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Mating Vocalizations of Female Frogs: Control and Evolutionary Mechanisms

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Key Words

Androgen · Brain · Evolution · Female vocalization · Frog · Larynx · Mating · Neural pathway · Vasotocin

Abstract

Vocalization behaviors of anuran amphibians are universally sexually dimorphic. Usually, only male frogs give an advertisement call, while female frog calls are limited to a soft and simple release call which is specifically suppressed at mating. In a very few species, however, female frogs also give mating vocalizations. We examined possible mechanisms for control of this rare heterotypical behavior. At the peripheral level, most differences in temporal and spectral characteristics between female mating calls and the calls of conspecific males related directly to sexual dimorphisms in laryngeal and oblique muscle morphology. At the neural and hormonal level, we first developed an integrated model for control of vocalizations, based primarily on male frog data. When this model is applied to females, female mating vocalizations were most similar to male advertisement calls, rather than being modified release calls. Females may have conscripted preexisting androgen-sensitive neural pathways typically used only by males but present in both sexes. Female mating calls have been heard only during courtship and amplexus. Androgen levels in females at this time are significantly higher than even those levels in males. Because this situation is common in frogs, female mating vocalizations likely evolved independently multiple times. Character optimization suggests that mate location is the most common biological role for female mate calling, but the particular aspects of reproductive biology vary widely across species.

Introduction

It is increasingly clear that sexual differences in the behavior of vertebrates result from a diversity of physiological processes and evolutionary pressures. This complexity has been particularly highlighted by studies of extreme or unusual cases of sexual dimorphism, and these studies have been among the most useful in providing insights into the mechanisms underlying these differences. The zebra finch, for example, with its striking sexual dimorphism in song, offered an excellent model system for classic work on steroid action in the brain [e.g., Arnold, 1997]. The unusual case of parthenogenetic lizards likewise offers a fruitful system for study of heterotypical behaviors [e.g., Crews, 1988; Crews et al., 1990]. In anuran amphibians there is a general sexual difference in vocal behavior that is robust and consistent across thousands of species – males give a conspicuous advertisement call and females do not [Duellman and Trueb, 1986]. On the other hand, the females of a handful of frog species do vocalize around the time of mating (see below). These vocal communications are patterned and clearly provide information to the receiver [e.g., Tobias et al., 1998a].

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The rare cases of mating vocalizations in female frogs represent an extreme example of ‘heterotypical’ behavior and, as such, may provide some important new insights into the processes and patterns of sexual dimorphism. In this paper, our first goal is to use knowledge of the control of vocalizations in male frogs to predict how calling in females may be controlled at neural, hormonal and laryngeal levels. Second, we will examine aspects of the mating systems of those species where females vocalize, in order to test for correlations between specific reproductive behaviors and the evolution of mating vocalizations in females.

Background

Mating vocalizations by female frogs during the breeding season have been heard in several contexts. Most commonly, females do not initiate calling but rather respond vocally to the advertisement calls of males [Dixon, 1957; Given, 1987; Marquez and Verrell, 1991; D. Roy et al., 1995; Bush, 1997; Orlov, 1997; Schlaepfer and Figeroa-Sandi, 1998; Tobias et al., 1998a]. These calls have thus been termed ‘reciprocation’ calls or reciprocal calls [Duellman and Trueb, 1986; D. Roy et al., 1995]. There are, however, a few instances of females initiating calling [Frazer, 1983; Given, 1993; Bush, 1997] or calling in the complete absence of males [Boistel and Sueur, 1997]. A female call that serves to solicit amplexus clearly occurs in one species, *Rana blythii*, where the male lacks an advertisement call [Emerson, 1992]. The female calls described above are noteworthy in that they occur without any physical contact with the male. In addition, patterned mating calls by females may also be given during amplexus [Marquez and Verrell, 1991; Linzana et al., 1994]. Finally, females in a few species give territorial calls [Capranica, 1968; Wells, 1980; Stewart and Rand, 1991]. These calls are loosely associated with mating in that they generally occur during the breeding season, but they are not as intimately associated with amplexus as the calls previously described for females.

Male frogs characteristically produce a species-specific ‘advertisement’ call that attracts females for breeding [Duellman and Trueb, 1986]. This advertisement call, often loud and complex, may also function in territory maintenance or attraction of other males to a breeding chorus as well as in interspecific recognition [Wells, 1977]. Generally, females do not give advertisement calls [Duellman and Trueb, 1986], but frogs of both sexes do produce ‘release’ calls. In contrast to other vocalizations, release calls only occur upon tactile stimulation [Bogert, 1960; Capranica, 1968; Kelley, 1982; Boyd, 1992]. Additionally, the social context in which release calls are given is gender-specific. Males give a release call when they are mistakenly clasped by other males. Non-gravid and sexually unreceptive females give release calls when clasped by males, but receptive females are silent.

Mating vocalizations in female frogs differ significantly from release calls in social context, timing, and call characteristics. Mating vocalizations in female frogs are unusual in that females call at a time that is specifically characterized by female silence in most species [Wells, 1977; Duellman and Trueb, 1986]. In this and other regards (see below), female mating calls are more similar to male advertisement calls, yet male advertisement calling is an androgen-mediated behavior of anurans [Kelley, 1986]. Display of mating vocalizations in female frogs thus raises interesting questions about how and why these females vocalize. Are the female vocalizations modified release calls, or are they a type of advertisement call? Are female mating vocalizations androgen-dependent? Are female vocalizations correlated with specific breeding systems and reproductive behaviors? Below, we review what is known about the control of vocalization in anurans and also the reproductive biology of species where female vocalization occurs.

Peripheral Morphology of Vocalization

Vocalizations by frogs are produced as air leaves the lungs and passes (back and forth) through the glottis [Schmidt, 1966a; Martin and Gans, 1972; Gans, 1973]. Several peripheral structures make critical contributions to this process [Schneider, 1988]. External and internal oblique muscles of the trunk pump air out of the lungs [Pough et al., 1992]. Laryngeal muscles open and close the glottis and move the vocal cords in and out of the air stream [McAlister, 1959; Martin and Gans, 1972; Schmidt, 1972a, b; Gans, 1973; Wilczynski et al., 1993]. Other non-muscular components may also affect the call [e.g., Drewry et al., 1982; Schneider, 1988]. Sexual dimorphisms are present in all these structures. Males have oblique and laryngeal muscles and laryngeal structures that are more than twice the size as those of females of the same body weight [Trewavas, 1933; Taigen et al., 1985; McClelland and Wilczynski, 1989; Kelley, 1996; McClelland et al., 1997]. Besides being larger, the oblique and laryngeal muscles of males are composed of different fiber types [e.g., Marsh and Taigen, 1987] and myosin heavy chain isoforms [Catz et al., 1992]. As a result, male oblique and laryngeal muscles have higher contraction velocities and are more resistant to fatigue [Marsh and Taigen, 1987; Kelley and Gorlick, 1990]. In one species, *Xenopus laevis*, organizational effects of hormones early in development generate sexually dimorphic laryngeal morphology [Kelley, 1996]. Larynx morphology in *X. laevis* is thus dependent on sexually-dimorphic hormone profiles. This includes not only the effects of androgens but also the influence of estrogens on the neuromuscular junction of the larynx [Tobias and Kelley, 1995; Tobias et al., 1998b].

The major temporal and spectral properties of the advertisement calls of male frogs are directly related to two factors. The first factor is the morphological and physiological characteristics of the oblique and laryngeal muscles. Pulse repetition rate is determined by the contraction velocity of the laryngeal or oblique muscles [Kelley and Gorlick, 1990 and references therein; Catz et al., 1992; Das Munshi and Marsh, 1996]. The duration of a call is partially dependent on the size of the hyolaryngeal muscle [Weber, 1976, 1977]. Total calling time and fatigue both vary depending on the muscle fiber type [Taigen et al., 1985; Marsh and Taigen, 1987; Gans and De Gueldre, 1992]. This applies as well to call intensity, which is partly related to force generated by the muscles pumping air out of the lungs and hence to oblique muscle cross-sectional area and fiber type [Gans and DeGueldre, 1992]. The second major factor that influences a call parameter is body size. Advertisement call frequency is inversely related to body mass [e.g., Ryan, 1985; Given, 1987; McClelland et al., 1996] and, partially, to vocal cord mass [Drewry et al., 1982; Wilczynski et al., 1993].

Variation in body size and peripheral morphology will thus alter call characteristics in predictable ways. Sexual differences in the release calls of *R. pipiens* and *X. laevis* are simply a result of such differences [Hannigan and Kelley, 1986; McClelland and Wilczynski, 1989]. Some interspecific and intraspecific differences in advertisement calls of males can also be accounted for by variation in the peripheral morphology [Drewry et al., 1982; Wilczynski et al., 1993; Das Munshi and Marsh, 1996; McClelland et al., 1996, 1998]. Female mating vocalizations should also differ from the conspecific male vocalizations in ways that can be predicted a priori by the sexual dimorphism in the periphery. For species where females are larger than males, the female mating vocalization should have a lower frequency than the male call. Generally, this has been observed [but see Schlaepfer and Figeora-Sandi, 1998], although data are limited [Wells, 1980; Stewart and Rand, 1991; D. Roy et al., 1995; Bush, 1997]. The smaller sizes of the laryngeal and oblique muscles of females suggest that mating vocalizations of females will be less intense and of shorter duration than male vocalizations. This has been documented in most species with female mating vocalizations [Dixon, 1957; Marquez and Verrell, 1991; Given, 1993; D. Roy et al., 1995; Boistel and Sueur, 1997; Bush, 1997; Orlov, 1997; Tobias et al., 1998a].

Neural Pathways Involved in Vocalizations

The neural and hormonal mechanisms controlling anuran vocalizations are much less understood than those of some other vertebrates, such as songbirds. Additionally, no current, comprehensive review is available that integrates information from the independent lines of investigation on several disparate species. Below we provide such an overview by developing a model for control of vocalization in frogs that accommodates both male and female mating vocalizations (fig. 1). The first component of the model is the putative neural pathways. Tract-tracing studies in *X. laevis* show a small set of interconnected areas proposed to function in the control of vocalizations (fig. 1) [Wetzel et al., 1985]. As described above, in most anurans, calling is ultimately produced by contraction of the laryngeal muscles [Martin and Gans, 1972; Weber, 1977; Tobias and Kelley, 1987] and the oblique muscles of the body wall [deJongh and Gans, 1969; Gans, 1973]. Only in Pipidae do oblique muscles not appear to be involved [Rabb, 1960; Yager, 1992]. These muscles are controlled by central motor neurons. Neurons that control the laryngeal muscles are located in the brain stem in the motor nucleus IX–X (n. IX–X), and axons from these cells travel to laryngeal muscles in nerve IX–X [Stuesse et al., 1984; Simpson et al., 1986]. Spinal motor neurons control the oblique muscles [Butler and Hodos, 1996]. Cells in the n. IX–X reveive input from three primary sources: the pretrigeminal nucleus (PTN), several rhombencephalic reticular nuclei, and the contralateral motor nucleus IX–X [Wetzel et al., 1985; Walkowiak, 1992]. Retrograde tract-tracing shows that the PTN, in turn, receives input primarily from the region of the ventral striatum and amygdala, the thalamus, and the preoptic area (POA). The PTN also receives considerable reciprocal input from the contralateral PTN and more downstream areas such as the motor nucleus IX–X and reticular nuclei. These central nervous system areas are thus candidate regions for control of frog vocalizations. This pathway is present in both male and female brains, although there are some anatomical sexual differences [see below; Wetzel et al., 1985].

The contribution of some of these areas to call generation has been determined. Control of laryngeal and oblique muscles by central motor nuclei is unambiguous [Schmidt, 1996a, 1974a; Hannigan and Kelley, 1981]. Lesion and

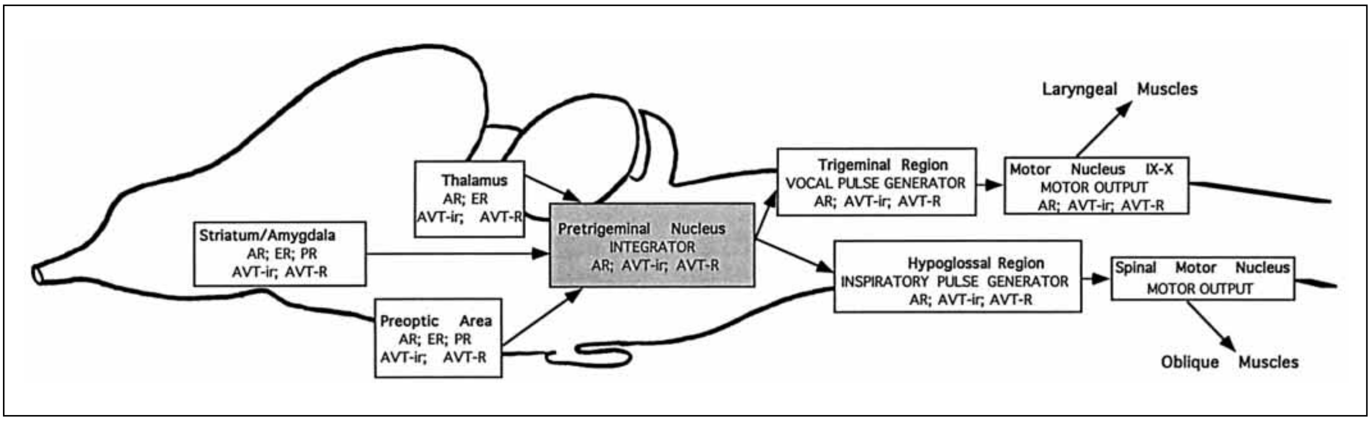

Fig. 1. Diagrammatic representation of the neural vocalization pathway and hormonal targets for frogs. Abbreviations: AR = androgen receptor; ER = estrogen receptor; PR = progesterone receptor; AVT-ir = arginine vasotocin immunoreactive cells and/or fibers; AVT-R = arginine vasotocin receptors. See text for references.

electrical stimulation studies in ranid frogs, however, show that the generator of the vocal and respiratory pulse patterns is located outside the motor nuclei [Schmidt, 1966a, 1973]. In most anurans, calls consist of alternations between a vocal phase and an inspiratory phase, the latter refilling the lungs with air [Gans, 1973]. It is likely that the pulse generators for these two phases are located in two distinct neuroanatomical regions, because these phases can be independently altered by lesions and electrical stimulation [Schmidt, 1974a, 1976, 1992]. Both anatomical and electrophysiological evidence suggests that the pulse generators are located in the rhombencephalic reticular formation, with the vocal pulse generator in the trigeminal region and the inspiratory pulse generator in the hypoglossal region [Schmidt, 1976, 1992; Wetzel et al., 1985]. Extensive connections between these areas [Wetzel et al., 1985] would allow the necessary coordination of vocal and inspiratory phases.

The pretrigeminal nucleus plays a central role in the generation of calls. The PTN is located slightly anterior and dorsal to the motor nucleus of the trigeminal nerve [Schmidt, 1980, 1982]. Neural activity in this area is correlated with calling movements of the larynx, and electrolytic lesions of the PTN abolish calling [Schmidt, 1974b]. Whether the PTN is independently able to generate the pulses of the vocal phase or whether the vocal pulse generator is just located very near the PTN is not clear [Schmidt, 1974b, 1976, 1992]. Most evidence indicates that the PTN acts as an integrative area for calling [Schmidt, 1976]. Anatomically, the PTN receives input from important sensory and integrative areas such as the striatum, amygdala, thalamus, and POA [Wetzel et al., 1985; Walkowiak, 1992]. Neurons that respond to auditory stimuli have been located in this region also [Schmidt, 1971; Aitken and Capranica, 1984]. Finally, sex steroid-concentrating cells are found in the PTN [Kelley et al., 1975; Kelley, 1980]. Thus, the PTN possesses characteristics that make it a plausible candidate for an integrator of external (e.g., auditory) and internal (e.g., androgen level) stimuli.

Some portions of the vocalization pathway must be shared in generation of all call types. Thus, the participation of the PTN, reticular formation pulse generators and motor nuclei is required for both release calls and mate calls [Schmidt, 1971, 1974a, 1976, 1992]. In the case of release calls, these areas are not only necessary for call generation, they are also sufficient. When the brain is transected just anterior to the PTN (thus removing all input from more anterior areas), release calls can still be elicited [Schmidt, 1966a, 1971]. Such lesions, in fact, appear to remove possible inhibitory control of release calling [Goltz 1865–1868, discussed in Holmes, 1954]. This supports the hypothesis that release calling, evoked by tactile stimulation, is the most basic of vocal patterns. Inhibition of the release call reflex, which normally occurs only in females at oviposition, would thus be an active process requiring input from outside the PTN [Schmidt, 1993].

For advertisement calling, the PTN and vocalization areas more posterior are necessary but not by themselves sufficient. The POA clearly plays a critical role in generation of the advertisement call. Ablation of the POA abolishes advertisement calling but not release calling [Schmidt, 1966a]. Electrical stimulation of the POA will elicit advertisement calling [Schmidt, 1966a, 1984; Knorr, 1976; Wada and Gorbman, 1977]. This distinction between advertisement call and release call circuits is supported by evidence of sexual differences in connections between the POA and the PTN. Tract-tracing studies in *X. laevis* show a clear input of fibers from the POA to the PTN in males [Wetzel et al., 1985]. No connections between the POA and PTN were found in female *X. laevis.* Such connections likely exist, although they are perhaps less robust, because androgen treatment and strong electrical stimulation of the POA can induce advertisement call-like vocalizations from females [Knorr, 1976; Hannigan and Kelley, 1986; Penna et al., 1992].

Neural mechanisms for control of mating vocalizations in female frogs have not been investigated. Vocalization brain areas and steroid-concentrating cells are present in both sexes, however, so it is likely that control mechanisms are similar in males and females [Kelley et al., 1975; Morrell et al., 1975; Kelley, 1981; Wetzel et al., 1985]. Differences in control mechanisms for release calling and advertisement calling make it possible to test whether female mating calls are more similar to release calls or to advertisement calls. For example, if female mating calls are modified release calls, then one would predict that they could be elicited in the absence of forebrain (POA) input. On the other hand, if female mating vocalizations are more similar to a male advertisement calls, then one would predict that the POA would be necessary and that POA stimulation of female frogs would elicit the reciprocation or solicitation call type.

Hormonal Control of Vocalizations

Gonadal steroids are required for the display of advertisement calling in anurans. Castration of males will abolish calling, and vocalization can be restored with androgen treatment [Schmidt, 1966b; Palka and Gorbman, 1973; Kelley and Pfaff, 1976; Wetzel and Kelley, 1983]. In addition, androgen treatment can sometimes induce advertisement-like calls in females [Schmidt, 1983; Hannigan and Kelley, 1986; Penna et al., 1992]. Steroid control of release calling is less clear. In *X. laevis,* ovariectomy increases release calling [Kelley, 1982]. In *R. pipiens,* on the other hand neither ovariectomy nor estrogen or progesterone treatments have any affect on release calling [Diakow et al., 1978]. It is unknown whether androgens influence release calling, but seasonal changes in release call rates in both sexes suggest that release calls may be androgen-sensitive [Boyd, 1992]. Based on what is presently known, one would predict that mating vocalizations of female frogs would be androgen-sensitive if they are more similar to male advertisement calls in their control. At the same time, androgen involvement in the female call does not rule out the possibility that female mating calls are modified release calls.

Gonadal steroids may influence calling directly by acting on vocal pathway neurons. Cells that concentrate the non-aromatizable androgen dihydrotestosterone (DHT) are located in the PTN in *X. laevis* brains [Kelley, 1980]. Such cells presumably possess androgen receptors. Androgen-concentrating cells were not found in the POA of *X. laevis* with autoradiography, but they were observed with androgen receptor immunocytochemistry [Boyd and Ebersole, 1997]. Androgen receptors are also found in the reticular formation, motor nucleus IX–X, some spinal nuclei, the thalamus, the striatum, and the amygdala in various frog species [Kelley et al., 1978; Kelley, 1980; Boyd and Ebersole, 1997]. There is thus the potential for androgen regulation of frog calling at all levels within the vocalization pathway [Kelley, 1980]. Estradiol-concentrating cells found in more anterior brain areas (stritum, POA, and thalamus) send projections to the PTN [Morrell et al., 1975; Kelley et al., 1978; E.J. Roy et al., 1986; DiMeglio et al., 1987]. Progesterone receptors are also found in the striatum and POA [E.J. Roy et al., 1986]. Estrogen and progesterone receptors have thus not yet been reported within the brainstem vocalization areas (from the PTN and more posterior). If these two steroids are responsible for inhibition of release calls in gravid females, such inhibition would likely come from a higher brain area and be superimposed on the PTN. Sexual differences in the distribution of steroid-concentrating cells have not been reported [Kelley et al., 1975; Morrell et al., 1975; Kelley, 1981].

In addition to steroids, vocalizations are also modulated by a variety of neuropeptide hormones. The peptide with the most consistent influence across species is arginine vasotocin (AVT), which stimulates advertisement calling in male frogs [Schmidt and Kemnitz, 1989; Penna et al., 1992; Boyd, 1994a; Marler et al., 1995; Propper and Dixon, 1997; Chu et al., 1998]. On the other hand, AVT inhibits release calling in female frogs [Diakow, 1978; Raimondi and Diakow, 1981; Boyd, 1992]. These data suggest that mating calls in female frogs may be facilitated by AVT if they are conscripted male advertisement calls but inhibited by the peptide if they are modified release calls.

Arginine vasotocin and AVT receptors are found in every brain area implicated in control of frog vocalization (fig. 1) [Boyd and Moore, 1992; Boyd et al., 1992; Boyd, 1994b, 1997]. Different effects of AVT on advertisement and release calling suggest that AVT does not act directly on pulse generator or motor output levels. As described above, these levels in the vocalization pathway are probably the same for both types of calls. Instead, it is likely that there is an interaction of steroids and AVT in higher brain areas, and this results in the different effects of AVT on the two call types. For example, males have higher AVT concentrations than females in the amygdala and PTN of bullfrogs [Boyd and Moore, 1992; Boyd et al., 1992; Boyd, 1994b]. Peptide concentrations in the amygdala are altered by androgen and estrogen, while the PTN is affected only by androgen [Boyd, 1994b]. The AVT receptor populations in these same brain areas are also steroid-sensitive [Boyd, 1997].

How and Why Female Frogs Call

We suggest that in species where females vocalize during mating, the calls may have evolved by co-opting the preexisting advertisement calling pathway which appears to be common to both sexes. One way this could be accomplished is by androgen stimulation of AVT receptors in the PTN. This postulated hormonal control mechanism is consistent with the data from androgen replacement experiments as well as what is known about circulating androgen levels in breeding female frogs. In *X. laevis* and *Hyla cinerea*, females will produce a ‘mating-like’ call when androgen treated. The call characteristics vary from those of a typical male call, but those differences are consistent with predictions based on sexual differences in peripheral morphology. The female mating calls are less intense and of shorter duration [Hannigan and Kelley, 1986; Tobias and Kelley, 1987; Penna et al., 1992]. In amphibians, unlike mammals, both adult males and females have substantial amounts of androgenic and estrogenic hormones [Norris, 1997]. In all anurans that have been examined, females show increasing levels of circulating androgens with follicle development [D’Istria et al., 1974; Licht et al., 1983; Iela et al., 1986; Emerson et al., 1993]. At ovulation and around oviposition, these values are often substantially greater than those reported for breeding males [Licht et al., 1983]. In *R. blythii*, a species with female mating calls, territorial breeding males have an average androgen level of 6 ng/ml, whereas one female with the most mature eggs had an androgen level of 31.4 ng/ml [Emerson, 1992; Emerson et al., 1993].

In the wild, female mating vocalizations have been heard only during that part of the breeding cycle when the females have mature eggs and are involved in courtship and amplexus [e.g., Emerson, 1992; D. Roy et al., 1995]. Furthermore, female frogs only initiate calling (rather than just respond to a male’s call) when they are within hours of oviposition [Emerson, 1992; Boistel and Sueur, 1997; Bush, 1997]. This is the same time frame over which androgen levels are highest in the females [e.g., Iela et al., 1986]. Perhaps the high levels of androgens associated with ovulation and oviposition provide an adequate hormonal stimulus to (potentially) evoke an advertisement call response in females. Thus, for example, AVT may not normally stimulate male-typical advertisement calling in females, because females have significantly fewer AVT receptors in the PTN. Under the influence of higher, ‘ovulation’ levels of androgens, however, AVT receptor concentration in this brain area may increase sufficiently to allow the potential for female mating vocalizations.

The combination of an androgen-sensitive advertisement call pathway in females and a temporally restricted pulse of high androgen levels could be considered an exaptation [sensu Gould and Vrba, 1982] for female mating calls. To the extent that these features occur in all female frogs, the potential for female mating vocalization is ubiquitous. This leads to the predictions that mating calls in females may have evolved a number of times independently and under a diversity of circumstances.

Female mating vocalizations have been reported in four families of frogs, to date [e.g., Dixon, 1957; Given, 1987; Marquez and Verrell, 1991; Tobias et al., 1998a]. Recently, enough examples have been documented to permit testing for general patterns of correlation with other aspects of the reproductive behavior. This kind of analysis is best done where there is an available phylogenetic hypothesis of relationship on which to map characters of interest [Lauder, 1981; Greene, 1986]. Using this approach, called character optimization [Brooks and McLennan, 1991], one can examine whether there is an interspecific pattern to the evolution of female vocalization, or, as predicted above, whether the evolution of each case of mating calls by females is idiosyncratic.

Locating mates, coordinating complex courtship, and providing information on physiological condition have all been suggested as reasons for female mating vocalization [Morris, 1970]. If any of these factors are related to the evolution of female calling in frogs, we would expect to see some shift in these characters at the points in the phylogenies where female vocalization evolves. There are three clades in which female vocalization is well-documented, and phylogenies are available that identify the sister taxa to the focal species: North American ranids [Hillis and Davis, 1986], Southeast Asian fanged frogs and relatives [Emerson and Berrigan, 1993; Emerson and Ward, 1998], and the midwife toads of the genus *Alytes* [Hay et al., 1995]. Figure 2

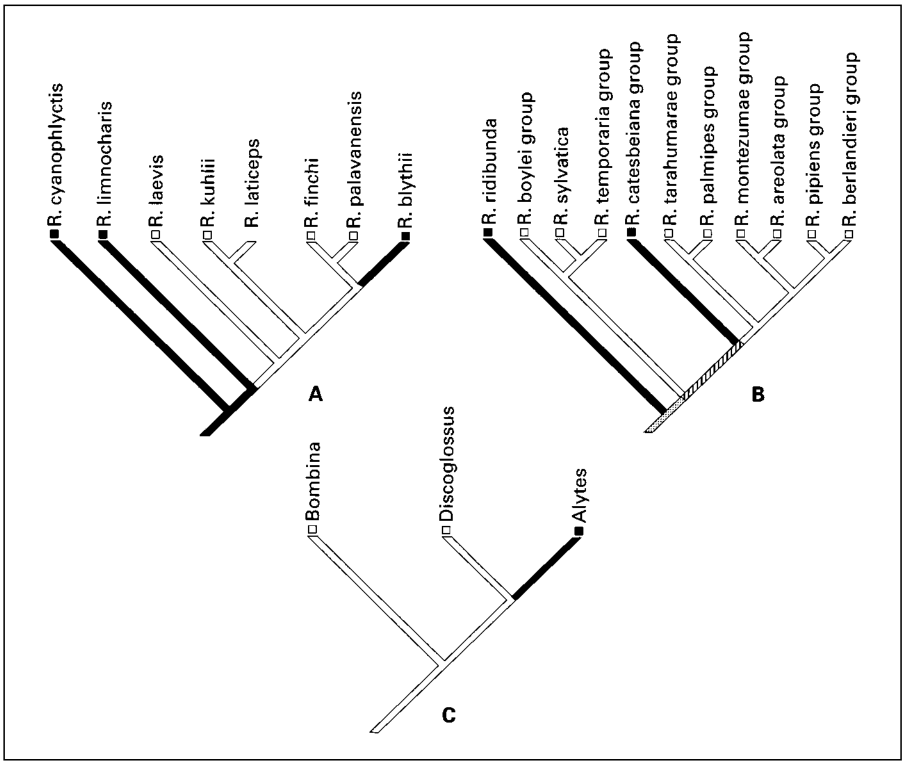

Fig. 2. Evolution of female vocalization in three groups of anuran amphibians: **A** Southeast Asian fanged frogs of the genus *Rana* [after Emerson and Berrigan, 1993; Emerson and Ward, 1998], **B** North American ranids [after Hillis and Davis, 1986] and **C** midwife toads and their relatives [after Hay et al., 1995]. Black lines indicate those species in which female vocalization occurs and white lines show taxa that lack female mating vocalizations. Other shaded lines indicate where the character state is equivocal.

shows the phylogenies of these groups and indicates where female vocalization has evolved.

In the three groups under study, mate location, in the broadest sense, emerges as the most probable biological role for female vocalization (fig. 3). Nonetheless, locating mates encompasses a diversity of scenarios, depending on whether males are territorial (fig. 4) or limited in their ability to use the customary phonotactic response of a gravid female to identify a potential mate. It has been suggested that female mating calls may inform aggressive, territorial males that a receptive female rather than a competing male is entering their territory [Wells, 1977]. Alternatively, female calling may provide a mechanism by which females can distinguish satellite males from territory holders [Given, 1993]. Based on character optimization, both situations are plausible. Male territoriality is common in all three groups (fig. 4) [Capranica, 1968; Heusser, 1968; Howard, 1978; Frazer, 1983; Given, 1987; Emerson and Inger, 1993; Kanamadi et al., 1995; Orlov, 1997; Tsuji, 1998], and satellite males are known to occur in the North American ranids [Capranica, 1968; Howard, 1978; Given, 1987]. Importantly, however, territoriality alone does not account for all the cases of female vocalization. Male midwife toads are not territorial (fig. 4) [Marquez, 1993], even though females vocalize, and, conversely, the males of at least one species of fanged frog, *R. kuhlii*, are territorial but the females do not vocalize (fig. 4).

Another type of mate location involves those situations where female calls function to inform the male of a female's presence and reproductive state. These might include cases where the males cannot see the females [e.g., Tobias et al., 1998a] or where gravid and non-gravid females are syntopic [e.g., Emerson and Inger, 1993]. In midwife toads, the males often call from underground [Marquez and Verrell, 1991], and a male would have no way of knowing whether a receptive female were present unless she provided an auditory signal. In the fanged frog, *R. blythii*, the male is aggressively territorial but does not give an advertisement call [Emerson, 1992]. Both reproductively active and inactive females are found along the stream where the male territories are located [Emerson and Inger, 1993]. Female vocalization in this species may alert the male that the frog entering his territory is both a female and gravid.

Complex courtship, including male parental care, does not appear to be a major correlation of female vocalization. Although the midwife toads and some fanged frogs do have derived reproductive behaviors involving nest building and other types of male parental care, such is not the case for the other species where the females vocalize. Additionally, complex courtship occurs in many taxa where females are

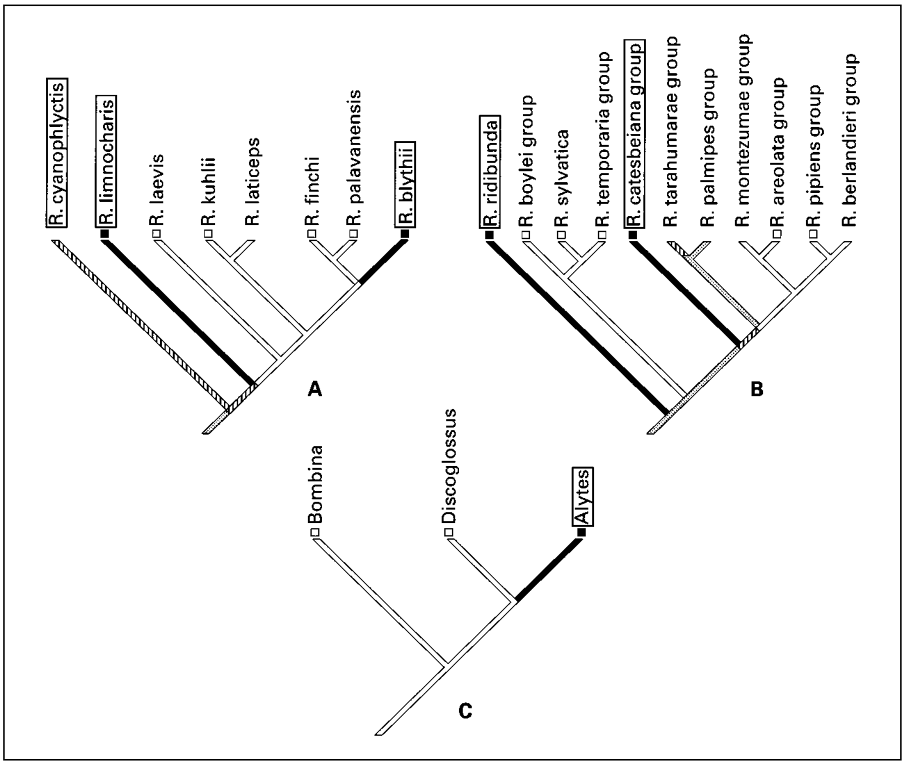

Fig. 3. Distribution of degree of mate location difficulty mapped onto phylogenies where female mating vocalizations have evolved. Boxes have been placed around names of taxa with female mating vocalizations. Black lines indicate species with unusual cases of mate location (see text for further elaboration). Shaded lines indicate character state is equivocal. No small boxes appear next to taxon names when the character state is unknown.

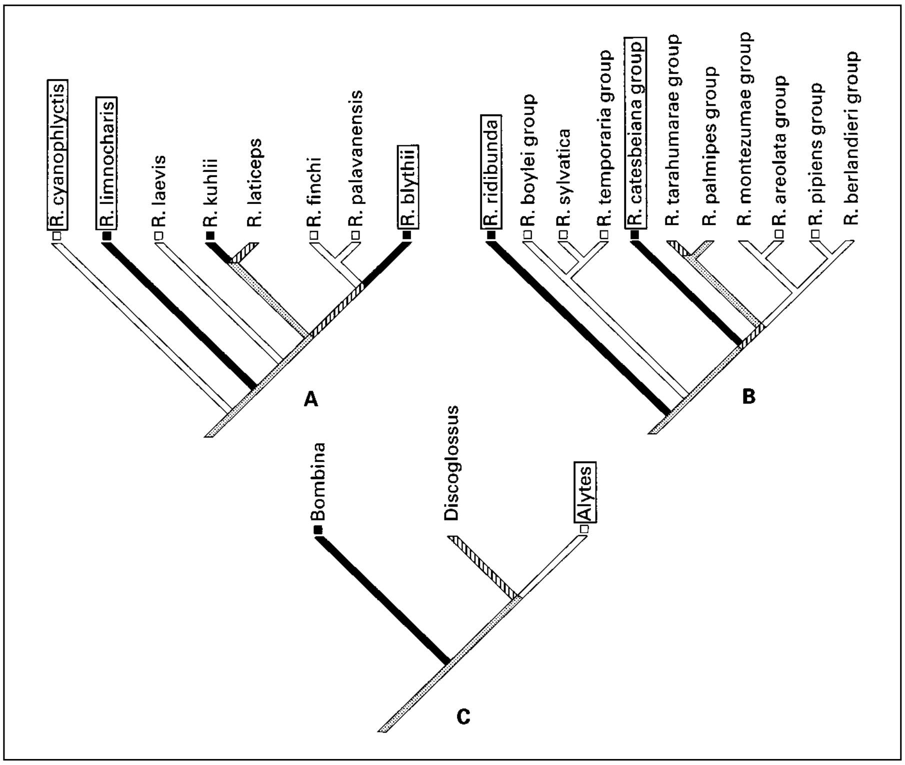

Fig. 4. Occurrence of male territoriality mapped onto phylogenies where female mating vocalization has evolved. Boxes have been placed around names of taxa with female mating calls. Black lines indicate species with territorial males. Shaded lines indicate character state is equivocal. No small boxes appear next to taxon names when the character state is unknown.

not known to vocalize [Duellman and Trueb, 1986]. For example, two fanged frogs, *R. palavanensis* and *R. finchi,* have extended male parental care [Inger and Voris, 1988], but the females do not vocalize (fig. 2).

In summary, while locating a mate appears to be the general, most common biological role for female vocalization, the aspects of reproductive biology that make this the case vary widely across species. Additionally, as more studies on the reproductive behavior of frogs have become available, the number of taxa reported to exhibit female mating vocalization has increased as well. Female mating vocalization thus appears to be more common than originally assumed. These findings are consistent with a priori predictions regarding the frequency and causes of female vocalization and lend support to the idea that mating calls in female frogs may have evolved by co-opting the pre-existing advertisement calling pathway common to both sexes, an exaptation for mate location that is present in most if not all species.

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