disrupted, they sink to the bottom and drown. Kluge observed females jumping onto males as if attempting to dislodge them from the nest. He suggested this behaviour might allow females to assess a male's commitment to guarding the nest.

Males also defend eggs in the Puerto Rican coqui frog, *Eleutherodactylus coqui*. In this species, however, females might be choosing poorer fathers as mates since a male's mating success and the hatching success of eggs he guards are negatively correlated (Townsend 1989).

Parental care is common in the family of dart-poison frogs, Dendrobatidae; both maternal and paternal care can occur. Summers (1989, 1990, 1992a,b) investigated the relationship between parental investment and sexual selection in detail in several species of *Dendrobates*. Theory predicts that the sex that invests most should be more coy and more choosy about its

mates than should the one that invests least (Williams 1966; Trivers 1972). Thus, males might choose females in species with male parental care. There is no evidence from any of Summers' studies to support this prediction. Furthermore, there are no data to support the notion that females choose males that are superior fathers, but there is some evidence to the contrary. Polygamous males in *D. auratus* often deposit tadpoles from several females in a bromeliad, with the result that the tadpoles have slower rates of development (Summers 1990).

3. Preferences for Increased Fertilization Rates

Even if males do not provide resources, either in the form of oviposition sites or direct care to offspring, they might still influence a female's reproductive success if they vary in their ability to fertilize eggs.

There is some evidence that the body size of the male may influence fertilization success. Davies and Halliday (1977) reported that in *Bufo bufo*, larger males fertilize more eggs, supposedly due to the mechanics of external fertilization. In these toads, as in most anurans, females are larger than males, and when this size difference is reduced, cloacae are more likely to be in juxtaposition during egg deposition. These experiments were conducted in the laboratory, and it is not known if mating between individuals disparate in size also results in unfertilized eggs in nature. In addition, male displacement, rather than female mate choice, seems to play the major role in determining size assortative mating under natural conditions.

In the túngara frog, *P. pustulosus*, females prefer larger males because, at least in part, they prefer lower frequency calls. In this species, as the absolute size difference between mates increases so does the number of unfertilized eggs; as with toads, females are larger than males so a remedy to this dilemma appears to be choice of larger males. Ryan (1983b, 1985) showed that the number of unfertilized eggs in laboratory experiments was the same as the number of unfertilized eggs in nature. Robertson (1990) demonstrated a similar, but more sophisticated, pattern of choice in *Uperolia laevigata*. In this species, fertilization is maximized when the male is 0.64–0.80 the size of the female. Instead of merely preferring larger males, a female uses a male's call frequency to estimate size and chooses a male 0.70 of her own size, thereby maximizing fertilization success.

Females also choose mates of a size ratio that maximizes fertilization rates in a neotropical treefrog, *Oolygon rubra* (Bourne 1992). The cues used in mate choice are unknown, but the advertisement call is a likely candidate. In one population of *Rana temporaria*, both male size and the ratio of male to female size influences fertilization success, but given the brief breeding period, the role of female choice in the mating system is unknown (Gibbons and McCarthy 1986). In a more recent study of a different population, Elmberg (1991) found no effect of male size on fertilization rate in *R. temporaria*. Similarly, in *Bufo americanus* neither male size nor male to female size ratio influences fertilization success (Kruse 1981).

Gibbons and McCarthy (1986) concluded that a male's ability to fertilize eggs is reduced by multiple mating in *R. temporaria*, and may be of importance in any mating decisions made by females. However, Elmberg (1991) found that males can mate with up to four females without a reduction in fertilization rate in this species (males have not been observed to mate with more than three females within a season, see Table 4). Elmberg reanalyzed the data presented by Gibbons and McCarthy and found no relationship between mating number and fertilization rate. In addition, no such effects were shown in the túngara frog, *Physalaemus pustulosus* (Ryan 1985) nor in the toads, *Bufo americanus* (Kruse and Mounce 1982) or *B. cognatus* (Krupa 1988).

These studies indicate that in at least some lek-like mating systems, there may be an opportunity for direct selection to influence female mating preferences due to potential differences in fertilization rates among males. Consequently, the lek appears less paradoxical (see also Reynolds and Gross 1990; Kirkpatrick and Ryan 1991).

4. Sexual Selection for Sensory Exploitation

A recent hypothesis for the evolution of female mating preferences, sensory exploitation, suggests that females have sensory biases or preexisting preferences, and males evolve traits that exploit these biases (Ryan 1990; also see Endler 1992). This hypothesis can be tested by reconstructing the phylogeny of trait-preference, and testing females for the preference of traits that exist in heterospecifics but are not exhibited by their own males. Sensory exploitation predicts that preferences exist prior to the evolution of preferred traits. This historical sequence differs from other hypotheses, such as those involving indirect selection, that predict coevolution of traits and preferences.

Studies of the túngara frog, its closest relatives (species in the *Physalaemus pustulosus* species-group) and its outgroup, support the sensory exploitation hypothesis (Ryan *et al.* 1990; Ryan and Rand 1993a,b). A preliminary phylogenetic analysis, using data from morphology, allozymes and mitochondrial DNA sequences, is shown in Figure 3; the calls are superimposed on this phylogeny. Although the calls of all species are similar in their whine-like form, there are some unique characters within the group. Only the túngara frog, *P. pustulosus*, and one population of its sister species, *P. petersi*, are known to add chucks to their calls. Only *P. pustulatus* has an extreme amplitude-modulated prefix to the call, and only *P. coloradorum* produces calls in doublets and triplets in response to calls of conspecific males.

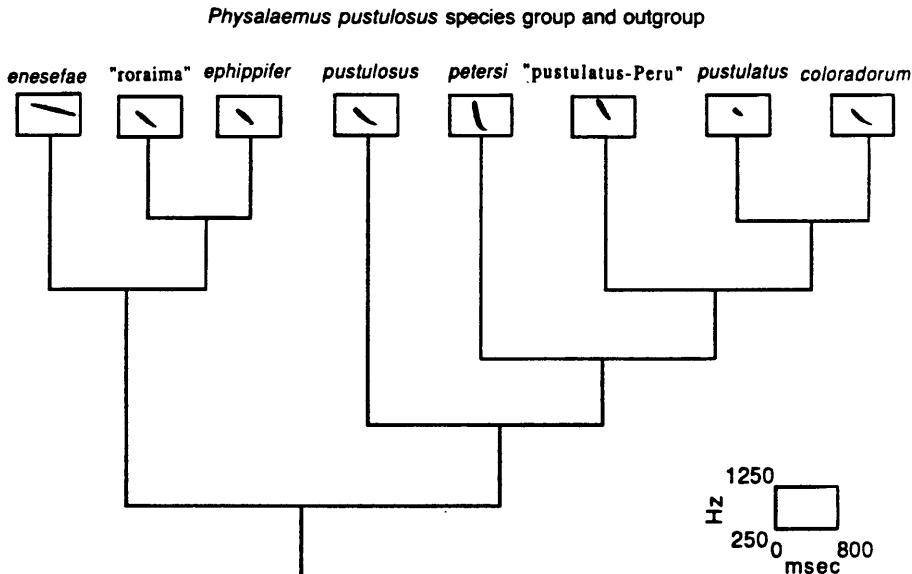


Fig. 3. A preliminary phylogeny of the *Physalaemus pustulosus* species group and some close relatives. Only whine-like calls are shown, although all *P. pustulosus* and one population of *P. petersi* can add chucks to the call. The designations "roraima" and "pustulatus-Peru" are not scientific names, but merely common names of populations from new species, as yet unnamed.

For each of these call characters there are examples of females of other species that would prefer their own males if they exhibited these characters. Female *P. coloradorum* prefer the call of their own conspecific males to which chucks are added over the normal conspecific call which lacks chucks. *Physalaemus pustulosus* females prefer the conspecific call to which the prefix of the *P. pustulatus* call is added over the normal conspecific call lacking such a prefix, and they prefer conspecific calls that are produced in doublets (as produced by *P. coloradorum* males) to the call pattern of their own males. When females of different species share preferences

it could be that the preferences evolved several times independently or that the preference evolved once and is shared by species through common ancestry. Since the latter hypothesis requires fewer evolutionary changes, the principle of parsimony suggests it to be the most likely hypothesis. Thus, in the *P. pustulosus* species group it seems that sensory exploitation is common and that female preferences for several traits existed prior to the evolution of those traits.

It might seem odd to have a preference for a trait as specific as a chuck existing prior to the trait itself. Experiments on the túngara frog by Ryan and Rand (1990) show, however, that this problem might result from how preferences are defined. One usually refers to a preference by the stimuli that will elicit it; however, it is possible that the preference is much broader, but that much of it is "hidden" because conspecific males do not exhibit other traits that might elicit it. This can be illustrated by female preference for chucks and "half-chucks". Half-chucks contain only half the frequency range of the normal chuck, either the low or the high half but with the same total energy as a full chuck. Nevertheless, half-chucks are equally attractive to females. Also, relative to a call with a normal chuck, females are equally attracted to calls in which a burst of white noise is substituted for the normal chuck. Thus, it appears that a preference might be rather broad relative to the conspecific stimuli that can elicit it. With this view of preferences the idea of preexisting or hidden preferences is more plausible.

C. Female Choice and Indirect Selection

In the above examples, preferences evolve because they are the targets of selection, either because they directly influence female reproductive success, or because, in the case of sensory exploitation, sensory biases arise in other contexts. The good genes and runaway sexual selection hypotheses, by contrast, suggest that preferences evolve because they are genetically correlated with other traits that are targets of selection.

1. Female Choice of Good Genes

One of the predictions of good genes is that a female's mate choice should increase the quality of her offspring, where quality refers not to the individual's attractiveness as a mate but to other components of fitness such as survivorship. Given the extreme energetic cost of calling (e.g., Taigen and Wells 1985; Wells and Taigen 1989; Pough *et al.* 1992), the observation that female anurans prefer males with high call rates is consistent with the notion that these males are advertising their phenotypic vigor, and by implication, their good genes. However, we are aware of no direct evidence of a link between male display behaviour, phenotypic and genetic quality, and female choice in amphibians.

Several studies of anurans have shown paternal effects on various larval life history characters, but the degree to which these studies support a good genes hypothesis is questionable. In some populations of *Bufo woodhousii* larger males have higher mating success and these males also father offspring that are larger at metamorphosis, but it is not known if females are choosing larger males or if the greater mating success of larger males derives from male competition (Mitchell 1990). Similar studies in two spadefoot toads, *Spea multiplicata* (Woodward 1986) and *Scaphiopus couchii* (Woodward 1987) and the spring peeper, *Pseudacris crucifer* (Woodward *et al.* 1988) also show heritable paternal effects on larval life history traits that might indicate greater survivorship. One problem with considering these studies as strong support for good genes, as these authors point out, is that different traits influencing fitness might be negatively correlated. For example, time to metamorphosis and size at metamorphosis are usually negatively correlated but faster development and large size each might be favoured by viability selection under certain conditions.

The popular "parasite resistance" hypothesis suggests that a trait such as bright plumage in male birds may be correlated inversely with parasite load so that by choosing brighter males, females coincidentally select those that are genetically resistant to parasites (Hamilton and Zuk 1982). If this is the case, then a correlation between genes for preference and genes for parasite resistance should occur, natural selection should increase the frequency of genes for parasite resistance, and the female preference genes should evolve as a correlated response.

The Hamilton-Zuk model is controversial (e.g., see Clayton 1991; Kirkpatrick and Ryan 1991; Sullivan 1991), and studies of amphibians have not supported it. In both the spadefoot toad, *Scaphiopus couchii* (Tinsley 1990) and the gray treefrog *Hyla versicolor* (Hausfaier *et al.* 1990) there is no consistent relationship between parasite load and male mating success.

Choosing mates with compatible genomes has long been thought to be an important selective force in mate choice between species (e.g., Littlejohn 1981) and it also could influence choice of partners among conspecifics. It has been suggested that individuals should avoid the deleterious effects of inbreeding. Waldman *et al.* (1992) offered some intriguing data suggesting this might be true in the American toad, *Bufo americanus*. Tadpoles of this species recognize their siblings, with whom they preferentially associate in the pond (e.g., Waldman 1988). It appears that toads continue to recognize close relatives as adults but avoid them when it comes to mating. By comparing mitochondrial DNA haplotypes among mated individuals, Waldman *et al.* (1992) showed a significant degree of "incest avoidance". They also showed that call characteristics might be indicative of relatedness. Using DNA fingerprints it was found that animals sharing more fingerprint bands, and thus assumed to be genetically more similar, also have more similar calls. This raises the intriguing possibility that females use call characteristics to avoid choosing closely related males as mates.

2. Female Preferences and Runaway Sexual Selection

Although runaway sexual selection has been a popular hypothesis there have been few empirical tests of it, and none in amphibians. Often, runaway seems to be treated as a null hypothesis: if a study can not support a good genes or direct selection hypothesis it is assumed that the preference has evolved under runaway sexual selection. This obviously is insufficient evidence. Empirically testing this hypothesis, however, is problematic. One approach would be to generate selection on a male trait and demonstrate a correlated change in female preference. Given their complex life-cycles, amphibians probably are not well suited to such an approach.

IV. EMPIRICAL CONTRIBUTIONS FROM THE AMPHIBIA: URODELA

A. Difficulties in Detecting Female Choice

In comparison with anurans, understanding of patterns of mate choice in urodeles is fragmentary. Several factors undoubtedly are responsible for the lack of information. First, many species are small and cryptic in their morphology and behaviour. Courtship and mating often take place in habitats that are relatively inaccessible, such as murky ponds or crevices in rock-faces. Second, behavioural interactions involved in mate selection invariably occur at close-range and may be subtle, such as the amount of stimulation provided by males to females during courtship. It would be difficult, if not impossible, to quantify the content of such interactions in the field. Third, even if a population of individually-marked animals could be observed satisfactorily, estimates of male mating success may not accurately reflect fertilization success. Multiple mating by females, and sperm storage with internal fertilization, render sperm competition a likely form of intrasexual selection in urodeles (Halliday and Verrell 1984). For these reasons, sexual selection in urodeles is understood only in a handful of the 350 or so species that have been described to-date. One must rely on a synthesis of laboratory and field data to predict likely (at best) or possible (at worst) patterns of mate choice and mating system structure in natural populations (Verrell 1989a). This section does not attempt to review all urodele studies relevant to these issues. Rather, in keeping with the discussion of anurans, concentration is on the few species that provide the most complete information.

1. Indirect Evidence of Female Choice

There are good reasons to suspect that sexual selection has operated in the evolution of the sexual behaviour of urodeles. As first recognized by Darwin (1871), the sexes are often dimorphic in epidermal structures such as glands and fins, and some species (especially in the family Salamandridae) are spectacularly sexually dichromatic (Fig. 7). More recent work has shown that courtship often is highly elaborate (Arnold 1977; Halliday 1977a, 1990). Table 2 summarizes the best data available for patterns of mate choice in urodeles. Note that only six species from

Table 2. Studies of mate choice in urodeles in which variation in male (and female) traits and preferences were examined in the laboratory. "No preference" indicates that an experiment failed to reveal a preference for the trait concerned.

Trait/Species	Results	Source
Male Body Size		
<i>Desmognathus ochrophaeus</i>	No preference	1,2
<i>Nothophthalmus viridescens</i>	No preference	3
<i>Triturus vulgaris</i>	Proximity preference for same-size males	4
<i>Triturus cristatus</i>	Mating preference for larger males if dorsal crest regressed	5
Male Age		
<i>Desmognathus ochrophaeus</i>	No preference	1
Male Prior Sexual Experience		
<i>Desmognathus ochrophaeus</i>	No preference	2
Male Courtship Display		
<i>Desmognathus santeellah</i>	Lengthy courtships more likely to result in successful mating	6
<i>Desmognathus ochrophaeus</i>	Transfer of male courtship pheromones increases rate at which female attains full sexual responsiveness	7
	Courtship pheromones <i>not</i> necessary for female to attain full responsiveness if duration of exposure to other courtship elements is sufficient	8
Male Courtship Display		
<i>Nothophthalmus viridescens</i>	Courtship pheromones decrease probability that female will flee	9
	Courtship pheromones necessary for female to attain full responsiveness	10
	Successful mating more likely when amplexus courtship display contains many individual elements	11
	Successful mating more likely after lengthy amplexus than after brief lateral display	11
<i>Triturus vulgaris</i>	Successful mating more likely when female exposed to multiple sequences of courtship display	12
	Successful mating more likely if courtship performed at a high rate	13
	Successful mating more likely if male has deep dorsal crest (more effective transfer of courtship pheromones?)	14
<i>Triturus cristatus</i>	Females unable to perceive male courtship pheromones fail to become fully responsive	15
	Males unable to transfer courtship pheromones fail to render females fully responsive	16
	Females orient to secretions associated with courting pairs	17
	Successful mating more likely if male has deep dorsal crest (more effective transfer of courtship pheromones?)	18
Resources Defended by Male		
<i>Plethodon cinereus</i>	Proximity preference for larger males holding superior territories	19
	Preferential investigation of males feeding on superior prey items	20,21
Female Body Size		
<i>Desmognathus ochrophaeus</i>	Mating preference for larger, more fecund females	22
<i>Nothophthalmus viridescens</i>	Mating preference for larger, more fecund females	23,24
	Males compete more intensely for larger, more fecund females	25
<i>Triturus vulgaris</i>	Proximity preference for larger, more fecund females	26
<i>Triturus cristatus</i>	Proximity preference for larger, more fecund females	27

1 = Houck and Francillon-Vieillot (1988); 2 = Verrell (1991a); 3 = Verrell (1983a, thesis); 4 = Verrell (1991b); 5 = Hedlund (1990a); 6 = Maksymovitch and Verrell (1992); 7 = Houck and Reagan (1990); 8 = Arnold and Houck (1982); 9 = Rogoff (1927); 10 = Paul Watson, unpublished; 11 = Verrell (1982a); 12 = Halliday (1975a); 13 = Teysedre and Halliday (1986); 14 = Green (1991a); 15 = Malacarne and Giacoma (1978); 16 = Malacarne *et al.* (1984); 17 = Malacarne and Vellano (1987); 18 = Malacarne and Cortassa (1983); 19 = Mathis (1991a); 20 = Walls *et al.* (1989); 21 = Jaeger and Wise (1991); 22 = Verrell (1989b); 23 = Verrell (1982b); 24 = Verrell (1985a); 25 = Verrell (1986b); 26 = Verrell (1986b); 27 = Malacarne (1984).

only two of the urodelan families (the Plethodontidae and Salamandridae) are represented. There are no species for which mate preferences are known to be related directly to patterns of mating success in the field because all such data have been collected in the laboratory. Thus, none of these studies satisfy the criteria of Searcy and Andersson (1986) for demonstrating that mate choice generates sexual selection in contemporary populations.

2. Female Choice and Male Body Size

There is little evidence that females choose mates on the basis of body size, age or prior sexual experience. Although it is commonly assumed that growth in amphibians is indeterminate, correlations between body size and individual age tend to be weak (Halliday and Verrell 1988; Verrell and Francillon 1986). The finding that female *Triturus vulgaris* exhibit proximity preferences for males similar to themselves in body size is intriguing (Verrell 1991b). The choreography of spermatophore transfer in these newts suggests that a reduction in size-disparity between partners might reduce the probability that spermatophores fail to adhere to the female's cloaca (Halliday 1975a), but this has yet to be tested empirically. It should be noted that male body size may be important in determining patterns of mating success, irrespective of mate choice, through its influence on the outcome of competitive interactions among males (e.g., Houck 1988; Verrell and Donovan 1991).

3. Female Choice and Male Courtship Intensity

Proximately, mate choice by female salamanders largely can be explained on the basis of differential responsiveness toward males producing the most intense short-range courtship displays. Presumably, a male's mating success is an increasing function of the relative intensity of his display, with a ceiling to intensity set by, say, the energetic cost of high activity (Halliday 1983).

The courtship of salamanders and newts typically involves stimulation of the female by the male via visual, tactile and chemical sensory modalities (Arnold 1977; Halliday 1977a). The transfer of chemical stimuli from males to females is almost ubiquitous in the families Plethodontidae and Salamandridae. These stimuli, termed courtship pheromones by Arnold and Houck (1982), are produced by glands that are most developed in males during the breeding season. In size at least, these glands can be almost as impressive as other, more obvious male, secondary sexual characters, such as the tails of African widowbirds (Andersson 1982). For example, the pheromone-producing dorsal gland of the male smooth newt (*Triturus vulgaris*) may represent almost 10% of his total mass at the height of the mating season (Verrell *et al.* 1986; Sever *et al.* 1990).

Courtship pheromones are thought to increase the rate at which females become fully responsive sexually, thus decreasing the time taken to reach the stages of spermatophore deposition and sperm transfer. This has been directly demonstrated in *Desmognathus ochrophaeus* and *Triturus cristatus* only; evidence for other species largely is correlative. Note that, in *D. ochrophaeus*, courtship pheromones are not necessary for courtship to be successful if females are exposed to other stimuli associated with courtship for sufficient periods of time (Arnold and Houck 1982). Nevertheless, merely "accelerating the inevitable" may be of importance in natural populations if the terrestrial courtship activity of these salamanders results in increased susceptibility to desiccation, injury through intermale competition, and/or injury or death through predation (Houck and Reagan 1990; Uzendoski *et al.* 1993).

Even aglandular morphological characters may be important in ensuring the effective transfer of courtship pheromones. For example, male newts in many species of the genus *Triturus* bear a crest of skin that runs along the dorsum and which may join with a fin along the upper surface of the tail. Darwin (1871) suggested the male crest to be a sexually selected character, and Halliday (1975b) showed how it may function in directing pheromone-laden water currents toward the female. It is interesting that female preference for larger males in *Triturus cristatus* is only seen when male dorsal crests are regressed (Hedlund 1990a).

In some urodeles mate preferences appear biased toward extremes, such as the most stimulating displays of males and the largest, most fecund females (Table 2). This is in accord with preferences for faster, longer, more intense calls in anurans, and patterns of mate choice for traits exceeding the mean found in other animals, both vertebrates and invertebrates (Ryan and Keddy-Hector 1992). However, there is insufficient information to determine whether or not mate choice is currently generating sexual selection in natural populations of any species of urodele.

4. Male Mate Choice

Male urodeles also may exercise mate choice, selecting larger and more fecund females as partners. Males in these species apparently provide their mates with nothing other than sperm, and so male mate choice might not be expected on the basis of "classical" sexual selection theory. However, as suggested by Dewsbury (1982), males might be selected to be choosy if investment in one mating limits further mating opportunities. One way in which this might happen is if ejaculates (or their equivalent) limit future ones, at least in the short-term. This appears to be the case for at least two of the species listed in Table 2. In both *Triturus vulgaris* and *Desmognathus ochrophaeus*, males are unable to produce spermatophores in successive encounters if they occur too close together in time (Verrell 1986c, 1988a). Although the physiological basis of this constraint is not understood (but may involve glandular synthesis of spermatophore components), short-term limitation of the mating capacity of males may select for male mate choice in these species. In principle, the temporal dynamics of spermatogenesis in *T. vulgaris* imposes a further, longer-term constraint because males begin each breeding season with a finite supply of mature sperm. However, in practice, availability of females bearing fertilizable ova probably ceases sometime before males risk exhausting their sperm supplies (Verrell *et al.* 1986).

Whether or not a preference for more fecund females translates into higher fertilization success for choosy males depends on the frequency with which females mate with multiple males, and on patterns of sperm storage and utilization. If females mate multiply and if they store sperm from successive males until the time of fertilization, then sperm competition is likely (Parker 1970; Halliday and Verrell 1984). Only for *Desmognathus ochrophaeus* is sufficient information on both of these factors available. Estimates of multiple paternity in the egg clutches of individual females range between 7% and 25% for natural populations (Labanick 1983; Tilley and Hausman 1976). In one laboratory experiment females mated with an average of 19 different males (Houck, Arnold and Thisted 1985). Preliminary work on sperm utilization in females mated with electrophoretically-distinct males suggests that the number of eggs a given male fertilizes depends on the relative numerical representation of his sperm in the female's spermatheca (Houck, Tilley and Arnold 1985); there is no obvious advantage to being a female's first or last partner, as occurs in many other animals (Smith 1984). Limited field data suggest a rate of multiple paternity of over 90% in the alpine newt, *Triturus alpestris* (Rafinski 1981), but the dynamics of sperm storage and utilization by females in this species are not understood.

An adverse effect of multiple mating by females on male mate choice could extend across successive breeding seasons if sperm are stored for sufficiently long periods (Halliday and Verrell 1984). However, in only one of three studies was positive evidence for such long-term storage of viable sperm obtained (*pro*: Houck and Schwenk 1984; *con*: Verrell and Sever 1988; Sever 1992).

B. Direct or Indirect Selection?

Only for *Plethodon cinereus* is there any evidence that female preferences might result in the acquisition of resources defended by territorial males, superior prey in this case (Table 2). Consideration of mate choice in *P. cinereus* will be deferred until mating systems are discussed. True territoriality apparently is restricted to the family Plethodontidae.

Whether female urodeles obtain any benefit in terms of good genes from choosing certain males as mates is unclear. Female urodeles may obtain nutrients from spermatophores, but this has yet to be examined. Preferences for larger males may be adaptive if such males bear

genes that contribute to survival. This argument is based on the questionable assumption that a male's size reliably "advertises" his age. Halliday and Verrell (1988) suggested that male size in anurans and urodeles may be determined largely by feeding experiences before sexual maturity, and that these may include a large stochastic element.

In terms of indirect selection, one can ask if there is any benefit to mating with males bearing well-developed secondary sexual characters, or with males producing particularly stimulating courtship displays. In *Triturus vulgaris*, the dorsal crest of the male is most highly developed during the time that courtship activity in natural populations is most intense (Verrell *et al.* 1986). The crest is believed to aid in directing currents of water toward the female's nares, which are produced by a fanning movement of the male's tail and probably carry courtship pheromones secreted from his dorsal gland (Halliday 1975b). Green (1991a) demonstrated that the dorsal crest is a condition-dependent secondary sexual character in *T. vulgaris*; degree of development depends on the male's recent feeding history. Well-fed males have deeper crests, which also may be true in another newt, *T. cristatus* (Baker 1992). Whether females responding differentially toward large-crested males may obtain some genetic benefit for their offspring is an intriguing, but untested, possibility. Such a benefit could come about for both sons and daughters of choosy females if the ability to procure/utilize food efficiently has a heritable basis.

A similar argument may be made for female preferences for high display rates, if these advertise some heritable capacity for sustaining high levels of (perhaps costly) metabolic activity. Interestingly, energetic costs of courtship and inter-male aggression in *Desmognathus ochrophaeus* are insignificant relative to a male's total energy budget (Bennett and Houck 1983; see also Marks and Houck 1989). Although lungless, this terrestrial species mates in an "infinite pool" of oxygen. Indirect data suggest that there may be a higher energetic cost to courtship for aquatic-breeding newts such as *Triturus vulgaris* (Halliday 1975a, 1977b; Halliday and Sweatman 1976), *T. cristatus* (Green 1991b) and *Notophthalmus viridescens* (Verrell 1982a, 1985b, 1985c). It must be stressed that, for urodeles as for anurans, there is no direct evidence of a link between male display, male genetic quality and female choice.

C. Overview

Studies of female choice in amphibians have provided a number of insights, both from the perspective of evaluating current theory, and perhaps more importantly, in the generation of new hypotheses. With respect to the former, in the late 1970s and early 1980s investigations of amphibians were instrumental in the refinement of sexual selection theory, especially with regard to the relative roles of, and interactions between, male-male competition and female choice. With respect to the generation of new theory, investigation of processes and patterns of sexual selection in the *Physalaemus* group greatly facilitated the development of the sensory exploitation hypothesis.

Empirically, investigations of amphibians have yielded some excellent examples of female choice; some anuran studies offer strong evidence of current selection on male traits under natural conditions (Table 1). Those investigations that document a lack of measurable selection on male traits under field conditions in spite of demonstrated female preferences are valuable, especially given current interest in the magnitude and consistency of sexual selection under different ecological conditions (Endler 1986; Moore 1990; Arnold and Duvall 1994).

Studies of mate choice in urodeles clearly are lagging behind those of anurans, both in quantity and quality, and especially for natural populations. Work on natural populations is needed, and until such studies are underway it will be impossible to determine the role of mate choice in generating sexual selection in these amphibians. At present, the greatest contribution of laboratory studies of urodeles may be to highlight the importance of male courtship behaviour in increasing female sexual motivation.

V. MATING SYSTEM STRUCTURE

A. Theoretical Considerations

Mating systems are traditionally classified according to levels of polygamy (Emlen and Oring 1977; Wells 1977a; Thornhill and Alcock 1983; Davies 1991). This approach is attractive given the expectation of an increase in the intensity of sexual selection associated with higher

Table 3. Mating system classification based on levels of polygamy. Modified from Emlen and Oring (1977) and Alcock (1993).

Mating Pattern	Mating System Type	Description/Predictions
Polygyny	Female Defence	Males defend groups of females; unpredictable OSR; intensity of sexual selection potentially high; increased role of male-male competition relative to female choice (?)
	Resource Defence	Males defend resources required by females and/or their offspring; male-biased OSR prior to male-male competition (?); intensity of sexual selection potentially high; male-male competition and female choice both important
	Lek	Males display at communal site and attract females; intensity of sexual selection potentially high; female choice and potentially male-male competition important
	Scramble Competition	Males locate and mate with as many females as possible; OSR potentially unbiased (unity); intensity of sexual selection potentially low; increased role of male-male competition relative to female choice
Polyandry	Male Defence	Females defend male mates in female aggregations; female-biased OSR (?); intensity of sexual selection potentially high; mate choice and mate competition potentially high
	Resource Defence	Females defend resources required by males and/or their offspring; female-biased OSR; intensity of sexual selection potentially high; mate choice and mate competition potentially high
Monogamy	Mate-Guarding/Assistance	Males mate with single females and defend them against other males; males may provide paternal care; OSR potentially unity; low intensity of sexual selection but mate choice and/or mate competition potentially operative
Polygamy	Resource Use	Either sex gains by multiple matings (e.g., sperm replenishment, nuptial gifts, access to resources); OSR potentially unity; mate choice potentially important

levels of polygyny or polyandry (Table 3). Hence, under such a scheme categories of mating systems are rough indicators both of the relative intensity of selection and the presumed target(s) of selection. For example, in a lek mating system it is presumed that relatively high levels of polygamy may be achieved by few males, resulting in a high intensity of selection acting on some component of male phenotype (e.g., display behaviour). However, like any simplified taxonomy, a classification scheme based solely on levels of polygamy provides little basis for an understanding of the evolutionary significance of differences in mating systems within or among taxa.

An adequate description and explanation of any mating system entails considerably more than a simple enumeration of the numbers of mates for each of the sexes. The temporal and spatial distribution of reproductively interacting individuals, and their behavioural tactics within the context of social competition for mates, together might be considered as constituting the essential elements of "mating system structure". Given that a great many ecological and historical (i.e., phylogenetic) factors can influence these components of reproductive behaviour, it is not surprising that an understanding of mating system evolution remains imperfect (Ims 1988; Rutowski *et al.* 1988; Arnold and Duvall 1994; Wagner and Hews, unpubl.).

The ultimate factors contributing to mating system structure have been examined from a variety of perspectives (see reviews by Ims 1988; Davies 1991; Arnold and Duvall 1994). For example, some investigators have focused on the factors causing sexual selection (e.g., parental investment) in an attempt to understand mating system variation (Gwynne 1991; Clutton-Brock and Vincent 1991). Thornhill (1986) provided an insightful discussion of the relationships between parental investment, sexual selection, and mating system structure. He argued that when parental investment by males is essentially zero (i.e., only genes are contributed to the next generation), then degree of mate monopolization controls sexual selection. In these mating systems, by monopolizing the parental effort of females, males increase their own fitness. Males appear to provide only sperm to females in many of the anurans and urodeles that have been studied (Wells 1977a; Arak 1983; Sullivan 1989a; Verrell 1989a). Accordingly, these forms should exhibit polygynous mating systems of one form or another (Table 3).

Clutton-Brock and Vincent (1991) suggested that differences in rate of reproduction (maximum number offspring produced sex per unit time) rather than relative parental investment *per se* are critical to differences in the intensity of sexual selection. An increased potential rate of reproduction on the part of males leads to a male-biased operational sex ratio (OSR) and thus males compete for access to the limited number of females available for reproduction at any given time. The views of Clutton-Brock and Vincent are compatible with those of Thornhill; it is reasonable to assume that reproductive rate will generally be higher in the sex with lower parental investment. In accordance with this perspective, Simmons (1992) documented that parental investment and reproductive rate are inversely related in a cricket with reversed sex-roles.

Studies of anuran amphibians have revealed that males typically have a potentially higher reproductive rate than females. In many North American toads (*Bufo*) males can mate repeatedly, night after night, and successfully fertilize the eggs of multiple females; however, females rarely produce more than two clutches within a season (Gatz 1981; Howard 1988; Sullivan 1989c; Wagner and Sullivan 1992). In the barking treefrog (*Hyla gratiosa*), Murphy (1992) found that occasionally females oviposit four separate clutches within a season; however, males can obtain up to 17 matings ($>4 \times$ maximal female mating success), indicating that the potential reproductive output of males still exceeds that of females (see review by Kluge 1981).

B. Ecology and Mating System Structure

In a seminal contribution, Emlen and Oring (1977) argued that environmental factors should significantly influence temporal patterns of reproductive activity of the sexes (i.e., cycling rates), and as a result, competition for mates. They stressed that the ability of one sex (usually males) to monopolize access to the other (usually females) is crucial to mating system structure. They emphasized that ecological variables can have a profound influence on the distribution of the sexes in space and time, and thereby determine the potential and extent of this "mate monopolization". In addition, they noted that historical or phylogenetic factors, such as the need for paternal care, can influence the ability of one sex to monopolize matings with the other.

Considerable corroborative evidence in support of the verbal model of Emlen and Oring has accumulated over the past 15 years. Predictable relationships between ecological variables, and variation in the spatial and temporal distribution of mates have been documented (see reviews in Thornhill and Alcock 1983; Rubenstein and Wrangham 1986; Clutton-Brock 1988). Numerous studies have found that female dispersion is linked to ecological variation and this in turn influences the dispersion of males and their mating strategies (see review by Davies 1991). Although it has been difficult to identify all of the salient environmental variables and their relationships to mating system structure for a single species (Duvall *et al.* 1993; Arnold and Duvall 1994; Wagner and Hews, unpubl.), strong support has been obtained for the general notion that ecological factors influence reproductive behaviour.

Emlen and Oring (1977) defined the operational sex ratio, or OSR, as the ratio of fertilizable females to males at a given time (since males typically compete for access to females). They suggested that OSR could be used as a measure of the potential intensity of sexual selection, assuming that the degree of polygyny of males will be limited by (1) the temporal availability of females, and by (2) the ability of males to monopolize matings with females. A higher level of polygyny, and therefore a higher intensity of sexual selection, should be associated with a male-biased OSR if females are available over an extended time period to allow multiple matings by successful males. Studies of a variety of organisms have documented relationships between OSR and alternative reproductive behavioural tactics of males, and by implication, the nature and intensity of sexual selection (but see Ims 1988). Crespi (1988, 1989) found that OSR directly influences the form of competition among males for access to females in an insect; changes in OSR are correlated with variation in the intensity of sexual selection (see also Lawrence 1986, 1987; Colwell and Oring 1988).

Emlen and Oring (1977) were the first to explicitly consider ecological, behavioural, and historical (phylogenetic) factors in an attempt to understand mating system structure (see also Bradbury and Vehrencamp 1977; Wells 1977a). Given the great number of relatively

thorough investigations of reproductive behaviour in amphibians, these vertebrates present an excellent opportunity for evaluation of the model of mating system structure developed by Emlen and Oring (1977). Paternal care is absent from many lineages, allowing direct evaluation of the significance of ecological variables for mating system structure. Below are reviewed the best-studied amphibian taxa (focusing primarily on the relatively well-studied anurans); their mating systems are described and the degree to which their reproductive behaviour conforms to the verbal model of Emlen and Oring is evaluated.

C. Anuran Mating Systems

Wells (1977a) suggested that anuran breeding periods can be arranged on a continuum from short duration (explosive) to long duration (prolonged). A great many temperate zone species have been surveyed, and most can be categorized as either explosive or prolonged breeders (see reviews in Kluge 1981; Arak 1983; Sullivan 1989a). Unfortunately, as noted by Wells, there is little understanding of the specific environmental variables (either abiotic or biotic) influencing the duration of breeding periods. Sinsch (1988) determined that environmental factors (e.g., temperature, rainfall, etc.) account for 23–41% of the temporal variation in breeding intensity in *Bufo calamita*.

Abiotic conditions might force taxa to adopt an explosive breeding period; for example, a lack of available water except during brief, unpredictable periods (e.g., in deserts). Conversely, the availability of water for an extended period presumably allows more prolonged breeding. However, a given mating system need not necessarily have evolved *in situ* as an adaptation to that environment and those particular abiotic conditions. In the southwestern deserts of the United States it appears that true toads (*Bufo*) exhibit an explosive mating system in part because it is an ancestral condition, and not solely as a result of recent adaptations to aridity (Sullivan 1989a). Although an explosive mating system is no doubt adaptive under arid conditions, it is apparently also adaptive under other more mesic ones (e.g., tropical forests; Crump 1974; Wells 1977a), presumably as a result of biotic factors (e.g., predation on larvae) favouring reproductive synchrony of females.

Regardless of the underlying basis, temporal variation in breeding period length should have profound consequences for the action of sexual selection in breeding aggregations. In accordance with the predictions of Emlen and Oring (1977), Wells (1977a) suggested that female choice should be reduced when females are temporally restricted in their egg-laying opportunities (explosive). The intensity of sexual selection also should be minimized given the inability of males to monopolize matings with females and achieve a high degree of polygyny. This should be especially true for anurans with external fertilization and the requisite participation of the male during oviposition. If an entire population breeds synchronously over a short time period, then given the time required for oviposition, males should be prevented from mating polygynously to any significant degree. Conversely, in forms with more extended breeding periods (prolonged), asynchronous arrival of females and the ability of males to mate repeatedly night after night establishes a male-biased OSR and greater opportunity for mate monopolization (Wells 1977a; Arak 1983).

1. Scramble Competition Polygyny

A scramble competition mating system is the norm for many anurans with explosive, temporally restricted mating systems (Table 4). In most of them breeding activity is limited to a few nights each year; males may or may not engage in advertisement calling to attract females. Often they spend considerable time actively searching for females and interacting with other males (Davies and Halliday 1979; Howard and Kluge 1985). As predicted by Wells (1977a), these alternative reproductive behaviours are often density dependent, with males adopting advertisement calling at low densities (Höglund and Robertson 1988; Sullivan 1989a; see Halliday and Tejedo 1995).

Observations of the Woodfrog (*Rana sylvatica*) reveal that few males mate polygynously in this highly explosive species (<1% mate with 2 females; Howard 1980). Similarly, in the common toad (*Bufo bufo*), successful males rarely obtain more than a single mating (1% mate

Table 4. Scramble competition polygyny in anurans. For each species an entire breeding season was monitored, and individuals were marked to allow determination of polygyny, OSR (no. breeding females/no. breeding males), and the nature of male-male competition. When multiple populations were investigated, they are listed together unless they varied substantially in mating system structure (see Tables 5 and 6), and OSRs represent the range in mean values for breeding seasons of the various populations. AS = active searching behaviour exhibited by males.

Taxon	OSR	Male-Male Competition	Source(s)
BUFONIDAE			
<i>Bufo americanus</i>	male-biased (0.27–0.60)	AS; opportunity for female choice in some aggregations; large males may mate 0–3 females	1
<i>Bufo boreas</i>	male-biased (0.38–0.67)	AS; large male mating advantage in some populations	2
<i>Bufo bufo</i>	male-biased (0.20–0.50)	AS; large male mating advantage in some populations; males may mate with 0–2 females	3
<i>Bufo cognatus</i>	male-biased (0.10–0.25)	Males may engage in satellite behaviour; opportunity for female choice	4
<i>Bufo exsul</i>	male-biased	AS; large male mating advantage in some aggregations	5
<i>Bufo gutturalis</i>	male-biased	AS; males attempt to displace other males in amplexus with females (51% of matings); large male mating advantage; relatively prolonged breeding period with multiple chorus bouts; males obtain 0–6 matings	6
<i>Bufo woodhousii</i>	male-biased (0.0–0.20)	AS; opportunity for female choice; males mate with 0–1 females	7
<i>Bufo typhonius</i>	male-biased	Males attempt to displace males in amplexus; large male mating advantage	8
RANIDAE			
<i>Rana sylvatica</i>	male-biased (mean = 0.18)	AS; large male mating advantage	9
<i>Rana temporaria</i>	male-biased (0.16–0.21)	Males attempt to displace other males in amplexus; large male mating advantage in some populations	10

1 = see reviews by Howard (1988) and Sullivan (1992); 2 = Olson *et al.* (1986); 3 = see reviews by Loman and Madson (1986) and Høglund and Saterberg (1989); 4 = Krupa (1989), Sullivan (1982a); 5 = Kagarise Sherman (1980); 6 = Telford and Van Sickle (1989); 7 = Sullivan (1989c); 8 = Wells (1979); 9 = Howard (1980); 10 = Arak (1983), Elmerg (1991).

with 2 females; Davies and Halliday 1979). Thus, as predicted by Emlen and Oring (1977), the reduced time available for reproduction prevents individual males from achieving high levels of polygyny by monopolization of females.

Explosively breeding anurans with obvious forms of direct male-male competition for mates are logically described as displaying scramble competition polygyny. However, it is important to recognize that in contrast to other organisms exhibiting this mating system, in which direct male-male struggles for females are dominant (e.g., insects), female mate choice may play a more important role for anurans. For example, Cherry (1992) documented that males do not displace other males in amplexus, or engage in behaviour that might limit the ability of females to freely select their mates in an explosively breeding population of *Bufo pardalis*. Even though temporal constraints might limit polygyny of males, and increase the potential for direct male-male competition for females, mate choice may represent an important factor in scramble competition mating systems of anurans (see below; Table 4).

2. Operational Sex Ratio (OSR) and Female Choice

Contrary to expectations, most explosively breeding anurans do not have OSRs approaching unity, although they are typically less male-biased than forms with more prolonged breeding (Gatz 1981; Kluge 1981; Sullivan 1989a; Wagner and Sullivan 1992; Tables 4, 5, 6). In *Scaphiopus couchii*, a desert anuran with an extremely short breeding period (1–2 nights), Woodward (1984a) found that the OSR ranged from 0.27–0.68 for six aggregations. This suggests a modest potential for sexual selection through either female choice or male-male competition. Although high levels of polygyny are not achieved in these taxa, mating failure on the part of most males indicates that some opportunity for sexual selection exists (Sullivan 1989a).

As noted above, it is widely thought that female mate choice is reduced in explosively breeding forms because male-male competition limits the opportunity for effective choice. Observations of a number of explosively breeding anurans indicate that direct male-male struggles for females, and interception of females approaching calling males by actively-searching males, can be commonplace (Table 4; Halliday and Tejedo 1995).

Table 5. Lek polygyny in anurans. For each species an entire breeding season was monitored, and individuals were marked to allow determination of polygyny (range in number of mates obtained by individual males within a season) and range in OSR over a breeding season (no. breeding females/no. breeding males), and the nature of female choice. If multiple populations were investigated, they are listed together unless they varied substantially in mating system structure (see Tables 4 and 6) and OSRs represent the range in mean values for breeding seasons of the various populations.

Taxon	OSR	Level of Polygyny (matings/male)	Source(s)
BUFONIDAE			
<i>Bufo calamita</i>	0.02-0.40	0-7	1
<i>Bufo canorus</i>	male-biased	0-3	2
<i>Bufo houstonensis</i>	<0.50	0-3	3
<i>Bufo variceps</i>	0.01-0.13	0-4	4
<i>Bufo woodhousii</i>	0.02-0.14	0-3	5
HYLIDAE			
<i>Hyla chrysoscelis</i>	0.05-0.82	0-4	6
<i>Hyla cinerea</i>	male-biased	0-7	7
<i>Hyla gratiosa</i>	0.15-0.30	0-17	8
<i>Hyla versicolor</i>	0.04-0.12	0-4	9
<i>Olotygon rubra</i>	mean = 0.06	—	10
<i>Pseudacris crucifer</i>	male-biased	—	11
LEPTODACTYLIDAE			
<i>Physalaemus pustulosus</i>	male-biased	0-6	12
MYOBATRACHIDAE			
<i>Uperoleia laevigata</i>	0.05-0.20	—	13
HYPEROLIDAE			
<i>Hyperolius marmoratus</i>	mean = 0.03	0-3	14

1 = Arak (1988), Tejedo (1992); 2 = Kagarise Sherman (1980); 3 = Jacobson (1989); 4 = Wagner and Sullivan (1992); 5 = Sullivan (1989c); 6 = see review by Ritke and Semlitsch (1991); 7 = Gerhardt *et al.* (1987); 8 = Murphy (1992); 9 = see review by Sullivan and Hinshaw (1992); 10 = Bourne (1992); 11 = Sullivan and Hinshaw (1990); 12 = Ryan (1985); 13 = Robertson (1986, 1990); 14 = see reviews by Telford (1985), Passmore *et al.* (1992).

Table 6. Resource defence polygyny in anurans. For each species an entire breeding season was monitored, and individuals were marked to allow determination, or at least the estimation, of polygyny, and the nature of female choice. When multiple populations were investigated, they are listed together. PC = paternal care observed; S = satellite behaviour observed in males.

Taxon	Resource Defended/Utilized	Source(s)
CENTROLENIDAE		
<i>Centrolenella fleischmani</i>	Terrestrial oviposition site; no PC?; males obtain 0-11 matings	1
DENDROBATIDAE		
<i>Dendrobates austruonicus</i>	Terrestrial oviposition site; PC?	2
<i>Dendrobates auratus</i>	Terrestrial oviposition site; PC?; females defend males	3
HYLIDAE		
<i>Hyla rosenbergi</i>	Aquatic nest site; limited PC; males obtain 0-6 matings	4
LEPTODACTYLIDAE		
<i>Eleutherodactylus coqui</i>	Terrestrial nest site; PC; males obtain 0-6 matings	5
RANIDAE		
<i>Rana catesbeiana</i>	Aquatic oviposition site; no direct PC; males obtain 0-4 matings	6
<i>Rana clamitans</i>	Aquatic oviposition site; no direct PC	7

1 = Greer and Wells (1980), Jacobson (1985); 2 = see review by Summers (1992b); 3 = Summers (1989, 1990); 4 = Kluge (1981); 5 = see review by Townsend (1989); 6 = Howard (1978a,b); 7 = Wells (1977b).

Somewhat unexpectedly, however, in many explosive breeders females have been observed to directly approach individual calling males and avoid non-calling ones (Sullivan 1982a, 1989a, 1992; Wagner and Sullivan 1992). No consistent relationships between male phenotypic characteristics and mating success have been found in these species. It may be that in spite of the opportunity for mate selection, temporal constraints increase the costs of highly discriminating behaviour by females. Consistent with this hypothesis, Sullivan (1989a) found that male mating success is unrelated to male phenotype in an explosively breeding population of *Bufo woodhousii* but not in a separate, prolonged breeding one.

Similarly, Wickman (1992) suggested that a reduction in female choice can influence both the intensity of sexual selection and the overall mating system structure. In the butterflies that he studied, a long-lived form exhibits a lek system, but a short-lived form, as a result of temporal constraints and less selective females, exhibits a scramble competition system. These observations support the view that female mate choice can be modified by duration of breeding period.

The data for butterflies also indicate that if a scramble competition mating system is consistently located in a particular area, a transition to a lek-like mating system only requires an increase in duration of breeding period and the ability of females to exercise mate choice. Standing water is required for breeding by many anurans, and as a result breeding aggregations often are located in the same general region each year, perhaps increasing the probability of such a transition (see Rutowski *et al.* 1988). At least two North American toads (*Bufo americanus* and *B. woodhousii*) exhibit intraspecific variation in reproductive behaviour (see reviews by Sullivan 1989c, 1992). Populations breeding explosively exhibit a scramble competition mating system with little opportunity for female choice and more obvious male-male competition for mates (e.g., active-searching behaviour; Table 4). Populations breeding over a more prolonged period exhibit lek-like mating systems in which females freely select their mates and there is little direct competition for females among males (Table 5).

3. Lek Polygyny

Lek mating systems have been described for a variety of vertebrates, including birds, mammals, fish, and amphibians. It has been questioned whether any anurans truly exhibit lek mating systems (Bourne 1992). However, as noted by Bradbury (1981, 1985) and Wells (1977a), many clearly fulfill the strictest definition (Table 5). In these forms males aggregate and attract females by displaying. Females move freely within aggregations to select a mate. Last, and most significantly, males provide only sperm since oviposition occurs away from their calling sites, thus eliminating the possibility that they are selected on the basis of other resources important to the female or her offspring (Sullivan 1983; Sullivan and Hinshaw 1992).

Lek mating systems have been described for representatives of at least five of the neobatrachian anuran families (Table 5). In some of these taxa males exhibit alternative reproductive behaviour as satellites that might limit the ability of females to exercise mate choice. The satellite behaviour of males in these forms reveals the similarities between anuran amphibians and other vertebrates in lek mating behaviour: satellite males are behaviourally similar in fish, amphibians, birds, and mammals.

4. Evolution of lek polygyny

The evolution of lek mating systems has received considerable attention over the past decade (Bradbury 1981, 1985; Queller 1987; Kirkpatrick and Ryan 1991). This attention has been due in part to the interest in the role of female choice in mating systems in which females receive no immediate benefits. In addition, the analysis by Bradbury (1981) emphasized that the benefits of communal display by males are not obvious.

Bradbury (1981, 1985) suggested that the traditional display site characteristic of a lek mating system largely may be determined by the spatial availability of females. Specifically, males should settle at sites ("hotspots") where females are expected in the highest numbers.

The observations of Thery (1992) of six species of birds (manakins) are consistent with this model: males exploit areas frequented by females in the development of leks (see also Höglund and Robertson 1990). In one obvious, but non-trivial, fashion anurans are consistent with the hotspot model. In species that require standing water to breed, females presumably will be attracted to particular ponds, lakes, streams, or rain-formed pools. Males simply may exploit the predictable occurrence of females in these particular locations. However, the observation that choruses of males often shift within sites (e.g., different shorelines; Howard 1978a; Sullivan 1982b) suggests that both males and females are attracted to the chorus, and are not haphazardly distributed around the body of water.

In addition to the hotspot model, a number of other hypotheses have been considered as likely explanations to account for the origin and/or maintenance of lek mating behaviour (Svensson and Petersson 1992). The female choice hypothesis posits that females prefer to mate with males participating in aggregations, and by extension, prefer larger rather than smaller groups of males (Alexander 1975; Sullivan 1985). Indirect evidence from analysis of the numbers of females present at choruses of different sizes in anurans indicates that, proportionately more females are present in larger choruses in some species, as predicted (*Physalaemus*: Ryan *et al.* 1981; *Bufo valliceps*: Wagner and Sullivan 1992), but not in others (*Bufo woodhousii*: Sullivan 1985; *Bufo calamita*: Tejedo 1992, 1993).

Unfortunately, no one has tested directly the hypothesis that females prefer larger choruses of males in anurans. Individual females often sample only a few males before making a selection under natural conditions (e.g., Sullivan 1983; Robertson 1986; Arak 1988; Morris 1989). This suggests that females do not take advantage of the wider range of males presumably available in a larger chorus.

A third hypothesis to account for lek evolution is the "hotshot" model. Under this view, preferred males are attractive to both females and less attractive males, who attempt to exploit the mate-attracting abilities of the preferred males. Hence, larger aggregations develop and are maintained as a result of selection on less attractive males to participate in larger aggregations (Arak 1988; Höglund and Robertson 1990). Consistent with this hypothesis, satellite males may disproportionately parasitize males preferred by females in the Great Plains toad (*Bufo cognatus*; Sullivan unpubl.; Krupa 1989).

A fourth, but not necessarily mutually exclusive, hypothesis concerns reduction of predation risk (Fig. 4). Observations of predation on displaying (calling) males in breeding aggregations have been documented for a number of taxa (Ryan *et al.* 1981; Hinshaw and Sullivan 1990; Woodward and Mitchell 1990). Males may be favoured to form aggregations if predation pressure on individuals is reduced in larger aggregations. Analyses of predation intensity in aggregations of *Physalaemus pustulosus* are consistent with this view of leks as "selfish herds" (Ryan *et al.* 1981). These neotropical frogs are subject to predation by a number of acoustically orienting predators; males experience a reduced predation risk as individuals when participating in larger choruses. Thus, all else being equal, and independent of any advantage accruing to females, males may benefit by participating in larger choruses.

In summary, observations on anurans are consistent with a number of hypotheses proposed to account for the evolution and/or maintenance of lek behaviour. First, it is clear that the hotspot model might account for the initial formation of male aggregations: females must gather at egg-laying sites. Second, predation pressure may secondarily favour larger aggregations. Third, males engaging in satellite behaviour may also favour larger aggregations, assuming a larger array of males for them to parasitize. In fact, the only hypothesis with no direct support is that of female preference.

5. Resource Defence Polygyny

Resource defence mating systems have been documented for relatively few anurans (Table 6). However, it is unclear if the paucity of examples is real or apparent. Additional studies of tropical forms in which males advertise from, or near, nest sites will no doubt reveal additional ones. For example, although only a small number of matings ($N = 7$) were observed

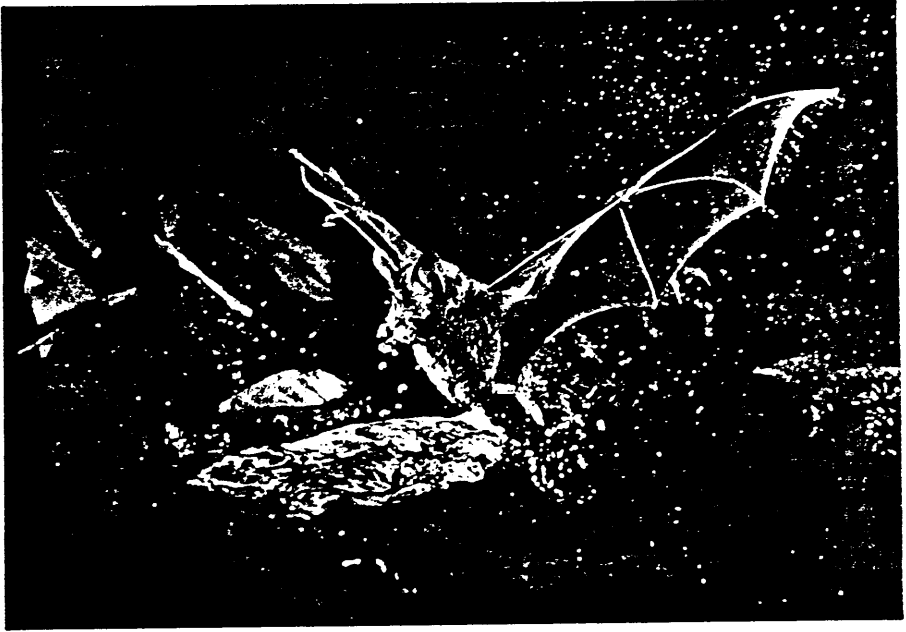


Fig. 4. A frog-eating bat (*Trachops cirrhosus*) having just captured a calling male túngara frog (*Physalaemus pustulosus*). (Photograph courtesy of Merlin D. Tuttle, Bat Conservation International).

(no males were polygynous), recent work with the neotropical dendrobatid *Epipedobates* (= *Phylobates*) *femorialis*, suggests that males defend territories used in courtship and terrestrial oviposition (Roithmair 1992).

In the North American ranids exhibiting this mating system, males defend oviposition sites (Wells 1977a; Howard 1978a,b). In the bullfrog (*Rana catesbeiana*), a prolonged breeding species, males defend oviposition sites that are preferred by females; there is increased survivorship of embryos deposited in the defended areas of the pond (Howard 1978b). Large males defend the territories preferred by females, but the role, if any, of female choice for large males (independent of resource quality) remains unknown.

In the gladiator frog (*Hyla rosenbergi*) of Central America, males defend nesting sites for females; again, egg survivorship is higher in attended nests (Kluge 1981). As in the bullfrog, it is possible that females prefer particular males on the basis of phenotypic characteristics in addition to or instead of nesting site features; however, Kluge (1981) found no obvious relationships between male traits and mating success.

Assuming an ancestral condition of some form of scramble competition mating system at a body of water, the evolution of these resource defense mating systems seems relatively straightforward. Given consistent variation in the survivorship of offspring associated with particular locations, females that recognize and mate at those sites will be favoured, and males that recognize and defend those sites will be secondarily favoured.

Summers (1989, 1990, 1992a,b) studied the complex social system of a number of Neotropical dendrobatid frogs. Some species (e.g., *Dendrobates histrionicus*) appear to have resource defence mating systems similar to those of the hylid and ranid frogs; males defend territories, and provide care for eggs and larvae, although the terrestrial nesting habits of these anurans is a departure from the previously studied ranids. In others (e.g., *D. auratus*), males are territorial, but females exhibit aggressive, "sex-role reversed" behaviour and

compete for access to males. Summers argued convincingly that in these species true sex-role reversal (in terms of parental investment) does not occur. Rather, females reduce the cost of polygyny by preventing additional females from mating with the male in possession of their own clutch. Summers (1990) documented that females suffer a reduction in offspring output if their mates are highly polygynous.

These studies of Neotropical anurans accent the paucity of information available on amphibian taxa lacking an aquatic egg and larval stage (e.g., terrestrial nesting). The reproductive behaviour typical of most temperate anurans studied to date is not necessarily the most widespread; Crump (1974) found that only 46% of 81 species of anurans from Santa Cecilia, Ecuador, deposit their eggs directly in water.

6. Polyandry

Multiple mating by females within a season, as observed in anurans such as *Afraxalus* (Backwell and Passmore 1990), *Dendrobates* (Summers 1992a,b), and *Hyla* (Murphy 1992), reveals that although the behaviour of males in these taxa is consistent with a polygynous mating system (as in Tables 4–6), strictly speaking, females exhibit polyandry. This aspect of mating system complexity has been recognized by many workers previously; unfortunately, a straightforward, readily used classification system allowing the incorporation of this diversity has yet to be developed. Although cumbersome, an alternative classification scheme would categorize the sexes separately to accommodate such variation (Thornhill and Alcock 1983).

Backwell and Passmore (1990) suggested that in the leaf-folding frog, *Afraxalus delicatus*, polyandry on the part of females may be adaptive if multiple nests increase overall reproductive output. However, little is known about the behaviour of females (e.g., sex-role reversal) in this anuran. Fukuyama (1991) documented that females of another terrestrially nesting anuran, *Rhacophorus schlegelli*, are polyandrous because additional males enter the nest burrows of ovipositing pairs and attempt to fertilize some of the eggs. The enlarged testes of rhacophorid frogs of Japan is consistent with the notion that male-male competition in the context of "sneak" fertilizations, rather than female mate choice, determines polyandry in these anurans (Kusana *et al.* 1991).

The mating system of some *Dendrobates* has been suggested as an example of polyandry, akin to the systems exhibited by some shorebirds (see review in Davies 1991). The work by Summers (1992a, b) discussed above indicates that females probably compete and limit the polygyny of their mates, rather than exhibit true sex-role reversal (see also Verrell and Brown 1993). Competitive behaviour among females in polygynous mating systems has received relatively little attention, although it is known to occur among birds and mammals (see reviews in Rubenstein and Wrangham 1986; Davies 1991).

Given the extensive parental care provided by males in a variety of amphibian taxa (Crump 1995), some forms might exhibit true sex-role reversal, i.e., greater parental investment in offspring by males than females, and a correspondingly reduced rate of reproduction of males relative to females. However, at present it appears that no amphibians exhibit a polyandrous mating system in which female behaviour is fundamentally similar to that of polygynous males.

7. Monogamy

In some anurans males may clasp females for extended periods prior to oviposition (see reviews in Wells 1977a and Crump 1988). Prolonged amplexus can be viewed as a form of mate-guarding monogamy in forms with highly male-biased OSRs and little opportunity for multiple mating by males. In *Ateolopus varius* males may enter into amplexus with females 32 days prior to egg-laying (Crump 1988). However, in some taxa with temporally constrained breeding periods, such as the explosively breeding spadefoot toads (*Scaphiopus* and *Spea*) and true toads (*Bufo*) of the Sonoran Desert, males may appear monogamous if only a single breeding episode is evaluated (Sullivan 1989a). If additional breeding opportunities occur within a season, males may return repeatedly, while females appear limited to the production

of a single clutch each year. Hence, over the entire breeding season males have the opportunity to mate polygynously. In the absence of temporal constraints it is likely that most monogamous anurans would tend toward some form of polygyny.

D. Urodelan Mating Systems

If understanding of mate choice in urodeles is limited, then the same must be said for the information currently available on the structure of urodele mating systems. Data are largely derived from laboratory studies, and based on inference as much as on direct observation.

1. Male-Male Competition

Competition among males apparently is intense in many urodeles species, and is undoubtedly an important determinant of mating system structure. Behavioural tactics used in competition range from simultaneous courtship of the same individual female by multiple males to overt aggression with the possibility of physical injury (reviewed by Verrell 1989a).

One very common form of intermale competition in ambystomatids, plethodontids and salamandrids is sexual interference, in which a male intrudes on a courting pair during the later stages of courtship and attempts to inseminate the female himself (Arnold 1976; Verrell 1983b, 1984a, 1988b, 1989a). In effect, sexually interfering males "parasitize" the efforts of others in rendering females sexually responsive, and are somewhat similar to the satellite males observed in many anuran mating systems. In many urodelan species sexually interfering males mimic behaviour normally shown by females toward courting males, perhaps escaping detection in this way. However, in the laboratory, the probability of a male securing an insemination is usually higher when he courts than when he interferes. Sexual interference thus appears to be what Dunbar (1982) has termed a "side-payment" strategy. Males primarily pursue the high-gain strategy of courtship, but will accept lower gains from interference in ongoing courtships as and when opportunities arise (gain is measured in terms of probability of insemination).

The extent to which interactions among males may thwart the effective expression of mating preferences in natural populations awaits detailed study. However, field observations have revealed that the majority of initiated courtship encounters fail to result in insemination for the newts *Triturus vulgaris* (Verrell and McCabe 1988) *T. cristatus* (Hedlund 1990b; Zuiderwijk 1990) and *Notophthalmus viridescens* (Massey 1988). It seems likely that patterns of mate choice seen in simplistic laboratory "habitats", whether shown by females or males (see Table 2), may be overwhelmed in the complexity of natural populations. These comments lead us to the tentative prediction that mate choice has little direct influence on the structure of mating systems in most contemporary populations of urodeles. This is not to deny that choice may have been important in the earlier evolution of these systems, as discussed above for anurans.

2. Breeding Period Duration

As with anurans (Wells 1977a), the breeding periods of urodeles in the temperate zone can be arranged on a continuum from relatively short, or explosive (usually aquatic-breeding species), to relatively prolonged (usually terrestrially-breeding species). Limited data suggest that there may be little opportunity for mate choice in taxa with breeding periods of short duration, regardless of the intensity of competition among males. For example, the total duration of all breeding activities in *Ambystoma maculatum* may be as short as one month (Sexton *et al.* 1986). Males arrive at breeding sites ahead of females, and each deposits a large number of spermatophores on the substrate. Males will even deposit spermatophores on top of others. Known as spermatophore covering, this appears to be a competitive tactic, for only the uppermost sperm masses of multiple spermatophores are available to females (Arnold 1976). Courtship interactions are virtually nonexistent, being limited to brief episodes of nudging. It seems likely that female *A. maculatum* have few, if any, opportunities for direct mate assessment. They simply move through the field of spermatophores, probably becoming inseminated almost at random with respect to male phenotypic characters. A male's mating success might be determined largely by his relative output of spermatophores.

At the other extreme are the relatively lengthy courtships that typify plethodontid salamanders with relatively prolonged mating seasons. Arnold (1977) showed that, as a rule, investment of effort in courtship (measured as time) is greater for species with prolonged seasons, and that the probability of a courtship ending in successful mating increases with effort.

Opportunities for female urodeles to sample multiple males and choose a partner are probably greatest for species exhibiting more prolonged breeding periods. A methodological caveat concerning the definition of breeding period must be introduced at this point. If mating activity does not occur throughout the total breeding period of a population, then the time available during which potential mates can be sampled may be much shorter than otherwise assumed. For example, populations of the newt *Triturus vulgaris* remain at the aquatic breeding site from as early as February to as late as November (Verrell and Halliday 1985a). However, mating activity largely is restricted to the months of April and May, with the rest of the time spent in egg-laying and feeding (Verrell 1984b, 1985d; Pecio 1992).

3. OSR and Polygyny

In general, adult sex ratios are skewed toward an excess of males for urodelan species that migrate to water to breed, at least partly because males often attain sexual maturity earlier than females (Halliday and Verrell 1984). As a rule, males arrive before and depart after females, and so operational sex ratios (OSR's) likely are also male-biased (Verrell 1989a). As proposed by Emlen and Oring (1977), the OSR of a population is an important determinant of the extent to which males may mate polygynously, and so it approximates the intensity of sexual selection. The most precise estimate of OSR for a urodele is that of Douglas (1979) for *Ambystoma jeffersonianum*, in which daily OSR's varied between 2.7 and 10.1 males per female. Had he observed behavioural interactions, it is likely Douglas would have noted the most intense wrestling among males for females and spermatophore covering on those days with the most skewed OSR's (see Kumpf and Yeaton 1932; Uzzell 1969).

Estimating the OSR of a urodelan population requires care since not all of the females present at the breeding site at any one time will be sexually responsive (and thus "fertilizable"). For example, they might be laying eggs, during which time they usually refuse courtship advances from males (e.g., Verrell 1984b), or they might exhibit a temporary refractory period between successive matings (e.g., Verrell 1991c). Set against this is the fact that, outside of the egg-laying period, initially unresponsive females may be rendered sexually responsive by exposure to male courtship. Sexual responsiveness at the start of a courtship encounter may thus be a poor predictor of whether a female might become inseminated by its end (Verrell 1982a). Finally, males experiencing temporary refractory periods after mating should not be included in the pool of presently sexually active males. Clearly, it is not easy to estimate OSR's accurately in natural urodelan populations.

It must be stressed that there is no information on the precise degree of polygyny in any natural population of urodeles. Indeed, it is only for one species, *Desmognathus ochrophaeus*, that there are any data describing variance in mating success among individuals (in this case, from a laboratory experiment in which the confounding effects of male-male competition were removed). Mating success is variable among individuals of both sexes in *D. ochrophaeus* but, as predicted by sexual selection theory, males are more variable than females (Houck *et al.* 1985). However, it is likely, especially in mating systems with intense male-male competition, that the issue may not be "how many mates does individual *x* obtain?" but more "does individual *x* obtain any mates at all?"

With these various cautions and caveats in mind, the putative mating systems of the better-studied urodeles are described below. These largely can be accommodated in the classification of Emlen and Oring (1977) as outlined in Table 3, including scramble-competition, lek, and resource-defense polygyny.

4. Scramble Competition Polygyny

This mating system appears to be characteristic of at least three species of salamandrids. It is typified by males actively searching for females and interacting with other males across wide areas of the breeding site. It must be stressed that, although males in these species clearly "scramble" for females, there are no field data available to determine actual levels of polygyny.

In natural populations of the red-spotted newt, *Notophthalmus viridescens*, males actively search for mates, perhaps using chemical cues to locate females (Dawley 1984; Verrell 1982b), and then engage them in amplexus courtship. Unpaired males attempt to court females already engaged in amplexus, and will sexually interfere with pairs during sperm transfer by mimicking female behaviour. The mating success of courting and interfering males is approximately equal (Massey 1988), suggesting that inter-male competition may thwart the effective expression of any mate preferences by males or females.

Observations of red-spotted newts in the laboratory indicate that a male will perform a brief lateral display rather than engage a female in amplexus courtship if initially she is sexually responsive (Verrell 1982a). However, lateral display only occurs in the absence of other males. Females are engaged in amplexus regardless of initial responsiveness if potential rivals are present, suggesting that, in this social context, amplexus represents a form of mate-guarding (Verrell 1983b). This response to a male-biased OSR may explain why lateral display was not observed in the natural population studied by Massey (1988), where inter-male interactions were frequent. In addition, laboratory observations indicate that unpaired males attempt to displace males engaged in amplexus, although they are seldom successful (Verrell 1983b, 1986a). Surprisingly, wrestling between paired and unpaired males was not observed by Massey (1988).

Active searching and pursuit of females by males also is apparent in natural populations of the smooth newt, *Triturus vulgaris* (Verrell and McCabe 1988). Males do not amplex females in this species, and interruption of ongoing courtship encounters by intruding males is very frequent. Intruders mimic female behaviour (Verrell 1984a). In the laboratory, females often flee from groups of males (Verrell 1984c), perhaps because sexual interference precludes effective expression of mate preferences.

Oviposition is quite sudden and synchronous in populations of smooth newts, and females laying eggs are at least temporarily unresponsive to courting males (Verrell and Halliday 1985a; Verrell *et al.* 1986). Verrell and McCabe (1988) showed that sexual interference is more frequent during the egg-laying period than before, and assumed that this reflected a sudden bias of the operational sex ratio toward an excess of males.

Finally, preliminary observations suggest that scramble competition polygyny may be the mating system of the rough-skinned newt, *Taricha granulosa*. Courtship in this species involves physical monopolization (amplexus) of the female by the male (Propper 1991). Short-term observation of a natural population revealed that males in amplexus are larger than unpaired males, and that the latter attempted to displace amplexant males through wrestling (Janzen and Brodie 1989).

5. Lek Polygyny

As discussed earlier, a lek is characterized by the aggregation of displaying males who contribute nothing but sperm to females that visit the lek to choose mates. The mating systems of several European newts of the genus *Triturus* seem to fit this description best although, as before, the occurrence of polygyny has yet to be documented in the field.

Male crested newts, *Triturus cristatus*, typically arrive at the breeding site before females (Verrell and Halliday 1985b). They then gather in clusters, each male defending a small patch of clear substrate with displays that resemble those given to females during courtship (Zuiderwijk and Sparreboom 1986; Hedlund and Robertson 1989). Interference in ongoing courtship encounters by intruding males is frequent, and invariably prevents successful insemination by courting males (Hedlund 1990b; Zuiderwijk 1990). Sexual interference may thwart the effective expression of mate preferences.

Similar clustering behaviour of displaying males has been observed in the marbled newt, *T. marmoratus*, and the banded newt, *T. vittatus*, and their mating systems might be characterized as leks (or lek-like). However, they differ from *T. cristatus* in an important respect; males defend their display sites from one another with aggressive behaviour. This includes biting and the infliction of physical injury, which may result in death in *T. vittatus* (Zuiderwijk and Sparreboom 1986; Raxworthy 1989; Zuiderwijk 1990).

A lek may also be the closest description of the mating systems of two plethodontid salamanders. The first is the mountain dusky salamander, *Desmognathus ochrophaeus*. Houck (unpublished data) studied a population residing on a rock-face, in which individual males maintained small "ranges" that were defended against same-sex intruders with aggressive behaviour. These ranges contained no obvious resources required by females and appeared to be temporarily fluid, in that males shifted them at intervals.

With this field information in mind, certain aspects of the reproductive behaviour of *D. ochrophaeus* in the laboratory may be interpretable. First, inter-male aggression is well-developed, including a threat display (Verrell and Donovan 1991), and is used by large males to prevent smaller males from gaining access to females (Houck 1988). Second, repeated encounters between familiar individuals result in a decreased probability of mating, although it is unclear which sex is responsible for this effect (Donovan and Verrell 1991). Such encounters may be quite frequent in natural populations, given the temporary site-tenacity of males.

The second species of plethodontid that may exhibit a lek-like system is the western red-backed salamander, *Plethodon vehiculum*. Individuals of both sexes show some site-tenacity in natural populations, although it is doubtful that home ranges contain important resources such as prey (Ovaska 1988). Females show little aggressive behaviour, but males engage one another in agonistic contests, especially during the breeding season (Ovaska 1987).

6. Resource Defense Polygyny

True territoriality, in which a resource crucial to survival and reproduction is defended, appears to be more-or-less limited to species in the family Plethodontidae (see review by Mathis *et al.* 1995). In general, plethodontid territoriality involves the defense of suitable cover objects and associated food supplies, and is shown by both sexes throughout the year. Whether the defense of resources of value to females and/or their offspring might influence male mating success is unclear, although a plausible, supportive scenario can be proposed for the red-back salamander, *Plethodon cinereus*, by integrating both laboratory and field studies.

Much is known about the behavioural ecology of territoriality in this species, as reviewed by Mathis *et al.* (1995); in the present chapter the focus is on its potential for influencing male mating success. Both sexes defend permanent territories containing cover objects and food supplies. Those of males seldom overlap, although female territories may overlap those of several males (Mathis 1991b). Site tenacity is strong, both within and between seasons (Mathis 1989; Gergits and Jaeger 1990a). Large cover objects are defended preferentially over smaller ones, and larger objects tend to be defended by larger individuals (Mathis 1990). In addition, males defending territories near females tend to be larger than solitary males (Mathis 1991a). That this might be due to female preference is suggested by laboratory studies showing that females spend more time investigating areas occupied by large males (Mathis 1991a). In addition, females are most interested in fecal pellets produced by males feeding on superior prey items (Walls *et al.* 1989; Jaeger and Wise 1991).

From this information, it appears that all of the elements are present for female *P. cinereus* to choose larger males with superior feeding territories as mates, although expression of preferences could be thwarted by interference from other males during courtship (Gergits and Jaeger 1990b). Female choice has yet to be demonstrated but, assuming it occurs, one may ask how females might benefit. They may obtain some genetic benefit for their offspring, if male ability to procure and defend a superior territory has some heritable component. Or, they may gain through immediate access to a superior food resource if their presence is tolerated. Indeed, males are more likely to tolerate females than other males in their territories, including females that are non-gravid and thus offering no immediate mating opportunities (Thomas *et al.* 1989). Female reproduction is biennial in *P. cinereus*, and it is interesting to speculate that males may tolerate non-gravid females in the expectation of future mating opportunities.

2. Breeding Sex Ratio (BSR) and Sexual Selection Intensity

Arnold and Duvall (1994) suggested that the breeding sex ratio (BSR), defined as the ratio of number of breeding males to number of breeding females (i.e., actual parents), rather than OSR, is a more accurate indicator of selection intensity and mating system structure. Using a selection theory and encounter rate approach, they found that the sex with less parental investment experiences stronger sexual selection, formally validating Trivers (1972). When males have lower investment in offspring relative to females, sexual selection increases with an increasingly male-biased BSR. In amphibians, at least those with external fertilization and easily observed oviposition, BSR potentially is estimated easily. In fact, in many anuran studies OSR is synonymous with BSR since females are often only present for a single night; hence, all females and males counted as part of the OSR breed, and therefore represent the BSR as well. If BSR is indeed a reasonable indicator of sexual selection, then this may explain why an assessment of OSR in relation to ecological variation has been fruitful in analyses of some anuran mating systems (Woodward 1984b; Sullivan 1986; Tejedo 1988).

Arnold and Duvall (1994) proposed that mating systems be recognized at two levels, first in a broad sense according to the strength of selection acting on each sex in the context of mating behaviour, and second, in a narrow sense according to local predictors of the extent of polygyny. When males experience a stronger selection gradient (i.e., stronger positive relationship between fecundity and number of matings), polygyny is expected; conversely, when females experience a stronger selection gradient, polyandry is expected. Monogamy results if neither males nor females experience increased fitness with increased mating success, and polygamy results if both sexes benefit by multiple mating (Fig. 6). Knowledge of the BSR is one way to estimate the intensity of sexual selection, and facilitate categorization of mating systems.

Presumably, in most anurans and urodeles, males invest less in offspring relative to females and thus experience stronger sexual selection; polygyny therefore is favoured. The precise form (i.e., lek versus scramble competition) of polygyny may be largely dependent on ecological factors determining the temporal distribution of mates, as suggested by Emlen and Oring (1977). Assuming that the ancestral condition centered on the need for an aquatic site for oviposition, and included modest, if any, parental investment by males, a transition from scramble competition to a lek or a resource defence polygyny system requires an increase in the duration of the breeding period, and variation in traits of males or oviposition sites used by females, respectively. In addition, females cannot be under strong selection for synchronous egg-laying, from either abiotic (e.g., restricted availability of water) or biotic (e.g., predation) factors. Selection for reproductive synchrony on the part of females reduces the opportunity for mate monopolization and presumably yields an explosive breeding period with a scramble competition mating system.

F. Overview: Mating System Structure

Analyses of amphibian mating systems have provided valuable data relevant to a general assessment of predicted relationships between ecological factors, sexual selection, and social behaviour. Most observations on North Temperate amphibians are largely consistent with expectations derived from the verbal model of Emlen and Oring (1977) regarding relationships between the ecology of reproduction and processes of sexual selection. For example, as noted by Wells (1977a), temporal constraints clearly limit maximal levels of polygyny in a number of anurans (Tables 4–6). However, additional study is necessary before one can assess the influence of specific ecological factors on mating system structure, such as the significance of breeding synchrony on the part of females in a scramble competition versus a lek polygyny system. As argued by Arnold and Duvall (1994), analyses of sexual selection and mating system structure would be facilitated by knowledge of breeding sex ratios.

The present survey retains a traditional classification scheme focusing on levels of polygyny among males, in part to facilitate comparisons with prior work. However, it is important to recognize that females may exhibit considerable variation in behaviour (e.g., mate defence in *Dendrobates*) which is obscured by this approach. In addition, the requirement of standing water for breeding for many amphibians sets them apart from other vertebrates such as birds and mammals, and may reduce the appropriateness of a parallel classification

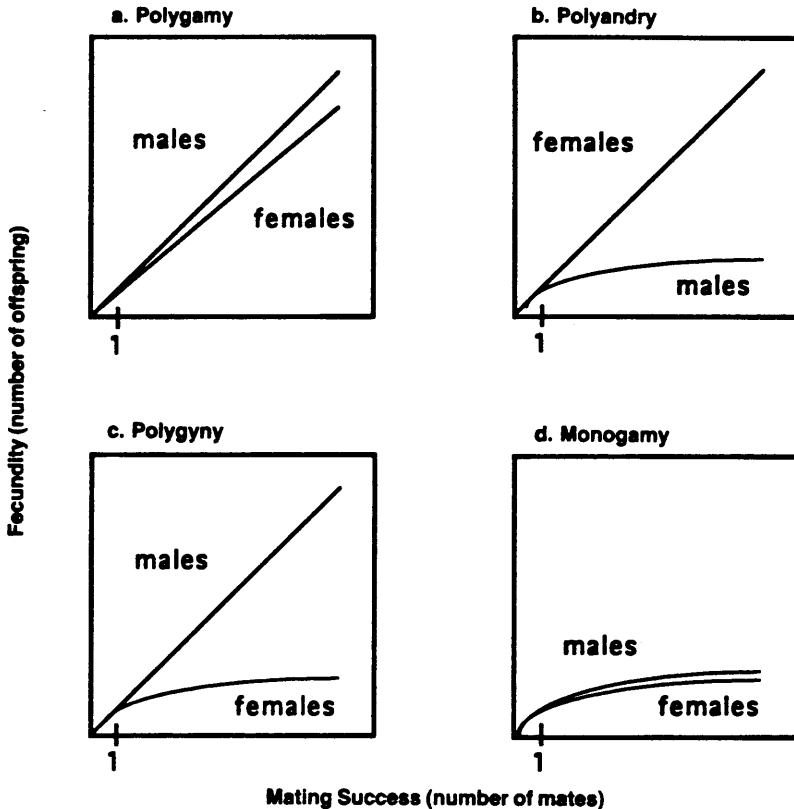


Fig. 6. Predicted relationships between fecundity and mating success for the two sexes of frogs (modified from Arnold and Duvall 1994). When fecundity increases with mating success for both sexes, polygamy is favoured; when fecundity increases with mating success for one or the other sex alone, polygyny or polyandry is favoured. If neither sex benefits from multiple mating, monogamy is favoured.

scheme. It is recognized that a simplified scheme does a great injustice to the complexity of the natural world. If future workers are stimulated to develop a classification system that adequately acknowledges and incorporates this complexity, the present effort will be rewarded.

VI. FUTURE DIRECTIONS

Most studies of female choice and mating system structure have been limited to single, or relatively few, breeding periods. With respect to evolutionary considerations, a need exists for studies that address mating system structure over longer periods of time. As stressed by many authors (e.g., Howard 1978a; Howard and Kluge 1985; Ryan 1985; Halliday 1990), short-term measures of individual reproductive success (RS) may not accurately reflect RS over an individual's total reproductive lifetime. It is lifetime RS that is the appropriate currency when considering evolutionary responses to mate choice and intrasexual competition. These data are also required for a complete assessment of polygyny (and thus the intensity of sexual selection) across mating systems. Long-term studies are also necessary if one is to determine the role that stochastic factors may play in determining individual differences in reproductive success. It is perhaps only for *Hyla rosenbergi*, a Neotropical hyliid that is apparently semelparous, that such information on life-time reproductive success is presently available (Kluge 1981).

In addition, multiple studies of the same species are needed. This apparent replication of research effort may at first seem inappropriate; however, studies of mating system variation among conspecific populations may be as valuable as those of different species in revealing ecological determinants of sexual selection and mating system structure. While it is true that species tend to differ more than conspecific populations, so many aspects of ecology, morphology, physiology and behaviour differ among species that diagnosis of crucial selective pressures may be difficult (Arnold 1992). Such confounding factors, which also may include historical effects due to phylogenetic relatedness, are less likely to affect comparisons of conspecific populations (e.g., Sullivan 1989b). Where interspecific comparisons are made, it is important that an explicit consideration of underlying phylogenetic relationships among species be undertaken. This is necessary for disentangling adaptation from historical constraint, for determining the direction of evolution and relationships among multiple traits, and in order to facilitate statistical analyses of independent evolutionary events (e.g., Sullivan 1989a; for a more detailed discussion see Brooks and McLennan 1992).

Studies of intraspecific variation also will be critical in advancing an understanding of proximate mechanisms of mate choice. When placed in a phylogenetic perspective such investigations can contribute to an evaluation of the sensory exploitation hypothesis, as well as other hypotheses accounting for the origin and elaboration of female mating preferences and sexually selected traits of males. Analysis of intrapopulation variation also will be vital to an assessment of the relationship between processes of female mate choice and the evolution of mate-recognition systems.

On a broader taxonomic level, if a plea can be made for further studies of anurans, then one can only beg for similar studies of urodeles. Little is known about the behavioural ecology of mating in families other than the Plethodontidae, Ambystomidae and Salamandridae. Even less is known about one whole amphibian order, the Apoda! For all species, laboratory studies of patterns of mate choice and inter-male competition obviously are necessary, and will be instrumental in guiding work on natural populations. Data should be collected from natural populations, preferably ones in which animals can be individually recognized and observed throughout at least a single breeding episode. A little ingenuity may be required for studying the least accessible species. For example, how can one determine patterns of mating if the act of mating cannot be directly observed? And even if one can observe matings, how can patterns of reproductive success be inferred reliably in the face of sperm competition?

The technique of DNA fingerprinting may be an extremely useful tool in this regard, for it allows access to the enormous variation of the nuclear genome that exists among individuals (Burke 1989). Studies of birds and mammals have demonstrated that this technique has enormous potential for assigning parentage, and thus revealing mating system structure, in natural populations. Estimation of operational and breeding sex ratios, and their relationships to the intensity of sexual selection, will be feasible with this methodology (Arnold and Duvall 1994; Duvall *et al.* 1993). Such efforts will advance an understanding of sexual selection in amphibians in particular, and elucidate more general aspects of sexual selection theory as well.

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