

THE SOCIAL BEHAVIOUR OF ANURAN AMPHIBIANS

BY KENTWOOD D. WELLS*

Smithsonian Tropical Research Institute, Box 2072, Balboa, Canal Zone

Abstract. Temporal patterns of anuran reproduction fall into two broad categories: prolonged breeding and explosive breeding. The spatial and temporal distribution of females determines the form of male–male competition. Males of explosive breeders in dense aggregations engage in ‘scramble competition’, attempting amplexus with every individual and struggling among themselves for possession of females. Males of prolonged breeders usually call from stationary positions to attract females and often maintain some sort of intermale spacing. Many aspects of vocal behaviour and chorus organization can be viewed as consequences of intrasexual competition. Males of some prolonged breeders defend all-purpose territories, oviposition sites, or courtship areas against conspecific males. Males with high quality territories may enhance their attractiveness to females and obtain several mates in one season. The social organization of some species resembles the lek behaviour of other vertebrates. Males or females of some tropical species care for eggs and tadpoles, but the evolution of parental care has not yet been studied in detail.

During the past few years our understanding of vertebrate social organization and its relationship to the environment has expanded at an ever-increasing rate. Many birds and mammals have been studied intensively, and there is a growing literature on the social behaviour of fishes, amphibians, and reptiles. Nevertheless, information on the so-called ‘lower vertebrates’ remains fragmentary and incomplete. This is particularly true of anuran amphibians (frogs and toads). Although there have been numerous reviews of anuran behaviour and communication (Jameson 1955a; Bogert 1960; Schneider 1966; Blair 1968; Lescure 1968; Heusser 1969b; Rabb 1973; Salthe & Mecham 1974), none has provided an evolutionary framework for understanding the relationship between social behaviour and ecology in these animals. Wilson (1975) presented a short summary of anuran social behaviour but provided few details.

In this paper, I attempt to point out patterns of similarity in the social behaviour of anurans from widely divergent families. In many species, social interactions occur almost exclusively during the breeding season, although this is not universally true. Much of my discussion will therefore be concerned with breeding behaviour and ecology, but I will mention other aspects of social behaviour as well.

As in many other animals, much of the social behaviour of anurans centres around competition among males for access to mates. The conditions which lead to such competition have been

discussed by Trivers (1972), Ghiselin (1974), Williams (1975), Wilson (1975), and Brown (1975). Male–male competition results from the disparity between very high energetic investment in gametes by females and low investment by males. Because of the low cost of gamete production, males are potentially able to mate with many different females. When males do not participate in parental care, they usually increase their reproductive output by attempting to mate with as many females as possible. Males therefore tend to compete among themselves for females as they would for any limited resource. A central thesis of this paper is that the form of male–male competition in a particular species depends to a large extent on the spatial and temporal pattern of reproduction in that species.

Temporal Patterns of Anuran Reproduction

The reproductive behaviour of anurans can be divided into two basic patterns: prolonged breeding and explosive breeding. Although it is convenient to distinguish these categories, they actually represent two ends of a continuum from single-night breeding in some species to year-round breeding in others. In general, prolonged breeding covers breeding periods of more than a month, whereas explosive breeding refers to breeding periods of a few days to a few weeks. In this paper, I am concerned with the ‘breeding period’ of a single population as opposed to the ‘breeding season’ of a species as a whole. This is an important distinction because some species may breed for several months even in a limited geographic area, but individual

*Present address: Biological Sciences Group, University of Connecticut, Storrs, Ct. 06268.

populations may have explosive breeding periods.

Of the two reproductive patterns, prolonged breeding is probably the more common, although information on tropical species is so sketchy that generalizations are hard to make. Many frogs in tropical regions breed during every month of the year (Church 1960a, b; Zeller 1960; Inger & Greenburg 1963; Berry 1964; Inger & Bacon 1968; Brown & Alcalá 1970; Duellman 1970; Crump 1974). Others breed only during wet or dry seasons (Lee 1967; Duellman 1970; Tandy & Keith 1972; Crump 1974). Many frogs from the northern hemisphere have breeding periods of two or three months duration. This is particularly true of summer breeders, including a number of ranids, hylids, and bufonids. The behaviour of some of these species is summarized in Appendices 1 to 3.

Explosive breeding periods are characteristic of many species that breed in temporary rain pools or other ephemeral habitats. These include many bufonids, pelobatids and microhylids (Appendices 5 and 6), some African ranids in the genera *Ptychocheilus*, *Phrynobatrachus* and *Cacosternum* (Balinsky & Balinsky 1954; Poynton 1964; Wager 1965; Stewart 1967; Balinsky 1969), the Australian leptodactylids, *Notaden* and *Neobatrachus* (Slater & Main 1963; Main 1968), and a variety of neotropical species in both semi-arid and forested habitats (Duellman 1970; Crump 1974).

Explosive breeding periods are also characteristic of many North American, European and Asian ranids and bufonids that breed in early spring (Appendices 4 and 5). Most of these species breed in temporary vernal ponds, but some breed in both temporary and permanent water. Many breed in very cold water, sometimes before ice has completely cleared off the water.

In addition to the species listed above, there are some anurans that breed in permanent water but have relatively short breeding periods. In the *Rana esculenta* complex in Europe, northern populations have one short breeding period each year (Forselius 1963). In warmer regions, a population may have several short periods of peak breeding activity within an extended breeding period lasting two to three months (Rühmkeorf 1958; Heusser 1961; Günther 1969; Smith 1969; Wahl 1969; Van Gelder & Hoedemaekers 1971). Obert (1975) attributed fluctuations in breeding activity in these ranids to changes in temperature.

Discoglossid frogs, on the other hand, apparently have an endogenous hormonal cycle (Obert 1973, 1974) which results in a series of brief breeding periods over a period of several months (Knoepffler 1962; Lörcher 1969).

The selective pressures favouring explosive breeding in some species and prolonged breeding in others are not yet clear. In many species, the length of the breeding period may be limited by the equability of the climate and the seasonal availability of suitable breeding sites. However, climatic factors only provide a framework for the evolution of reproductive strategies. Ecological factors such as larval competition and predator abundance, and demographic factors such as age specific mortality of adults, age at first reproduction, clutch size, and frequency of reproduction by individual females must also be considered (Tinkle, Wilbur & Tilley 1970; Andrews & Rand 1974). Such data are not available for most anurans, although the work of Collins (1975) provides a useful starting point for this type of analysis.

It is beyond the scope of this paper to provide a more detailed discussion of the adaptive significance of explosive and prolonged breeding in different species. The question is not unimportant, however, because the factors that determine the length of a species' breeding period are those which ultimately determine the temporal availability of females and the form of male-male competition. Any future quantitative treatment of the evolution of anuran social systems should include some consideration of these problems. For the present discussion, I will simply take these basic temporal patterns as a starting point and discuss their influence on male-male competition.

Mate-Locating Behaviour and Male-Male Competition

Explosive Breeders

In the following discussion I refer primarily to examples from the northern hemisphere. The behaviour of explosive breeders in the tropics is not well known, although brief accounts are available for some species. The behaviour of some species from the northern hemisphere and Africa are summarized in Appendices 4 to 6.

Explosive breeding is usually associated with marked spatial clumping around suitable oviposition sites. These are generally aquatic sites, although some treefrogs in the genera *Agalychnis*, *Pachymedusa*, *Phyllomedusa* (Central

and South America) and *Chiromantis* (Africa) lay eggs in trees overhanging temporary ponds (Rivero & Esteves 1969; Duellman 1970; Pyburn 1970; Pyburn & Glidewell 1971; Wiewandt 1971; Coe 1974; Scott & Starrett 1974).

Males of many species vocalize in choruses that probably advertise the locations of breeding sites to females in surrounding areas (Bogert 1960; Blair 1968). This would be particularly important for species that breed in temporary pools which change in location from year to year. However, females of some species are not strongly attracted to male choruses (Savage 1961; Lörcher 1969; Oldham 1974). In some species, females arrive at the breeding site long before males begin to call (Obert 1975). In such cases, male vocalizations may be important in triggering ovulation in females, but little experimental evidence is available on this point (Rabb 1973; Salthe & Mecham 1974). I will discuss certain aspects of vocal chorusing in more detail in a later section.

Aggregations of explosive breeders are frequently very dense and may include hundreds of individuals. This is true of *Bufo*, *Scaphiopus*, *Gastrophryne*, and other forms that breed in temporary rain pools, including some tropical species (Appendices 5 and 6; Rivero & Esteves 1969; Scott & Starrett 1974). Among cold-water breeders, the densest aggregations seem to occur in species that clump their eggs into huge 'communal' masses that may contain the eggs of more than a hundred females (Wright & Wright 1949; Eibl-Eibesfeldt 1950; Bragg 1953; 1954; Heusser 1961; Savage 1961; Herreid & Kinney 1967; Licht 1969, 1971; Smith 1969; Van Gelder & Hoedemaekers 1971; my personal observations on *R. sylvatica*). Clumping of eggs in sunny areas near the water's surface may provide some thermal advantage to developing embryos (Herreid & Kinney 1967; Licht 1971).

In many species from the northern hemisphere, the total number of males breeding each year greatly exceeds the number of females (Turner 1960; Savage 1961; Merrell 1968; Calef 1973). The reason for this is unknown, although individual females of some species do not breed every year (Turner 1960; Savage 1961). Whether this pattern also occurs in tropical frogs is not known because no data are available on frequency of reproduction by individual females.

Behaviour at high densities. The behaviour of males in breeding aggregations varies with male density. At high densities, males usually search

actively for females in or around the breeding area. The males apparently cannot discriminate visually between males and females, so the search for mates is a trial-and-error process. Males approach and attempt to clasp practically any moving object. Other males are frequently clasped but released after giving stereotyped release calls or vibrations (Bogert 1960; Blair 1968; references in Appendices 4 to 6).

In most of the species listed in Appendices 4 to 6, and in many other explosive breeders, males move around the entire breeding area in search of females. In some species, however, individual males stay in roughly the same place for several hours at a time and attempt to clasp only those frogs that approach to within a few centimetres. This type of limited-area searching has been reported in *Rana aurora*, which calls under water (Calef 1973), *R. esculenta* (Wahl 1969), *Bufo boreas* (Black & Brunson 1971), *B. regularis* and *B. rangeri* (Tandy & Keith 1972), some *Scaphiopus* (Bogert 1960; Bragg 1965), *Pelobates fuscus* (Eibl-Eibesfeldt 1956), *Discoglossus pictus* and *D. sardus* (Knoepffler 1962; Weber 1974), *Bombina bombina* and *B. variegata* (Heusser 1961; Lörcher 1969). I have also observed such behaviour in *Bufo typhonius* in Panama.

Limited-area searching sometimes produces a regular spacing pattern among males resembling that of territorial frogs. 'Territorial calls' and apparent aggressive interactions among males have been reported for several species with relatively short breeding periods, including *Scaphiopus hammondi* (Whitford 1967), *Rana esculenta* (Wahl 1969), and two species of *Bombina* (Lörcher 1969). Yet in *R. esculenta* and *Bombina*, calling males are usually only a few centimetres apart and they retain the active searching and trial-and-error clasping behaviour characteristic of other explosive breeders (Wahl 1969; Lörcher 1969). If males of these species do maintain small individual territories, then the adaptive significance of the behaviour remains unclear.

Active searching is usually accompanied by intense competition among males for possession of females. Several males may try to mate with a single female, struggling with one another and attempting to dislodge the male most securely fixed to the female's back (Liu 1930b, 1931; Savage 1934, 1961; Wright & Wright 1949; Eibl-Eibesfeldt 1950, 1956; Heusser 1968a; Smith 1969; Calef 1973; personal observations on *B. americanus* and *R. sylvatica*).

These contests usually consist of vigorous pushing and shoving among the males, but in the African frog, *Pyxicephalus adspersus*, and the South American bull frog, *Leptodactylus pentadactylus*, males fight violently among themselves for possession of females (Balinsky & Balinsky 1954; Wager 1965; Rivero & Esteves 1969).

Females in dense aggregations apparently do not approach individual calling males. Any female attempting to do so would usually be intercepted by a searching male before reaching her goal. Consequently, males that called from stationary positions to attract females would probably be unsuccessful. On the other hand, males must allocate some time for calling if vocalizations attract females to the breeding site. Males of some species alternate between bouts of calling and searching. This has been observed in *Bufo bufo* (Eibl-Eibesfeldt 1950) and *B. americanus* (C. Richard Tracy, personal communication, and personal observations). It probably occurs in other species as well, but few observers have paid close attention to the behaviour of individual males in choruses.

Behaviour at low and intermediate densities. Males in low-density aggregations often space themselves around the periphery of a pond or other breeding site and call from stationary positions. Consequently, active searching may be rare or absent in low-density aggregations. Females can approach individual males at their calling sites and select them as mates. This strategy would reduce direct male-male competition for females and may be a more efficient way for males to obtain mates at low densities. Males may also reduce their vulnerability to predation by calling from concealed locations in vegetation instead of searching in exposed areas (Nelson 1973).

The use of different mate-locating strategies in high- and low-density aggregations has been reported in *Bufo woodhousei* (Bragg 1940; Thornton 1955, 1960), *B. valliceps* (Thornton 1960), *B. cognatus* (Bragg 1936, 1937, 1940; Brown & Pierce 1967), *B. canorus* (Karlstrom 1962), *Hypopachus variolosus* (Nelson 1973), and *Gastrophryne olivacea* (Awbrey 1965). These changes in behaviour are similar to those observed in some acoustical insects, which may switch from stationary signalling to active searching as densities increase (Alexander 1975).

Within an aggregation, the mate-locating behaviour of males may change as the density of males changes. For example, male *B. bufo*

arriving early at a breeding pond take up isolated calling stations along the shore, but most calling activity ceases as densities increase. Males then begin actively searching for females on land and in the water (Eibl-Eibesfeldt 1950; Heusser 1969a). Presumably there is some density threshold at which the advantages of active searching surpass those of calling from stationary locations. This 'switching threshold' could be measured relatively easily in a number of species, but to my knowledge, this has not been done.

At intermediate densities, some males may adopt a strategy incorporating elements of both vocal attraction and active searching. In *Bufo cognatus*, *B. houstonensis*, *B. valliceps*, *B. speciosus*, *B. woodhousei*, and *Gastrophryne olivacea*, silent males are reported to gather around calling males and attempt to intercept approaching females (Axtell 1958; Awbrey 1965; Brown & Pierce 1967). This probably occurs when males are switching from a vocal attraction to an active searching strategy.

A similar 'parasitic' strategy has been observed in some acoustical insects, where non-courting males attempt to mate with females as soon as they demonstrate receptivity to courting males (Otte 1972; Alexander 1975). In the poeciliid fish, *Poeciliopsis occidentalis*, small males attempt to 'steal' copulations with females attracted to larger territorial males (Constantz 1975). Silent males have also been observed sitting near calling males in several hylid and ranid frogs with prolonged breeding periods, but the selective advantage of the behaviour may be different in these species and will be discussed later.

Prolonged Breeders

In contrast to explosive breeders, males of virtually all prolonged breeders use vocalizations to attract females to their calling sites. Gravid females are able to seek out individual males and select them as mates. Field observations of females approaching calling males are available for a number of species, including some listed in Appendices 1, 2 and 3.

That vocalizations play a role in attracting females to males can no longer be doubted. Controlled experiments have shown that gravid females will approach loudspeakers playing conspecific calls. These include experiments in which only the conspecific call was played (Martof & Thompson 1958; Awbrey 1965; Schmidt 1969, 1971) and choice situations in

which females discriminated between the calls of their own and other species (e.g. Littlejohn & Michaud 1959; Blair & Littlejohn 1960; Littlejohn, Foquette & Johnson 1960; Littlejohn 1961; Straughan & Main 1966; Littlejohn & Loftus-Hills 1968; Forester 1973; Gerhardt 1973; Littlejohn & Watson 1974).

I know of no examples of active searching behaviour in prolonged breeders. Males of most species apparently do not rush forward and attempt to clasp every frog that moves nearby. In *R. clamitans* (Wells 1976), *R. catesbeiana* (Emlen 1968) and many hylids (references in Appendix 3), a male will clasp a female only after she initiates physical contact, in some cases by jumping on the male. The common notion that male anurans attempt to clasp any moving object of appropriate size (Martof 1953; Blair 1958a; Bogert 1960; Littlejohn & Martin 1969) does not hold for many species with prolonged breeding periods.

Direct male-male competition for possession of individual females is rare or absent in most prolonged breeders, although it may occur occasionally (e.g. Pyburn 1970). For the most part, competition is indirect. Males engage in vocal competition for the attention of females and may defend territories around calling sites, courtship areas, or oviposition sites. This type of competition forms the basis of most of the more elaborate social interactions described in the remainder of this paper.

Evolutionary Comparisons

Before discussing more elaborate forms of social behaviour, it will be useful to make some evolutionary comparisons between the basic mate-locating behaviour of explosive and prolonged breeders. Previous comparisons of active searching and vocal attraction have focussed on differences in 'sex recognition mechanisms,' with little reference to their implications for male-male competition (Martof & Thompson 1958; Heusser 1961, 1968a; Hotz 1970). In comparing these two strategies, we need to consider factors that influence the reproductive success of individual males.

Speed versus efficiency. The mating system of explosive breeding frogs is essentially a form of 'scramble competition' that often occurs when resources are concentrated in space and time (Wilson 1971, 1975). An extremely short breeding period places a selective premium on rapid acquisition of mates. Male reproductive success is probably determined by the rate at which

males encounter other individuals and by direct competition for possession of females. Hence, the advantage of being the first to encounter an incoming individual probably outweighs the disadvantages of repeatedly clasping other males. The emphasis is on speed rather than efficiency.

This system is analogous to the mating system of dung flies (*Scatophaga stercoraria*), where males gather in dense groups at oviposition sites (fresh dung) which are usable for very short periods of time. As in frogs, male dung flies search for females around the oviposition site, and those that capture females as soon as the females enter the area achieve the highest reproductive success (Parker 1970).

Such a system allows little time for the exchange of communication signals between individuals (Otte 1974). While aggressive competition may occur, it is less likely to be preceded by elaborate threat postures and displays than the aggressive behaviour of prolonged breeders. One might expect the vocal repertoires of explosive breeders to be less complex than those of some prolonged breeders. Finally, high male densities and the short time available for breeding probably means that individual territories would not be economically defensible in most explosive systems.

In prolonged breeders, the arrival of receptive females is spread over a long period of time. Selective pressures for rapid acquisition of mates would be relaxed. If relatively few females are present at any given moment, then a male would be unlikely to improve his reproductive success by trying to maximize his encounters with other frogs. Instead, a male's reproductive success probably depends on his ability to attract females to his calling site and to prevent interference from other males. In many species, this has led to vocal competition, maintenance of intermale spacing, or defence of individual territories. These are discussed in a later section.

Energetic considerations may be more important for prolonged breeders than for explosive breeders, although very little is known about the energetic costs of various types of behaviour in frogs. An explosive breeder can afford to 'waste energy' and even go without food during the breeding period (Savage 1961; Heusser 1963, 1968a; Oldham 1966), because the low metabolic rates of frogs allow rapid replacement of energy reserves when breeding has stopped (Seymour 1973). During a prolonged

breeding season, males may be on a tighter energy budget, particularly if they are restricted to breeding territories with inadequate supplies of food (Wells 1976). In general, one would expect the behaviour of prolonged breeders to emphasize efficiency rather than speed.

Female choice. The form of male-male competition can be strongly influenced by the operation of female choice (Trivers 1972). As I have already mentioned, females appear to have few opportunities to choose among potential mates in explosive breeders. Consequently, there would be no way for a male to improve his reproductive success by enhancing his attractiveness to females.

In prolonged breeders, female choice might be crucial in determining male reproductive success and males should try to make themselves more attractive to females. At present, very little is known about the criteria that females use to choose among potential mates in most animals (Trivers 1972), and virtually nothing is known about it in frogs. One likely possibility is that males could defend territories around favourable oviposition sites, as occurs in many fishes, dragonflies, and other animals (Barlow 1974; Wilson 1975). This seems to be the case in *Rana clamitans* (Wells 1976), and I will discuss other possible examples later.

Intensity of sexual selection. The intensity of sexual selection is directly related to the variance in the potential reproductive success of individual males. Elaborate male displays, vocalizations, courtship, aggressive behaviour, and territoriality are most likely to evolve when the variance in male reproductive success is very high, as in the polygynous mating systems of many birds and mammals (Trivers 1972; Wilson 1975; Brown 1975). Selection will favour increasing levels of male reproductive effort as long as the potential reward in increased fitness outweighs the potential cost in decreased future reproductive success.

Among frogs, the variance in male reproductive success is likely to be higher in prolonged breeders than in explosive breeders. In explosive breeders, many females are in amplexus simultaneously, particularly in species where the oviposition period is even more synchronous than the male calling period. In many species, almost all females breed within a one- to five-day period (Rühmekorf 1958; Heusser 1961, 1963, 1968b; Savage 1961; Forselius 1963; Smith 1969; Wahl 1969; Geisselmann, Flindt & Hemmer 1971; Van Gelder & Hoedemaekers

1971; Meeks & Nagel 1973; Martha & John Paton, personal communication and personal observations on *R. sylvatica*).

A male that completes oviposition with one female may find that most other females have already mated. Therefore he could do little to increase substantially his reproductive success no matter how hard he competed against other males. I should point out that some male-male competition would be expected even in species that breed for only one day if a heavily skewed sex ratio makes it impossible for some males to mate at all. Indeed, one might find a correlation between intensity of male-male competition and the degree of sex ratio bias in many explosive breeders.

When the availability of receptive females is spread over a long period of time, each male should be able to compete for many different females during the breeding period. Some males may be very successful; others may not mate at all. This assumes that individual males are present at the breeding area for a substantial portion of the breeding period. This is true of *Rana clamitans* (Martof 1953; Wells 1976), *R. catesbeiana* (Emlen 1968; Wiewandt 1969), *Hyla regilla* (Whitney & Krebs 1975b), *H. versicolor* (Gary Fellers, personal communication), *Syrhophus marnocki* (Jameson 1955b), *Eleutherodactylus coqui* (Drewry 1970), and some *Centrolenella* (Roy McDiarmid, personal communication).

At present, few data are available on male reproductive success in frogs. Savage (1961) reported that of 33 male *Rana temporaria*, an explosive breeder, only one mated more than once, while 16 did not mate at all. Martha and John Paton (personal communication) found that of 129 male *Bufo americanus* marked in 2 years, only three mated more than once in a season, 33 mated once, and 93 did not mate. In contrast to this, I found that three male *R. clamitans* out of a population of 25 mated between two and five times in one summer and accounted for nine of the 19 matings (47%) that occurred (Wells 1976). Even greater variance in male reproductive success may occur in some tropical species that breed throughout the year.

Modifications of Mate-Locating Behaviour Prolonged Amplexus as 'Female-Guarding'

A number of workers have reported that males of some explosive breeders may remain in amplexus for many days, in contrast to the usual pattern of a few hours in most prolonged

Table I. Duration of Pre-spawning Amplexus in Several Anurans from the Northern Hemisphere

Species	Breeding period	Length of amplexus	Sources
<i>Pseudacris nigrita</i>	3-4 months	< 1 h	Martof & Thompson 1958
<i>Hyla arborea</i>	2-3 months	A few hours	Eibl-Eibesfeldt 1952
<i>H. cinerea</i>	2-3 months	5-6 hr	Garton & Brandon 1975
<i>H. andersonii</i>	2-3 months	< 1 h	Noble & Noble 1923
<i>Bufo calamita</i>	2-3 months	A few hours	Smith 1969
<i>Rana clamitans</i>	2-3 months	A few hours	Wells 1976
<i>B. b. bufo</i>	6-14 days	1-14 days	Eibl-Eibesfeldt 1950; Heusser 1963
<i>B. b. asiaticus</i>	14-21 days	1-10 days	Liu 1930b
<i>B. americanus</i>	3-5 days	12-24 h	Martha, & John Paton, personal communication
<i>R. temporaria</i>	12-14 days	1-12 days	Heusser 1961; Geisselmann, et al. 1971
<i>R. esculenta</i> (may have more than one peak of breeding per year)	5-14 days	Several days	Eibl-Eibesfeldt 1956; Heusser 1961; Smith 1969; Van Gelder & Hoedemaekers 1971
<i>R. pretiosa</i>	14-21 days	Several days	Turner 1958
<i>R. sylvatica</i>	4-14 days	1-4 days	Wright 1914

breeders (Table I). In some cases, a male may spend most of the breeding period in amplexus with a single female.

Prolonged amplexus is analogous to the 'female-guarding' behaviour of dung flies and some other insects (Parker 1974). Such behaviour can evolve when high male densities at a breeding site reduce the frequency with which individual males encounter unmated females. Females may arrive at a breeding site long before they are physiologically ready to mate (Heusser 1963, 1968a) or before weather conditions are suitable for oviposition (Obert 1975). When males greatly outnumber females in the breeding population, there may be strong selective pressures on males to seize females early and stay with them until oviposition occurs (Parker 1974).

Once a male had seized a female, he would have to guard against attempted takeovers by unmated males. In most species, amplexed males adopt a characteristic 'guarding' posture, with the hind legs flexed in a position to kick away other males that try to dislodge them (see illustration in Rabb 1973). This may favour the evolution of enlarged nuptial pads in many explosive breeders, a point made by Savage (1961) in his study of *R. temporaria*. It seems

unlikely that such pads would be needed simply for holding the female, because females are usually passive and do not attempt to escape from clasping males (see numerous references in Appendices 4 and 5). Selection for female-guarding probably also explains the tenacity of males holding onto dead females, bits of floating debris, and other inappropriate objects (Wright 1914; Liu 1930b; Eibl-Eibesfeldt 1950, 1952; Smith 1969).

Prolonged amplexus also occurs in neotropical frogs in the genus *Atelopus*. In *A. oxyrhynchus*, pairs may stay in amplexus for many months, and males become extremely emaciated because of the restriction imposed on their food intake (Dole & Durant 1974a; Durant & Dole 1974). Amplexus lasting at least 19 or 20 days has been reported in several other species in the genus (Sexton 1958; Starrett 1967).

The selective advantage of prolonged amplexus in *Atelopus* is not known. Males do not gather in dense groups for breeding, and direct male-male competition seems to be non-existent. It seems likely that for some unknown reason, the male-female encounter rate is extremely low in these species, perhaps because males and females spend much of their time in different habitats (McDiarmid 1971). Males of *A.*

oxyrhynchus apparently encounter females in random wanderings in their home ranges and may be forced to grab them whenever they are available. Dole & Durant (1974a) believed that males that were unpaired when they reached the breeding site (a mountain stream) were unable to mate during that breeding period.

Reduction of Vocalizations

Although vocalizations have an important role in the mate-locating behaviour of most anurans, there are some species which produce very weak mating calls or no mating calls at all. The tailed frog, *Ascaphus truei*, has no mating call. Males find females by searching under water in streams (Jameson 1955a). Neotropical frogs in the genus *Atelopus* produce very weak calls, but their role in mating behaviour is unknown (McDiarmid 1971).

Several authors have noted the relatively weak nature of the mating calls of some ranids, including *R. temporaria* and *R. cascadae* (Savage 1961; Altig & Dumas 1971). Some ranids, including *R. dalmatina* (Geisselmann et al. 1971) and some species in the *R. boylii* group (Zweifel 1955) lack functional vocal sacs. This may relate to their habit of calling under water, where vocal sacs might not be needed for effective sound transmission.

A number of bufonids lack mating calls or produce very weak calls. These include *B. alvarius*, *B. boreas*, *B. exsul*, *B. nelsoni*, the *B. spinulosus* group, *B. holdridgei*, *B. rosei*, most subspecies of *B. bufo*, and others (Blair & Pettus 1954; Heusser 1961, 1969a; Schuierer 1962; Hotz 1970; Black & Brunson 1971; Martin 1972; Tandy & Keith 1972). Some authors have attributed the loss of mating calls in these bufonids to the absence of sympatric species of similar size and hence a reduced need for species-specific vocalizations to serve as isolating mechanisms (Blair & Pettus 1954; Blair 1958a, 1968; Martin 1972). However, at best this can only be a partial explanation, because species identity is only one type of information communicated by a frog's call.

All of the ranids and bufonids listed above for which behavioural data are available have three major features of their breeding behaviour in common: they breed in permanent water, or in temporary ponds that do not change in location from year to year; they have explosive breeding periods; and they locate females by active searching at the breeding site (Appendices 4 and 5).

I suggest that the reduction of mating calls in these species is related to the spatial and temporal pattern of their reproductive behaviour. Since they breed in relatively permanent sites, vocalizations may not be important in guiding females to the breeding site. Individual populations may develop strong ties to traditional breeding areas, possibly because adults return to ponds from which they emerged as juveniles. Male and female *B. bufo* have been observed returning to traditional breeding sites even after ponds have been drained and replaced by highways and parking lots (Heusser 1960, 1961, 1969a). Because these species are explosive breeders and use an active searching strategy to obtain mates, vocalizations would not be needed to guide females to individual males in an aggregation. If predation pressures or other factors made continued use of vocalizations disadvantageous, they might eventually be lost or reduced. Similarly, Alexander (1975) suggested that crickets that live in dense, relatively sedentary clusters sometimes lose their long-distance calling songs.

Acoustic Interactions and Chorus Organization

Since Goin (1949) reported that male *Hyla crucifer* sometimes call in duets and trios, a number of workers have reported apparent 'social organization' in the choruses of many other frogs (Bogert 1960; Duellman 1967; Wilson 1975). However, there have been few attempts to examine the evolutionary implications of acoustic interactions between individuals in a chorus. In the following discussion, I will not present a comprehensive review of chorusing behaviour in anurans, but I will mention a number of problems that require further investigation. An extensive review of chorusing behaviour in acoustical insects by Alexander (1975) includes many ideas which are applicable to anuran choruses, and that paper should be consulted for more details.

Synchronous Chorusing

No species of anuran is known to exhibit the extreme degree of synchrony found in some cicada choruses (Alexander 1975), but some species are reported to call in rhythmic bursts of vocal activity (Lörcher 1969; Wahl 1969). In some species, such as *Bufo americanus*, the calls of one male seem to stimulate calling by other males, resulting in considerable overlap in the calls of different individuals (personal observations). Synchronous or nearly synchronous

choruses may occur in other species, but few workers have paid close attention to this aspect of vocal behaviour.

What could be the advantage to an individual male in having his calls overlap, partially or completely, the calls of other males? If females used vocalizations as cues to locate individual males in a chorus, then highly synchronized chorusing would appear to be disadvantageous because it would produce maximum acoustic interference between competing males. Otte (1974) suggested that some animals might try to interfere with the signals of other individuals to prevent them from mating, but Alexander (1975) pointed out that such a strategy would reduce the signalling efficiency of both the original caller and the male attempting to interfere.

I would suggest that the greatest degree of synchrony in anuran choruses might occur when males attract females to a breeding area with vocalizations, but obtain mates by active searching rather than vocal attraction from stationary calling sites. In this type of mating system, a synchronous burst of calling from all of the males in a pond would presumably be more effective in attracting females from a distance. If females did not approach individual calling males, then acoustic interference would not be a serious problem. This hypothesis is largely speculative at this point, although the vocal behaviour of active searchers such as *B. americanus* (personal observations) and *Bombina* (Lörcher 1969) seem to support this view. Future workers should pay close attention to the amount of call overlap within choruses of other explosive breeders.

Phonoreponse and Spacing of Calls

Many male anurans tend to space their calls so that the vocalizations of one individual do not overlap those of nearby individuals. In *R. clamitans*, for example, the calls of different individuals are usually spaced at intervals of 2 to 10 s, and the calls of near neighbours seldom overlap (Wells 1976). In some species, one male may be stimulated to call at some fixed interval after another male has called. If the response time of the second male is one half the intercall interval of the first male, the result is a pattern of antiphonal alternation between two calling males (duets). In other species, several males may respond successively to one another, producing a pattern of trios, quartets or pentets in a chorus (Goin 1949; Eibl-Eibesfeldt 1952;

Anderson 1954; Jameson 1954; Martof & Thompson 1958; Hardy 1959; Bogert 1960; Snyder & Jameson 1965; Capranica 1965; Duellman 1967; Foster 1967; Schneider 1967, 1968; Heinzmann 1970; Lemon 1971; Loftus-Hills 1971, 1974; Rosen & Lemon 1974; Whitney & Krebs 1975a).

This pattern of phonoreponse to another male's calls seems to be a mechanism that allows each male to maximize his signalling efficiency by minimizing acoustic interference from other males. Loftus-Hills (1974) presented a neurophysiological model to explain this type of behaviour. He suggested that anurans may have a neural pacemaker similar to those of some acoustical insects. Each individual would have a set calling rate, but this could be altered by interactions with other calling males. Calling by one male might inhibit calling by a second male until a fixed interval after the end of the first male's call. This would enable the second male to place his calls between successive calls of the first frog. Experiments on several species have shown that males will adjust their calling rates in response to playbacks of tape-recorded calls (Lemon 1971; Rosen & Lemon 1974; Loftus-Hills 1974).

Phonoreponses leading to spacing or alternation of calls would be most likely to evolve in species where females approach and select individual calling males. It is in these species that minimization of acoustic interference would be most important for individual male reproductive success. The most precise patterns of alternation should occur in species with regularly spaced, repetitive calls. In a species such as *R. clamitans*, where males call at irregular intervals, precise alternation of calls would occur only occasionally (Wells 1976).

Chorus Leadership

Several authors have reported that certain individuals tend to initiate bouts of calling more frequently than others and therefore serve as 'chorus leaders' (Anderson 1954; Hardy 1959; Bogert 1960; Brattstrom 1962; Duellman 1967; Brattstrom & Yarnell 1968; Whitney & Krebs 1975a). It has been suggested that chorus leaders may obtain more mates than other males. For example, Brattstrom & Yarnell (1968), working with *Physalaemus pustulosus*, reported that the 'leader' in a chorus of four males had more egg masses near its calling site than other males. These results are inconclusive, however, because pairs of this species may

move around before ovipositing (A. S. Rand, personal communication). The placement of egg masses is influenced by the structure of the habitat (Sexton & Ortleb 1966), and in some cases, pairs may attach their eggs to previously laid masses (A. S. Rand, personal communication).

In an experimental study of *Hyla regilla*, Whitney & Krebs (1975a) presented females with an artificial chorus consisting of four speakers playing the same call. The speaker that initiated the 'chorus' was changed with each trial. They reported that females consistently approached the speaker that initiated the chorus. The application of these results to field situations is unclear. Whitney & Krebs reported that certain individuals in the field tended to initiate choruses more often than others, but the same frogs also called more frequently, ended choruses more frequently, and called louder than other frogs. Although females may have located chorus leaders more easily in the experimental situation, this does not prove that chorus leadership is the principal cue for mate selection in natural choruses.

If 'chorus leaders' do enjoy greater mating success than other frogs, this does not necessarily imply that females 'prefer' these males because they make 'better' mates. The most successful males may be those that outsignal their competitors and are therefore easiest to locate in a large chorus (Alexander 1975). Chorus leaders are sometimes referred to as 'dominant' individuals, and ordered sequences of calls have been termed 'hierarchies' (Duellman 1967; Brattstrom & Yarnell 1968; Wilson 1975). However, there is no evidence that call-order is determined by agonistic encounters among males, so there is no reason to suppose that organized choruses are analogous to dominance hierarchies of other animals.

Aggression and Social Spacing

Encounter Calls and Maintenance of Intermale Spacing

In many anurans, there is some degree of spatial separation between calling males, and the role of vocalizations in maintaining this separation has received considerable attention. Since Bogert (1960) included a category of 'territorial calls' in his classification of anuran vocalizations, this term has been rather loosely applied to a wide variety of calls which occur in different contexts. In general, any call that occurs in close-range encounters between males

has been termed a 'territorial call'. I prefer to use the term 'encounter call', suggested by McDiarmid & Adler (1974). In some species, the 'mating call' is thought to have a territorial function in that it advertises a male's spatial location to other males. I would suggest that such vocalizations be termed 'advertisement calls'. By using this term, we can avoid specifying the intended recipient of these signals (i.e. males or females) when their precise social functions are unknown.

As Tinbergen (1957), Crook (1973) and others have pointed out, territoriality normally involves two distinct tendencies, site attachment and intolerance of intruders. It is important to realize that either tendency can occur independently. Animals may show strong attachment to particular locations, such as preferred perches, shelters, or feeding sites, without defending them, and they may show hostility toward conspecifics for reasons other than defence of particular sites. Hostility without site attachment sometimes leads to the maintenance of individual distance. At any given moment, individuals in a population may be relatively evenly spaced throughout the appropriate habitat, but their locations may change over more extended periods of time. Site-specific territoriality occurs when intolerance of other individuals centres around particular locations. Although it is often difficult to distinguish between individual distance and territoriality in the field, the distinction is not merely semantic, for these types of behaviour may have different functions governed by different selective pressures (Kummer 1971; Crook 1973).

The difficulty of distinguishing individual distance from territoriality is shown by the behaviour of many temperate-zone hylids. Calling males are usually spaced 50 to 200 cm apart in bushes and other vegetation around ponds. Spacing is probably maintained largely through mutual avoidance by calling males. The mating or advertisement calls produced by one male probably inhibit calling by other males perched nearby (Whitney & Krebs 1975b). Occasionally, two males begin calling within 10 to 50 cm of one another. One or both of the frogs may then give encounter calls, which are usually low frequency trills. Examples of hylid encounter calls and the contexts in which they occur are given in Table II.

Experimental work by Allan (1973) showed that tape playbacks of the encounter call of *Hyla regilla* inhibited calling by nearby males

Table II. Examples of Hylids Having Encounter Calls and the Contexts in Which the Calls Occur

Species	Context of vocalization	Sources
<i>H. crucifer</i> *	In response to males calling within 10–20 cm	Rosen & Lemon 1974; Fellers 1975
<i>H. versicolor</i> *	In response to males calling or moving nearby	Pierce & Ralin 1972; Fellers 1975
<i>H. chrysocelis</i> *		
<i>H. arenicolor</i>		
<i>H. cadaverina</i> *	In response to males calling nearby	F. T. Awbrey, personal communication
<i>H. avivoca</i> *	In response to males calling or moving within about 45 cm	Altig 1972; Pierce & Ralin 1972
<i>H. cinerea</i> *	In response to males calling within 45–75 cm	Fellers 1975; Garton & Brandon 1975
<i>H. regilla</i> *	In response to males calling within 50 cm and in response to playbacks of advertisement calls	Snyder & Jameson 1965; Allan 1973; Whitney & Krebs 1975b
<i>H. a. arborea</i> *	In response to males calling within 20–30 cm and in response to playbacks of advertisement calls	Schneider 1967, 1968; Paillette 1970; Schneider & Nevo 1972; Blankenhorn 1972
<i>H. a. savignyi</i>		
<i>H. meridionalis</i> *		
<i>Pternohyla fodiens</i> *	In response to males calling within 60–90 cm and in response to playbacks of advertisement calls	T. A. Wiewandt, personal communication
<i>Smilisca baudinii</i> *	In response to males calling within 30–50 cm and in response to playbacks of advertisement calls	T. A. Wiewandt, personal communication
<i>Pachymedusa dacnicolor</i> *	Given by males in amplexus when other males approach; occasionally given in choruses	Pyburn 1970
<i>Agalychnis callidryas</i> *		

*Male–male aggressive encounters observed.

and were often followed by withdrawal of intruders. Field observations of males retreating after being 'threatened' with encounter calls are available for many of the species listed in Table II (Schneider 1967, 1968; Paillette 1970; Schneider & Nevo 1972; Allan 1973; Rosen & Lemon 1974; Fellers 1975; Whitney & Krebs 1975b; T. A. Wiewandt, personal communication). The encounter call probably serves as a warning to an intruder that he is calling too close to a resident male.

When intruders fail to respond to vocal threats, males will generally defend their calling sites with aggressive behaviour. Fighting males may jump at one another, butt against one another with their heads, push at one another with their forelimbs, or engage in bouts of clasp and kicking. Behaviour of this kind has been observed in most of the species listed in Table II (Paillette 1970; Altig 1972; Blankenhorn 1972; Rosen & Lemon 1974; Fellers 1975; Garton & Brandon 1975; Whitney & Krebs 1975b; T. A. Wiewandt, personal communication; Frank T. Awbrey, personal communication).

In addition to North American and European hylids, encounter calls and fighting occur in *Pachymedusa dacnicolor* and *Agalychnis callidryas* (Pyburn 1970) and the Australian treefrog *Litoria peroni* (Norbert Danks, personal communication). Many African treefrogs in the genera *Afrixalus*, *Leptopelis*, and *Hyperolius* (Rhacophoridae and Hyperoliidae) also have trills or buzzes that probably serve the same function as the encounter calls of hylids (Wager 1965; Schiøtz 1967; Stewart 1967).

In many of the hylids listed in Table II, aggressive behaviour is not necessarily connected with defence of fixed territories. Males often occupy different calling sites on successive nights (Blankenhorn 1972; Whitney & Krebs 1975b; Garton & Brandon 1975), although some individuals may be found in the same place for several nights in a row (Paillette 1970; Rosen & Lemon 1974). It may be that maintenance of a minimum distance between calling males is more important than possession of a particular calling site.

The maintenance of intermale spacing may reduce interference between males and may

enable females to localize individual males more easily (Pierce & Ralin 1972; Whitney & Krebs 1975b). Perhaps more important is the ability of males to reduce the number of potential competitors by preventing nearby males from calling. In this sense, males that fight with one another would not be competing for calling sites per se, but for the opportunity to call. If a male must search from place to place for a calling site at a suitable distance from other males, he may lose valuable time that could be used for attracting females.

More research is needed to determine whether males occupying certain sites obtain more mates than those at other sites, perhaps because some calling perches are more favourably located. When males call in bushes, females might approach them along certain preferred routes, and males near these routes would be more likely to obtain mates. It is also possible that males space themselves without site specific territoriality when calling perches are abundant, but defend more permanent territories when sites are scarce.

Territoriality

Territoriality is best understood in the context of resource competition (Brown 1964, 1975; Rand 1967; Wilson 1971, 1975; Crook 1973). Attachment to a fixed site will be advantageous if this gives the occupant exclusive or priority access to resources in short supply. These may be resources needed for individual survival or for reproduction. When males defend territories against conspecific males, females are often the ultimate limiting resource. However, females themselves are usually not defendable, except in the limited sense of female guarding during amplexus. Possession of a territory may give a male direct access to females in the area or it may enhance his attractiveness to prospective mates.

Aggressive behaviour related to site-specific territoriality has been reported in a number of anuran families. Data are summarized in Table III. As in the hylids discussed above, many species have encounter calls that often precede physical combat between individuals. *Rana catesbeiana*, *R. clamitans*, and several species of *Eleutherodactylus* and *Pseudophryne* have more than one type of close-range encounter call (Capranica 1968; Emlen 1968; Jenssen & Preston 1968; Wiewandt 1969; Drewry 1970; Pengilley 1971; Wells 1976).

Many territorial frogs also employ stereotyped postural and other visual displays as threat signals in agonistic encounters. In *R. clamitans* and *R. catesbeiana*, for example, territorial males maintain high, inflated postures in the water, whereas non-territorial males maintain low postures with only the tops of their heads out of the water (Emlen 1968; Wells 1976). Emlen (1968) reported that model frogs in high posture elicited aggressive responses from territorial males, whereas models in low posture did not. Males of these species also have bright yellow throats, which are prominently displayed by males in high posture and are probably important in territorial advertisement during daylight hours (Emlen 1968; Schroeder 1968; Wiewandt 1969; Wells 1976).

Territorial female *Colostethus trinitatis* and *C. collaris* also display bright yellow throats when challenging intruders (Test 1954; Sexton 1960; Durant & Dole 1975). In *C. inguinalis*, males have pearly white throats which may be important in territorial displays (personal observations). Many territorial dendrobatid frogs adopt an erect posture with stiffened limbs when challenging intruders (Test 1954; Sexton 1960; Duellman 1966; Goodman 1971; Crump 1972). A similar display is employed by male *Centrolenella*, which approach intruders with a series of jerky rocking movements (McDiarmid & Adler 1974). In *Leptodactylus melanonotus*, territorial males raise the posterior portion of their bodies, exposing a dorsal, rusty coloured patch (Brattstrom & Yarnell 1968).

The form and intensity of aggressive behaviour involving physical contact is quite variable. In some species, such as *Centrolenella valerioi*, residents clasp intruders with amplexus-like grips (McDiarmid & Adler 1974). In others, residents jump on intruders or charge at them and push them out of the territory (Test 1954; Sexton 1960; Duellman 1966; Drewry 1970; Durant & Dole 1975). Male *Pseudophryne* butt against intruders and attempt to toss them out of their burrows (Pengilley 1971). Male *P. pipa* and *Leptodactylus melanonotus* may bite intruders in fights (Rabb & Rabb 1963b; Brattstrom & Yarnell 1968).

Wrestling bouts have been observed in pipids, leptodactylids, dendrobatids, hylids and ranids. In the aquatic pipids, males charge at each other head on and interlock their forelimbs while pushing against one another (Rabb 1969). Semi-aquatic forms such as *R. catesbeiana*, *R. clamitans*, and *Limnodynastes peroni* wrestle

Table III. Examples of Territorial Behaviour in Anurans. When Both Sexes Defend Territories, the Behaviour is Most Conspicuous in the Sex Listed First in Column 2

Species	Sex	Territory location	S	E	D	C	J	W	O	Sources
Pipidae										
<i>Hymenochirus boettgeri</i> *	♂	Underwater calling site	×	×	×	×	×	×	n	Rabb & Rabb 1963a; Österdahl & Olsson 1963
<i>Pipa pipa</i> *	♂	Underwater calling site		×	×	×	×	×	n	Rabb & Rabb 1963b
<i>P. parva</i> *	♂	Underwater calling site		×	×	×	×	×	?	Rabb 1969
Leptodactylidae										
<i>Leptodactylus bolivianus</i>	♂	Foam nest in water					×		×	Sexton 1962
<i>L. melanonotus</i>	♂	Under rocks on shore of ponds or streams	×	×	×	×	×	×	×	Brattstrom & Yarnell 1968
<i>Limnodynastes dorsalis</i>	♂	Small pools or burrows	×	×		×	×	×	×	Clyne 1967, 1969
<i>Pseudophryne corroboree</i>	♂	Terrestrial burrows	×	×			×		×	Pengilley 1971
<i>P. dendyi</i>	♂	Terrestrial burrows	×	×			×		×	Pengilley 1971
<i>P. bibroni</i>	♂	Terrestrial burrows	×	×			×		×	Pengilley 1971
<i>Eleutherodactylus coqui</i>	♂♀	Tree holes, in moss on tree trunks, etc.	×	×		×	×		×	Drewry 1970
<i>E. hedricki</i>	♂	Tree holes	×	×		×	×		×	Drewry 1970
Hylidae										
<i>Pachymedusa dacnicolor</i>	♂	Abandoned rodent burrows	×	×		×	×		n	Wiewandt 1971
<i>Hyla faber</i>	♂	Mud nests near water	×				×	×	×	Lutz 1960
<i>H. paradalis</i>	♂	Mud nests near water	×				×	×	×	Lutz 1973
Centrolenidae										
<i>Centrolenella valerioi</i>	♂	Plants over mountain streams	×	×	×	×	×		×	McDiarmid & Adler 1974
<i>C. viridissima</i>	♂	Plants over mountain streams	×	×	×		×		?	McDiarmid & Adler 1974
Ranidae										
<i>Rana clamitans</i>	♂	In vegetation at edge of ponds and in marshes	×	×	×	×	×	×	×	Martof 1953; Brode 1959; Schroeder 1968; Jenssen & Preston 1968; Wells 1976
<i>R. catesbeiana</i>	♂	Well vegetated areas of lakes and ponds	×	×	×	×	×	×	?	Durham & Bennett 1963; Blair 1963; Emlen 1968; Wiewandt 1969
Dendrobatidae										
<i>Dendrobates pumilio</i>	♂	Low plants, logs, and ground	×	×	×	×	×	×	?	Duellman 1966; Bunnell 1973
<i>D. granuliferus</i>	♂	Logs, leaves, plant stems, or other elevated sites	×	×	×	×	×	×	?	Goodman 1971; Crump 1972
<i>D. histrionicus</i>	♂	Logs, leaves, plant stems	×			×	×	×	?	Silverstone 1973
<i>Colostethus inguinalis</i>	♂♀	Rocks in streams	×	×	×	×	×	×	?	Duellman 1966; Wells, personal observations
<i>C. trinitatis</i>	♀♂	Rocks in streams	×		×	×	×	×		Test 1954; Sexton 1960
<i>C. collaris</i>	♀♂	Rocks in streams	×		×	×	×	×		Durant & Dole 1975

Abbreviations: S = site attachment. E = encounter calls. D = postural or other visual displays. C = residents chase intruders. J = jump attacks. W = wrestling. O = oviposition in territory. × = behaviour present. n = behaviour not present. ? = behaviour may occur. Blank spaces = behaviour not reported. * = captive animals.

while clasped venter to venter, often standing out of the water with snouts pointed straight up (Brode 1959; Clyne 1967, 1968; Emlen 1968; Schroeder 1968; Wells 1976). Terrestrial dendrobatids stand on their hind limbs and push against one another with their forelimbs, in postures reminiscent of human wrestlers (Test 1954; Sexton 1960; Duellman 1966; Goodman 1971; Silverstone 1973). The most violent wrestling occurs in *Hyla faber* and *H. pardalis*, which have sharp claw-like pollex rudiments that serve as weapons against opponents (Lutz 1960, 1973). *H. faber* is the only species of frog in which serious injuries have been observed that may have resulted from fighting between males.

In many of the examples cited above, the adaptive significance of territoriality is unclear. Nevertheless, it is possible to speculate on the advantages of territoriality in some species. I will discuss three general categories of territorial behaviour: defence of resources needed for survival, defence of oviposition sites, and defence of courtship areas. In some species, a territory may serve more than one function.

Resources needed for survival. Many terrestrial dendrobatids may defend all-purpose territories that include feeding sites, shelter, and oviposition sites. For example, although Test (1954) and Sexton (1960) referred to the territories of *Colostethus trinitatis* as feeding territories, it was clear that the presence of adequate shelter was an important criterion in choice of territory sites (Sexton 1960). The same may be true for *C. collaris* (Durant & Dole 1975). In *C. inguinalis* in Panama, both males and females defend territories on rocks and in crevices near water (personal observations). In the dry season, this may be particularly important in providing access to adequate sources of moisture.

In *Eleutherodactylus coqui*, both males and females defend tree holes used as daytime shelters, and the same holes can be used as oviposition sites. Some females of this species also defend favourite feeding perches (Drewry 1970). Defence of burrows is probably widespread in frogs, and has been reported in a number of species, including several species of *Pseudophryne* in Australia (Pengilly 1971) and *Pachymedusa dacnicolor* in Mexico (Wiewandt 1971). In *Pseudophryne*, the burrows are used both for shelter and as oviposition sites, while in *Pachymedusa* they are used only as daytime shelters.

Oviposition sites. As a general rule, one would expect territorial defence of oviposition sites to be widespread in animals with external fertilization, because the male must be present when eggs are laid. By defending a favourable oviposition site, a male might enhance his attractiveness to females (Trivers 1972). Defence of oviposition sites by males is common in fishes (Barlow 1974), most of which have external fertilization. In salamanders, apparent defence of oviposition sites by males has been reported in primitive cryptobranchoids (*Cryptobranchus*, *Andrias*, *Hynobius*) that have external fertilization (Kerbert 1904; Bishop 1941; Thorn 1962), but has not been reported in species with internal fertilization.

Many of the frogs listed in Table III probably defend territories centred around oviposition sites. This is most obvious when the territory consists of a defended burrow, nest, or tree hole used for reproduction. For example, males of the large neotropical hylids, *Hyla faber* and *H. pardalis*, build and defend large mud nests where the eggs are laid (Lutz 1960, 1973). Other species, such as *H. boans* and *H. rosenbergi*, also build mud nests and may defend them, although aggressive behaviour has not been reported in these forms (Breder 1946; Duellman 1970). These species have sharp claw-like pollex rudiments similar to those reportedly used as weapons by male *H. faber* (Lutz 1960; Duellman 1970).

In *Rana clamitans*, eggs are laid at the male's calling site, which usually contains a dense mat of *Elodea* or other vegetation used for attachment of the eggs (Wells 1976). In some instances, this may also be the case in *R. catesbeiana* (Wright 1914; Emlen 1968; Wiewandt 1969), although females apparently lay eggs away from male calling sites in dense populations (S. T. Emlen, personal communication). Male *Limnodynastes peroni* defend territories in small pools or burrows (Clyne 1967, 1968), and eggs have been found in similar locations (Moore 1961). It is not known whether the territories of male dendrobatids always include an oviposition site, but male *D. granuliferus* apparently lead females to oviposition sites under leaves near the male calling site (Crump 1972).

Courtship areas. For some frogs, there may be no shortage of oviposition sites, but males may defend relatively large areas that enable them to court females without interference from other

males. This would be particularly important in many dendrobatids, which have complex courtship consisting of extended sequences of stimulus-response interactions between males and females. Amplexus is absent in those *Dendrobates* for which mating has been observed. Courtship includes following of one partner by the other, touching, rubbing, circling, and elaborate postural displays (Senfft 1936; Dunn 1941; Hoogmoed 1971, 1972; Crump 1972; Silverstone 1973; Dole & Durant 1974b; Polder 1974a). Presumably any interruption of the normal courtship sequence would terminate the sequence and result in considerable time waste or even loss of a mate by the courting frog. Therefore, there might be strong selection for territorial defence even when oviposition sites are plentiful.

Complex courtship and mating is also characteristic of pipid frogs, and territories in these species may serve primarily as courtship areas. In some species, females do not lay eggs in spatially fixed oviposition sites. In *P. pipa*, eggs are placed on the back of the female through an elaborate interaction with the male (Rabb & Rabb 1961, 1963b). In *Hymenochirus* and *Pseudohymenochirus*, eggs are laid at the surface of the water in a complex process involving mid-water turnovers by the amplexed pair. In all of these species, oviposition commonly lasts for many hours, and a pair of *Hymenochirus* may make as many as 350 turnovers before egg laying is completed (Österdahl & Olsson 1963; Rabb & Rabb 1963b; Sughrue 1969). An exclusive territory might be important in insuring uninterrupted courtship and mating. The mating process in *Xenopus* is much less elaborate, and it is not known whether males of this genus are territorial in nature. Aggressive behaviour has been reported in *Xenopus* confined to small aquaria (Rabb & Rabb 1965).

Lek behaviour. Emlen (1968), Rabb (1973), Wilson (1975), Whitney & Krebs (1975b) and others have suggested that the choruses of many frogs are analogous to the 'leks' of some birds and mammals. In species that form leks, males display on small territories, while females move among the displaying males before choosing a mate. In many species, a few males are chosen repeatedly by females and achieve very high reproductive success, while other males obtain no mates at all (Wilson 1975). In birds and mammals, the term 'lek' is usually applied to communal display groups that are removed from feeding and nesting sites of females.

Alexander (1975) argued that male display groups in acoustical insects that form around oviposition sites, food plants, or other resources needed by females should also be considered leks. If this criterion is accepted, then the choruses of many prolonged breeding frogs that form around ponds or other breeding sites may be analogous to leks in other vertebrates. This would be particularly true of species that call in bushes or other vegetation but oviposit in water (i.e. many hylids). The dense population of *Rana catesbeiana* studied by Emlen (1968) could also be considered a lek, since amplexed pairs apparently left the main chorus before depositing eggs (S. T. Emlen, personal communication).

The lek analogy does not seem to be appropriate for *R. clamitans*, because males of this species defend individual oviposition sites (Wells 1976). Thus the social system of this species is essentially the same as that of many 'typical' territorial birds, fishes, and insects (Wilson 1975). It is possible that some species such as *R. catesbeiana* show a change from territorial to lek organization with increasing density, perhaps because individual oviposition sites would not be economically defensible at high male densities (Emlen, personal communication). This might be paralleled by a shift in the criteria used by females to select mates. At low densities, female choice might be based primarily on the quality of a male's territory (Wells 1976). At high densities, females would have to depend on some other cue, such as a male's position in the chorus or individual differences in display behaviour (Emlen 1968).

In considering possible lek behaviour in anurans, we need to consider the following question: Are breeding aggregations of male anurans always resource-based aggregations caused by males gathering at suitable breeding habitats, or are some aggregations favoured because of the action of female mate selection? It is conceivable that aggregation and chorusing itself could be advantageous to individual males if males in large groups obtained more mates than those in small groups. This might occur if (1) females were attracted from greater distances by large choruses, or (2) females perceived males in large choruses to be 'better' mates (Alexander 1975). The second possibility is purely speculative at this point.

At first glance, it would appear that aggregations of pond- or stream-breeding frogs fit Alexander's (1975) definition of resource-based aggregations, since these species must breed

in water. However, one often observes choruses of frogs concentrated in one small part of a large pond or along part of a lake shore, while other areas apparently equal in quality are not used (for example, *Hyla regilla*, Whitney & Krebs 1975b). In *Rana catesbeiana*, male choruses sometimes form in one part of a pond, break down after a few nights, and reform in some other part of the pond (S. T. Emlen, personal communication). These observations, although inconclusive, suggest that aggregation itself may be advantageous to males of some species.

One might test this possibility by examining the distribution of calling males in terrestrial breeding tropical frogs in relatively homogeneous environments. If males of any of these species show a tendency to aggregate, then this might be the clearest analogy to the lek behaviour of other vertebrates.

Peripheral males. In many animals, male territoriality or spacing limits the number of reproductively active males and leaves an excess of non-breeding males in the population. Such males often establish territories in sub-optimal habitats, wait for resident males to vacate their territories, or adopt alternate strategies for obtaining mates. I have already mentioned the groups of silent males that seem to 'parasitize' calling males in dense aggregations of explosive breeders. A similar phenomenon occurs in some prolonged breeders, but its adaptive significance may be somewhat different.

Silent males have been reported to sit near calling males in *Pseudacris nigrita*, *Hyla versicolor*, *H. chrysoceles*, *H. cinerea*, *H. crucifer*, *R. catesbeiana*, and *R. clamitans* (Martof & Thompson 1958; Emlen 1968; Pierce & Ralin 1972; Fellers 1975; Garton & Brandon 1975; Wells 1976). In the case of *R. catesbeiana* and *R. clamitans*, these males adopt low postures and move into the territories of other males, sometimes sitting for hours within a few centimetres of resident males (Emlen 1968; Wells 1976).

Silent males have not been observed intercepting females in any of the species listed above, although they may do so occasionally. I suspect that in many cases, silent males may simply wait for territory residents to leave and then occupy vacated sites. This behaviour has been observed in *R. clamitans* (Wells 1976), *R. catesbeiana* (Emlen, personal communication), and *H. versicolor* (Fellers 1975). Male *R. catesbeiana* and *R. clamitans* that move from one territory

to another may be monitoring the availability of sites in the pond (Emlen 1968; Wells 1976).

In many frogs, it would probably be very difficult for males to 'steal' matings with females, particularly when females can exercise some choice in selection of mates. In *R. clamitans*, females are extremely wary when approaching calling males and are easily driven away by excessive movements of males (Wells 1976). A silent male that attempted to intercept females might only succeed in driving most of them away. Furthermore, a male that clasped a female in another male's territory would probably be attacked immediately by the resident.

Whether or not a male attempted to intercept females approaching other males might depend in part on the rate of turnover in territory ownership. In a system where changes in territory ownership were relatively frequent, a male might find it advantageous to wait for a site to become available. This would be particularly true in a very prolonged breeding period, where there would be a high probability of additional females becoming available. This may well be the situation in such species as *R. clamitans* (Wells 1976) and *H. versicolor* (Fellers 1975). On the other hand, if territory ownership were relatively stable throughout the breeding period, with the largest males monopolizing the best sites, then a strategy of intercepting females might be the only one available to smaller males.

Parental Care

Many authors have listed examples of parental care of eggs and tadpoles by adult anurans, and Salthe & Mecham (1974) have reviewed much of the important literature. Unfortunately, most accounts of parental care in anurans are anecdotal, and the details of the behaviour are unknown for most species. In most cases, the precise contribution of the adults to increased survivorship of eggs and young is not known. I will not attempt to summarize all of the varieties of anuran parental care. Instead, I will focus on a number of evolutionary problems that have received scant attention in the past.

In many anurans, parental care is performed by the female, but male parental care is probably as common, if not more common than female parental care in some genera. The selective factors that favour parental investment by one sex or the other have not been explored. Among animals in general, parental care performed exclusively by males is relatively rare (Trivers

1972). This never occurs in mammals, for obvious reasons, and in birds, males usually care for young in conjunction with females. Male parental care is also rare or absent in lizards, snakes, turtles, crocodiles and salamanders with internal fertilization. By contrast, male parental care is relatively widespread in fishes.

Male parental care in many anurans and fishes is probably an outgrowth of territorial defence of oviposition sites by males. As I mentioned earlier, this in turn is probably related to external fertilization of eggs. A male defending a suitable oviposition site might care for eggs already laid while continuing to attract additional females into his territory (Trivers 1972). Such behaviour might be particularly common in species that breed in crevices, burrows, or specially constructed nests. For example, male *Eleutherodactylus coqui* and *E. hedricki* sit on eggs in their nest chambers and may care for the eggs of more than one female at a time (Drewry 1970). Males of some species of *Colostethus* remain with egg masses until they hatch (Stebbins & Hendrickson 1959; Mudrack 1969), but whether they guard the eggs or care for them is not known.

In some frogs, adults carry tadpoles until they complete development or carry them from terrestrial oviposition sites to water. In *Rhinoderma darwini*, tadpoles are carried in the male vocal sac (Busse 1970). In the Australian frog, *Assa darlingtoni*, males carry tadpoles in brood pouches in the skin (Straughan & Main 1966; Ingram, Anstis & Corben 1975). In *Sooglossus* of the Seychelles Islands and in many dendrobatids, adults carry tadpoles on their backs (Salthe & Mecham 1974).

The parental behaviour of dendrobatids needs to be investigated in more detail. In many cases, the sex that carries the tadpoles is unknown. Most reports are of males carrying tadpoles (Senfft 1936; Dunn 1941; Eaton 1941; Breder 1946; Hoogmoed 1972). However, only females carry tadpoles in *Colostethus inguinalis* (personal observations), and both sexes have been reported to carry them in other *Colostethus* (Mudrack 1969), *Dendrobates azureus* (Hoogmoed 1972; Polder 1974b), and *D. pumilio* (A. Stanley Rand, personal communication).

Tadpole carrying in dendrobatids may have originally evolved from the habit of 'brooding' or guarding eggs after deposition, but many questions concerning the adaptive significance of this behaviour remain unanswered. What

factors favour parental care by one sex or the other in different species? Has co-operative parental care evolved in any species? Do adults care for eggs in some way, or simply wait for them to hatch? Are tadpoles carried for long periods of time or transported directly from the oviposition site to water? When males assume the parental role, to what extent does this interfere with their ability to attract additional mates? Do males sometimes care for the eggs of more than one female within a territory?

Finally, the relationship between parental investment patterns and intrasexual competition needs to be explored. Trivers (1972) pointed out that when males invest more effort than do females in care of young, there may be a reversal of the usual sex roles in social behaviour. If the availability of males to carry tadpoles limits female reproductive success, then females might compete among themselves for males. This might take the form of active courtship of males by females or female aggressiveness and territoriality.

There are scattered observations in the literature suggesting sex-role reversal in some dendrobatids. For example, females seem to initiate courtship in *D. azureus* and females have been observed fighting with one another (Polder 1974a). Dunn (1941) reported several females following a single calling male in *D. auratus*, and Senfft (1936) saw females of the same species jumping at each other and wrestling in an apparent attempt to gain access to a single calling male. Female aggressiveness and territoriality also occurs in several species of *Colostethus* (Test 1954; Sexton 1960; Durant & Dole 1975). This behaviour is not always correlated with male parental care, however. In *C. inguinalis*, females defend temporary territories near water, but they also carry the tadpoles (personal observations). Female territoriality in some species may be related to ecological factors such as availability of moisture, shelter, or favourable feeding sites.

At present, data on parental care in dendrobatids is too fragmentary to provide a coherent evolutionary picture. Nevertheless, the presence of parental care in conjunction with complex courtship and aggressive behaviour suggests that dendrobatids would be an ideal group for future research on the evolution of anuran social systems. This would provide an opportunity to test theories of parental investment and sexual selection proposed by Williams (1966, 1975), Trivers (1972) and others. In investigating these

problems, we should bear in mind that the social system of a particular species often represents an evolutionary compromise between the conflicting interests of males and females attempting to maximize their own fitness.

Conclusion

In this review, I have tried to describe the major features of anuran social behaviour and to point out the selective pressures that may be important in shaping the evolution of anuran social systems. It is now essential that future workers move from a purely descriptive to a more quantitative approach to anuran behaviour. In this respect, there can be no substitute for long-term field studies of marked individuals. Researchers should pay close attention to competitive relationships among individuals of both sexes, because intrasexual competition provides the key to many of the most elaborate forms of anuran behaviour.

Problems that require special attention include the relative importance of vocal signalling and searching in mate acquisition, changes in mate-locating behaviour with changes in male density, competitive strategies of individual males in choruses, the adaptive significance of aggression and territoriality, the relative importance of female choice in different social systems and the criteria used by females to select mates, the development of complex courtship interactions between males and females, ecological factors governing the evolution of parental investment patterns, and the influence of parental investment on mating systems and sexual selection.

There is also a need for additional quantitative studies on all aspects of anuran life histories, ecology, and demography, since these factors are important in the evolution of social behaviour. Age at first reproduction, age specific mortality, relative growth of males and females, age specific fecundity, and frequency of reproduction by individual females are unknown for most species. It is especially important to have additional information on tropical species, since the vast majority of anurans live in tropical regions. Finally, additional experimental investigations of acoustic communication and auditory neurophysiology would shed light on functional aspects of call structure and the location of calling males by females.

Some of the generalizations that I have made in this paper may have to be modified in light of additional research, particularly in tropical species. Nevertheless, I hope the ideas expressed

in this review will provide a stimulus for more extensive field studies in the future. At present, the study of anuran social behaviour is many years behind similar studies on birds and mammals. Yet these animals occupy a crucial position in vertebrate evolution, and their behaviour should form an integral part of any unified theory of sociobiology.

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Appendix 1. Breeding Behaviour of Some Ranids with Prolonged Breeding Periods

Species and area	Breeding period	Male behaviour	Female behaviour	Sources
<i>R. clamitans</i> Eastern U.S.	2–3 months in summer	Call from sites near shore 2–4 m apart; territorial	Approach and contact calling males; eggs laid at calling site	Wright 1914; Martof 1953; Brode 1959; Schroeder 1968; Wells 1976
<i>R. catesbeiana</i> Eastern U.S.	2–3 months in summer	Call from sites 3–6 m apart; territorial	Approach and contact calling males	Wright 1914; Blair 1963; Emlen 1968; Wiewandt 1969
<i>R. grylio</i> Georgia, Florida	3–6 months	Call from widely spaced sites in open water	Unknown	Wright 1932; Duellman & Schwartz 1958
<i>R. capito</i> Georgia, Florida	6–9 months	Call from widely spaced sites among roots and at base of trees in water	Unknown; eggs found in sites similar to male calling sites	Wright 1932; Wright & Wright 1949
<i>R. adenopleura</i> China	3–4 months	Call from shallow water or burrow	Approach calling males; eggs probably laid at male calling site	Liu 1950
<i>R. Boulengeri</i> China	3–5 months	Call from isolated pools in streams; usually only one male per pool	Unknown; eggs found under rocks in pools where males call	Liu 1950

Appendix 2. Breeding Behaviour of Some Bufonids with Prolonged Breeding Periods

Species and area	Breeding period	Male behaviour	Female behaviour	Sources
<i>B. woodhousei fowleri</i> Indiana	About 75 days in late spring	Call from widely spaced sites in vegetation or on shore; no active searching	Unknown; probably approach calling males	Cory & Manion 1955; Jones 1973
<i>B. canorus</i> California	About 1½ months in late spring	Call from sites 7–14 m apart; some active searching in dense groups	Unknown	Karlstrom 1962
<i>B. calamita</i> Europe	3–4 months in spring and summer	Call from sites spaced along shores of ponds streams; no active searching	Approach calling males	Rühmekorf 1958; Heusser 1963, 1969a; Smith 1969; Heusser & Miesterhans 1969
<i>B. maculatus</i> Africa	Throughout rainy season	Call from widely spaced sites concealed on land around ponds; no active searching	Apparently approach calling males; will approach speakers playing calls	Tandy & Keith 1972
<i>B. garipeensis</i> Africa	2–3 months in rainy season	Call from widely spaced exposed sites on shore	Unknown	Tandy & Keith 1972

Appendix 3. Breeding Behaviour of Some Hylids with Prolonged Breeding Periods

Species and area	Breeding period	Male behaviour	Female Behaviour	Source
<i>Pseudacris nigrita</i> Southeastern U.S.	3-6 months	Call from sites spaced several centimetres apart in vegetation in shallow water	Approach and contact calling males	Livezey 1952; Martof & Thompson 1958; Hardy 1959
<i>P. streckeri</i> Southeastern U.S.	3-5 months	Call from sites spaced several centimetres apart in vegetation in shallow water	Move toward speakers playing calls; no field observations	Bragg 1942
<i>Hyla crucifer</i> Eastern U.S.	1-2 months	Call from tufts of vegetation spaced several centimetres to several metres apart	Approach calling males	Gerhardt 1973; Rosen & Lemon 1974
<i>H. versicolor</i> <i>H. chrysocelis</i> Eastern U.S.	1-3 months	Call from shrubs or water's edge in sites spaced 0.75 m or more apart	Approach and jump on calling males	Noble & Noble 1923; Littlejohn 1958; Pierce & Ralin 1972; Fellers 1975
<i>H. andersonii</i> New Jersey	2-3 months	Call in shrubs or at water's edge; sites spaced several metres apart	Approach and contact calling males	Noble & Noble 1923
<i>H. arenicolor</i> Western U.S.	2-3 months	Call from rocks near water; spaced 1 m or more apart	Approach and sometimes contact calling males	Brown & Pierce 1965
<i>H. cinerea</i> Southeastern U.S.	2-4 months	Call in shrubs near water; spaced 0.5 m or more apart	Approach and contact calling males	Blair 1958b; Garton & Brandon 1975
<i>H. regilla</i> Western U.S. and Canada	3-5 months	Call in shrubs near water; spaced at least 40-200 cm apart	Approach and contact calling males	Snyder & Jameson 1965; Allan 1973; Whitney & Krebs 1975a, 1975b
<i>H. arborea</i> <i>H. meridionalis</i> Europe and Israel	2-5 months	Call from land, shrubs, or water; spaced at least at least 30 cm apart	Approach and contact calling males	Eibl-Eibesfeldt 1952; Heusser 1961; Schneider 1967 1968; Schneider & Nevo 1972; Blankenhorn 1972
<i>H. elaechroa</i> Costa Rica	All year in rains	Call from low bushes around ponds; spaced at least 1 m apart	Unknown	Duellman 1967
<i>H. rosenbergi</i> Panama	5-6 months	Call from mud nests irregularly spaced along streams	Approach calling males in their nests and jump on them	Breder 1946
<i>Agalychnis callidryas</i> Mexico	1-2 months	Call from branches over water; spaced at least 50 cm apart	Approach calling males; males may move toward females or females may contact males	Pyburn 1970

Appendix 4. Breeding Behaviour of Some Ranids with Short Breeding Periods

Species and area	Breeding period	Male behaviour	Female behaviour	Sources
<i>R. sylvatica</i> Alaska, New York, Tennessee	4-14 days in early spring	Call in dense groups in shallow water; active searching and struggling for females	Passive; eggs laid in communal masses in full sunlight	Banta 1914; Noble & Farris 1929; Wright & Wright 1949; Herreid & Kinney 1967; Meeks & Nagel 1973
<i>R. pipiens</i> Minnesota, New York	7-28 days in early spring	Call in dense groups in shallow water; active searching and struggling for females	Passive; eggs laid in separate masses or in clumps	Wright 1914; Wright & Wright 1949; Merrell 1968
<i>R. palustris</i> New York	14-21 days in early spring	Call under water or on surface; amount of searching and struggling unknown	Unknown; eggs laid in limited area of pond	Wright 1914; Wright & Wright 1949
<i>R. pretiosa</i> British Columbia	10-14 days in early spring	Call in dense groups in shallow water; active searching and struggling for females	Passive; eggs laid in communal masses in full sunlight	Turner 1958; Licht 1969, 1971
<i>R. areolata</i> Oklahoma	A few days in spring	Call in dense groups in shallow temporary water; active searching and struggling for females	Probably passive, eggs laid in communal masses in shallow water	Bragg 1953, 1954
<i>R. aurora</i> British Columbia	9-21 days in early spring	Call under water in dense groups in ponds and lakes; approach and clasp nearby frogs	Unknown; eggs laid in isolated clutches or clumped together under water	Licht 1969, 1971; Calef 1973
<i>R. temporaria</i> Europe and England	12-14 days in early spring	Call in dense groups in ponds, active searching and struggling for females	Passive; eggs laid in communal masses in shallow water	Eibl-Eibesfeldt 1956; Rühmekorf 1958; Savage 1961; Heusser 1961; Smith 1969; Günther 1969; Van Gelder & Hoedemaekers 1971; Geisselmann et al. 1971
<i>R. arvalis</i> Europe	5-14 days in early spring	Call in dense groups in ponds; active searching and struggling for females	Unknown; eggs laid in communal masses in shallow water	Eibl-Eibesfeldt 1956; Rühmekorf 1958; Günther 1969; Van Gelder & Oömen 1970; Van Gelder & Hoedemaekers 1971
<i>R. dalmatina</i> Europe	5-30 days in early spring	Call under water; amount of searching and struggling unknown	Unknown; eggs laid on plants under water	Geisselmann et al. 1971; Schneider 1973
<i>R. esculenta</i> complex Europe and England	5-10 days in early spring in cold regions; may have longer breeding period with several peaks in some areas	Usually call in dense groups in ponds, with active searching; may maintain individual distance in some choruses	Passive in dense groups; may approach calling males in lower densities; eggs clumped at surface in vegetation	Rühmekorf 1958; Heusser 1961; Forselius 1963; Smith 1969; Wahl 1969; Van Gelder & Hoedemaekers 1971
<i>R. plancyi</i> China	14-21 days in spring	Call in dense groups in ponds; some active searching and struggling for females	Unknown; eggs laid on plants at surface	Liu 1930a, 1930b
<i>R. nigromaculata</i> China, Japan	10-21 days in spring or early summer	Call in dense groups in shallow water; active searching and struggling for females	Unknown; eggs laid on plants at surface	Liu 1930a, 1930b, 1931, 1950; Okada 1966
<i>R. japonica</i> Japan	21-35 days in spring	Call in dense groups in rice fields or ponds; amount of searching and struggling unknown	Unknown	Okada 1966

Appendix 5. Breeding Behaviour of Some Bufonids with Short Breeding Periods

Species and area	Breeding period	Male behaviour	Female behaviour	Sources
<i>B. americanus</i> Eastern North America	3-6 days in spring	Usually call in dense groups in shallow water; active searching and struggling for females	Usually passive; may approach calling males in small choruses	Cory & Manion 1955; Oldham 1966; Jones 1973; Wells, personal observations
<i>B. w. woodhousei</i> Texas	A few days after summer rains	Call in very dense groups in temporary water; active searching and struggling for females	Unknown	Thornton 1955, 1960
<i>B. cognatus</i> Southwestern U.S.	A few days after summer rains	Often call in dense groups in shallow water, but density varies; active searching at high densities	Unknown	Bragg, 1936, 1937, 1940; Brown & Pierce 1967
<i>B. alvarius</i> Southwestern U.S.	A few days after summer rains	Form dense groups in semi-permanent water; reduced mating calls; active searching and struggling for females	Probably passive	Blair & Pettus 1954
<i>B. exsul</i> California	14-21 days in spring	Form groups of 10-100 males in permanent water; reduced mating calls; amount of searching unknown	Unknown	Schuieler 1962
<i>B. marinus</i> Panama	Opportunistic during rainy weather	Call in large groups or individually; active searching and struggling in dense groups	Unknown	Breder 1946
<i>B. bufo bufo</i> Europe	6-14 days in early spring	Form very dense groups in shallow water; reduced mating calls; active searching and struggling for females	Do not approach calling males; passive during struggles	Eibl-Eibesfeldt 1950; Rühmekorf 1958; Huesser 1960, 1961, 1963, 1968a
<i>B. bufo asiaticus</i> China	14-21 days in early spring	Call in dense groups in shallow water; active searching and struggling for females	Passive during struggles among males	Liu 1930a, 1930b
<i>B. raddei</i> China	14-21 days in spring	Call in dense groups; active searching and struggling for females	Passive during struggles among males	Liu 1930a, 1930b, 1931, 1950
<i>B. regularis</i> Africa	Beginning of rainy season	Call in dense groups in shallow water; approach and clasp nearby toads	Do not approach individual calling males	Tandy & Keith 1972
<i>B. rangeri</i> Africa	End of rainy season	Call in dense groups; males randomly spaced on rock outcrops; approach and clasp nearby toads	Unknown	Tandy & Keith 1972
<i>B. carens</i> Africa	After rains	Call in dense groups on surface of water; amount of searching unknown	Unknown	Tandy & Keith 1972
<i>B. rosei</i> Africa	End of rainy season	Form extremely dense groups in well-vegetated semi-permanent water; amount of searching unknown	Unknown	Tandy & Keith 1972

Appendix 6. Breeding Behaviour of Some Pelobatids, Microhylids, and Discoglossids

Species and area	Breeding period	Male behaviour	Female behaviour	Sources
Pelobatidae				
<i>Scaphiopus bombifrons couchi hammondi hurteri holbrookii</i> Southwestern and eastern U.S.	All species breed for a few days after heavy spring and summer rains	Usually call while on surface of water; some call on land; form very dense groups; very active searching and struggling for females in some species	Probably largely passive in dense choruses, although some may approach calling males in small groups	Ball 1965; Bragg 1945, 1965; Blair 1947; Wright & Wright 1949; Hansen 1958; Axtell 1958; Bogert 1960
<i>Pelobates fuscus</i> Europe	A short period in early April	Call under water; males usually about 1 m apart approach and clasp nearby frogs	Unknown	Eibl-Eibesfeldt 1956; Rühmekorf 1958
Microhylidae				
<i>Gastrophryne olivacea</i> Oklahoma, Kansas	1-2 days after summer rains	Call in very dense groups in shallow water; active searching at high densities	Probably do not approach calling males in dense groups	Bragg 1950 & Fitch 1956; Awbrey 1965
<i>Gastrophryne carolinensis</i> Eastern U.S.	Late spring and summer	Call from concealed isolated sites in vegetation or shallow water	Approach individual calling males	Bragg 1950; Anderson 1954; Jameson 1955a
<i>Hypopachus variolosus</i> Mexico, Central America	A few days after summer rains	Variable chorus size: males in dense choruses actively search for females on water's surface; call from stationary sites in small choruses	Probably approach calling males only in small choruses	Wiewandt, Lowe & Larson 1972; Nelson 1973
Discoglossidae				
<i>Discoglossus pictus</i> <i>D. sardus</i> Europe	Several short periods during the year	Call above or under water; approach and clasp nearby frogs	Probably do not approach individual calling males	Knoepffler 1962; Weber 1974
<i>Bombina bombina</i> <i>B. variegata</i>	Several short periods from April to July	Call at surface of water; maintain small individual distance; approach and clasp nearby frogs	Do not approach individual calling males; not strongly attracted to male calls played experimentally	Heusser 1961; Lörcher 1969
<i>Alytes obstetricans</i> Europe	Several short periods from April to August	Call on land; males spaced at least 10-20 cm apart; move around while calling	Give courtship calls while approaching individual calling males	Heinzmann 1970