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Breeding ecology and behavior were investigated in a field study of three sympatric anuran amphibians in the Oregon Cascade Mountains: the western toad (*Bufo boreas*), the Cascades frog (*Rana cascadae*) and the Pacific treefrog (*Hyla regilla*).

A comprehensive study of the western toad mating system was conducted at three populations during five years (15 explosive-breeding aggregations). Two size-dependent pairing patterns (a large male mating advantage and size assortative mating) occurred variably among aggregations and among breeding days within aggregations. Body size variation and the degree of sexual size dimorphism explained much of the mating pattern variability. Field observations and experiments suggest nonrandom mating resulted from male-male exploitative competition for mates and passive female choice of mates. Density and sex ratio had little affect on pairing behavior. Sporadic mass-predation on breeding toads was associated with pair-separations and may have influenced pairing patterns. Toads showed sex and site differences in multiyear breeding schedules, recapture/survival rates, and yearly and multiyear cumulative mating success.

The opportunity for selection on toads was partitioned into 3 selection episodes: adult survival, mating success, and fertility. The largest contributors to selection opportunity were mating success for males, and clutch size (fertility) for females. At some aggregations, the opportunity for sexual selection on males was the lowest recorded for anurans.

Temporal and spatial synchrony of breeding occurred with Cascade frogs and Pacific treefrogs. During two years, interspecific interactions resulted in the displacement of treefrogs by Cascade frog males from the warmer areas of the ice-covered pond.

The Ecological and Behavioral Dynamics of Breeding in Three Sympatric Anuran Amphibians

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I would like to make an addition to the Chinese Proverb that has hung on my office door the last six years:

> Never try to catch two frogs with one hand,
> unless you rudely interrupt their nuptials.

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THE ECOLOGICAL AND BEHAVIORAL DYNAMICS OF BREEDING IN THREE SYMPATRIC ANURAN AMPHIBIANS

GENERAL INTRODUCTION

Variance in reproductive success (lifetime fitness) is the basis of evolutionary change. Variation in mating success is the key result of Darwin's (1871) concept of sexual selection. Darwin considered two proximate mechanisms of sexual selection, mate choice and mate competition, from which mating success variation arises. Although Darwin initially used his theory of sexual selection to explain sexually dimorphic characters in animals, it has also become the basis of studies of mating system evolution (e.g. Halliday 1978; Borgia 1979; Payne 1979; Partridge and Halliday 1984).

The use of the two components of sexual selection, mate choice and mate competition, for the description of intra- and inter-sexual associations during breeding provides a framework for mating system classifications. However, unlike previous classification systems, sexual selection has been useful in the generation of predictions of mating system evolution. Mating systems can be largely determined by the intensity and form of sexual selection (e.g. Orians 1969; Emlen and Oring 1977).

Components of animal life history, demography and ecology are important for the operation of sexual selection. The intensity of sexual selection is affected by the necessity of parental care for young survival, and ecological and demographic conditions of breeding populations. The importance of parental investment in sexual selection and mating system theories was considered by Trivers (1972). He proposed that the sex investing less in offspring should compete for the high-investing sex, and the degree of mate competition should vary with the sexual disparity of parental investment. Ecological factors can affect mating systems by altering the extent of sociality during reproduction and constraining the operation and intensity of sexual selection. Emlen and Oring (1977) suggested mating systems be defined by the behavioral potential of individuals to monopolize mates. This "potential" depends on the temporal and spatial distribution of mates and resources (e.g. food, nesting sites), as well as demographic conditions of breeding populations such as density and sex ratio. For example, variance in reproductive success should increase with an increasing breeding sex ratio, resource clumping, or an asynchronous mate distribution. Additionally, density may affect the cost of mate or resource defense, change the types of sexual interactions and cause mating system variation (Emlen and Oring 1977).

Theoretical development of sexual selection theory has progressed in recent years (e.g. Wade 1979; Wade and Arnold 1980; Arnold and Wade 1984a, 1984b). Mathematical treatments by Wade and Arnold (op. cit.) of reproductive success have provided an operational measure of the intensity or opportunity for sexual selection based on the mean and variance in mating success, defined as the number of mates per individual. Potential problems with this definition are outlined by Koenig and Albano (1986). Furthermore, Wade and Arnold (1984a, 1984b) provided an assessment of the opportunity for selection, including the effects of both natural and sexual selection. By partitioning fitness into components (e.g. viability, mating success, fertility), the distinction of the contributions of natural selection (based on differential survival and fertility) and sexual selection (based on differential mating success) to the total opportunity for selection within a population can be estimated. The opportunity for sexual selection (e.g. Kluge 1981; Trail 1986) or the relative importance of selection episodes to the total opportunity for selection (Vehrencamp and Bradbury 1984) may be useful for quantitative mating system classifications.

The theoretical framework now available with regard to sexual selection and breeding behavioral ecology has allowed the study of mating systems to become a predictive rather than descriptive science. To examine mating system theory, analyses of interactions between ecological, behavioral (e.g. mate choice and mate competition) and fitness components of animals should be conducted (Vehrencamp and Bradbury 1984). However, such comprehensive data on animal breeding behavior and ecology are rare in the literature. Additionally, the opportunity for selection and the partitioning of selection into episodes (including sexual selection) can be addressed with empirical data on lifetime reproductive success of individuals (e.g. Arnold and Wade 1984b). Estimates of lifetime reproductive success are available from few previous studies of animal mating systems. Longitudinal studies conducted on animals throughout their lives most adequately assess variation in lifetime reproductive success (Arnold and Wade 1984b). Additionally, intraspecific variation in the ecological, demographic, and behavioral components of animal populations emphasize the importance of multi-site studies. For the empirical examination of mating system theory, comprehensive field studies of animal ecology, mating behavior, and fitness considerations conducted at several populations over individual lifetimes are needed.

Organization of Thesis

This thesis reports results of a field study examining several aspects of breeding ecology and behavior of three sympatric anuran amphibians in the Oregon Cascade Mountains: the western toad (*Bufo boreas*), the Cascades frog (*Rana cascadae*), and the Pacific treefrog (*Hyla regilla*). I conducted a comprehensive, multisite, multiyear study of the western toad mating system in which both observational and experimental techniques were used at natural breeding sites. Comparative issues of breeding behavioral ecology were addressed in a field study of Cascades frogs and Pacific treefrogs at one site in several years.

Western toad breeding was monitored during a longitudinal study of three large populations. Using mark-recapture methods, breeding individuals were censused throughout breeding during five years, 1982-1986. Chapters I-V of this thesis address specific aspects of the structure of the western toad mating system at the 15 breeding aggregations (3 sites x 5 years):

Chapter I reports variable occurrences of two nonrandom mating patterns at the 15 breeding aggregations. The variation in degree of nonrandom mating is largely explained by the demographic conditions of the breeding aggregations.

Chapter II examines the dynamics of western toad breeding behavior by observations at the natural breeding sites and by field experiments. Both behavioral components of sexual selection, mate choice and mate competition, may influence pairing in this anuran. The potential influence of three demographic factors (density, sex ratio, and toad body size distribution) on toad pairing behavior are addressed. Western toad mating behavior can result in the observed patterns of nonrandom mating (Chapter I).

Sex and site differences in the multiyear breeding schedules and survival estimates of western toads are reported in Chapter III.

Chapter IV provides estimates of western toad lifetime reproductive success and opportunity for selection in the three populations. Variation in the yearly and multiyear cumulative mating success of males greatly exceeds that of females. Two aspects of fertility, clutch size and fertilization efficiency, are assessed. The opportunities for both natural and sexual selection are estimated from data on mating success, fertility and adult survival (Chapter III). Measures of selection opportunities may be useful for limited classifications of anuran mating systems.

Chapter V reports the incidence of predation on breeding toads, and changes in toad mating behavior associated with predation.

The breeding dynamics of Cascades frogs were examined at a pond-population during four breeding seasons, 1983-1986. There is spatial and temporal synchrony of anuran-species breeding at this pond, unlike at the three western toad sites investigated. Chapter VI reports the interspecific interactions between two anurans, Cascades frogs and Pacific treefrogs, during breeding. The dominance of Cascades frogs during aggressive encounters with Pacific treefrogs may have resulted in the apparent competitive exclusion of treefrogs from the warmer Cascades frog breeding area.

Natural History and Breeding Biology of Study Animals

Western Toad

The western toad belongs to the cosmopolitan genus *Bufo*, which is present in Africa, Southern Asia, Europe, North and South America. It is one of about 30 bufonids inhabiting North America (Blair 1963) and is one of two species found in the Pacific Northwest of the United States (Nussbaum et al. 1983). The subspecies *B*. *b*. *boreas* (the boreal toad) is the only bufonid in Central and Western Oregon.

Little is known of western toad breeding biology. In Montana, only diurnal breeding activity was observed at several ponds between May and July (Black and Brunson 1971). Their daily activity pattern showed seasonal changes in California, where they had diurnal activity during the spring months (typical breeding times) and nocturnal activity in the summer (Smits 1984). At communal breeding aggregations in Montana and Oregon, males clasped each other as they searched for mates, and males gave "release calls" when clasped by other toads, but did not give "true mating" (i.e. advertisement) calls (Black and Brunson 1971; Nussbaum et al. 1983). In the Oregon Cascade Mountains, breeding occurs from May to July, females produce an average of 12,000 eggs per clutch (Samollow 1980), tadpoles form dense aggregations (e.g. O'Hara and Blaustein 1982; Blaustein 1988), and metamorphic aggregations along lake shores are found between August and September. Prereproductive mortality may reach 99% (Nussbaum et al. 1983). Western toad adults are insectivorous and their toxic skin secretions may deter predators (Nussbaum et al. 1983).

Cascades Frog

The Cascades frog belongs to the cosmopolitan family Ranidae, and is a member of the only American ranid genus, *Rana*. Of the 250 *Rana* species, 21 occur in North America and 5 are found in Central and Western Oregon. The Cascades frog is found in the Olympic Mountains of Washington and the Cascade Mountains of Washington, Oregon and Northern California. The Cascades frog is not generally found in sympatry with other ranids, although it shares part of its range with the yellow-legged frog, *R. pretiosa*.

The Cascades frog is an "explosive" breeder, having a short breeding season lasting from a few days to two weeks (Nussbaum et al. 1983; Briggs 1987; personal observations). In Oregon, breeding occurs when the ice begins to melt from breeding ponds (Briggs 1976, 1987; personal observations). In a study conducted in Jefferson County, Oregon, males gave release calls and three other types of calls during breeding: series clucks, double clucks, and mews (Briggs 1976, 1987). The function of these calls was not determined. They may play a role as potential advertisement calls to attract mates, for mate selection by females, in male territorial disputes, or as factors affecting male-male mate competition. Females oviposit in communal egg masses (Briggs 1976, 1987; O'Hara and Blaustein 1981), and larvae form small aggregations (e.g. Blaustein 1988) and metamorphose within about two months (Nussbaum et al. 1983). The Cascades frog has a fine-tuned kin recognition ability (e.g. Blaustein 1988): both larvae and new metamorphs prefer to associate with kin over non-kin. At one population (Jefferson Co., Oregon), age at sexual maturity was estimated at 3+ years, frogs lived 1-2 years and had annual mortality rates from 0.41-0.54, and few individuals lived more than 4-5 years (Briggs and Storm 1970).

Pacific Treefrog

The Pacific treefrog belongs to the very diverse family Hylidae, and to the genus, Hyla, which occurs in both the Old and New World (Nussbaum et al. 1983). It is the one Hyla species inhabiting the Pacific Northwest of the United States, having a very widespread distribution in this region.

There is variation in many aspects of Pacific treefrog life history and breeding biology. During their spring breeding season, they can be found in or near large lakes, small ponds, or flooded fields and ditches. Breeding activity at any one location begins from November to July, depending on habitat and elevation. Breeding can be prolonged, lasting 2-3 months (e.g. in the Willamette Valley, Oregon; Nussbaum et al. 1983) or more protracted, lasting a few weeks to one month (e.g. in the Oregon Cascade Mountains; personal observations). Males produce advertisement calls in breeding choruses which attract females and upon which mate selection by females is based (e.g. Whitney and Krebs 1975). Male call characteristics show geographic variation (Snyder and Jameson 1965). Three male mating tactics have been reported: (1) site-specific calling males, (2) noncalling satellite males, and (3) opportunistic males (Perrill 1984). Differential mating success among males with the various mating tactics has not been demonstrated (Perrill 1984). Females lay from 9 to 70 eggs (Nussbaum et al. 1983). Larvae usually metamorphose within two months and frogs can breed in their first year after metamorphosis. Pacific treefrogs eat small invertebrates and are preyed on by a variety of species during all life stages.

Study Sites

I investigated anuran breeding ecology and behavior at four locations in the Oregon Cascade Mountains. Western toad breeding biology was studied at three lakes: Lost Lake, Little Three Creeks Lake, and Todd Lake.
The interactions between Cascades frogs and Pacific treefrogs during breeding was examined at a small unnamed temporary pond.

Lost Lake

Lost Lake is located in the Santiam Pass of the Oregon Cascade Mountains (Linn County) at 1220 m elevation. It is a large lake, measuring over 1 km in its longest dimension and typically covering over 100 ha at its greatest level during the spring snow-melt. The water surface is frozen and snow-covered in winter, melting in May-June.

The lake is in the Willamette National Forest, and lake shore vegetation is dominated by Douglas fir (Pseudotsuga menziesii) and grand fir trees (Abies grandis). Cottonwood (Populus) and alder (Alnus) are also present. Vegetation along the shore breeding areas used by anurans at Lost Lake are primarily willows (Salix) that have been partially submerged from the spring high-water levels.

Western toads are the first amphibians to become active at the lake during the Spring snow-melt. Later in the spring and early summer, a large Pacific treefrog population inhabits the opposite (eastern) side of the lake from the western toad breeding area (north-west section). Rough-skinned newts (Taricha granulosa) also inhabit the lake, and I found one Cascades frog at the lake in my five study years. During the western toad breeding season, most other animals are dormant or in their winter hibernation because the surrounding areas are still snow-covered. Leeches (family Hirudinea) were abundant at the lake in one of five study years. Aquatic insects generally became active in the weeks following western toad breeding, and were not abundant at the oviposition site. Ravens (Corvus corax), ospreys (Pandion haliaetus), gray jays (Perisoreus canadensis), and

Barrow's goldeneye ducks (Bucephala islandica) were the most conspicuous birds present at the site during toad breeding. Their interactions with toads were usually minimal (but see Chapter V). The only mammal seen within the breeding area in my five study years was a single river otter (Lutra canadensis). The lake is stocked yearly with trout (Salvelinus species). The lake location adjacent to the Santiam Highway makes it easily accessible to people.

Little Three Creeks Lake

Little Three Creeks Lake is located in Deschutes County, Oregon, east of the Three Sisters mountain peaks, at an elevation of about 2000 m. It is a smaller lake than Lost Lake, measuring approximately 20 ha. Little Three Creeks is ice-covered until early July, and snow in the surrounding forest is usually melted by late July. Shore vegetation includes Douglas fir, grand fir, sedges (Carex), and grass-like quillwort (Isoetes).

A small Pacific treefrog breeding population becomes active after western toads breed at the lake. In two years, I saw a single Cascades frog at the lake. Spotted sandpipers (Actitis macularia) and red-winged blackbirds (Agelaius phoeniceus) are occasionally present along the lake shore. Aquatic insects are not abundant in the early spring, and the lake is stocked with trout. The area is not heavily trafficked by people because it is over 1 km from the nearest road and campsite.

Todd Lake

Todd Lake is located along the Cascades Lakes Highway in Deschutes Co., Oregon, at 1860 m elevation. During my five study years it was ice-covered until early-to-mid July. Western toads and Cascades frogs breed along the western shore of the lake adjacent to a sloping meadow. Their oviposition sites are located in small shallow alcoves newly-opened from snow-melt. Sedge grass from the previous year lines these alcoves. The surrounding forest includes fir and pine trees. Pacific treefrogs are also present in meadows adjacent to the lake, and become active soon after western toads and Cascades frog breeding activities abate. Spotted sandpipers and ravens are regularly seen in or near the meadow next to anuran breeding areas. This lake is stocked with trout, and has moderate-to-heavy human foot-traffic along the shore during the summer.

Small Pond

A small (100 x 90 m) temporary pond in Linn Co., Oregon, was used for the study of Cascades frog and Pacific treefrog breeding dynamics. Breeding of both anurans begin when the pond is partially melted from winter snow and ice.

Cascades frogs cease breeding when about half the pond is free of ice and snow, and Pacific treefrogs continue breeding until the pond is completely melted. Single western toads were seen at the pond in two years and a single clutch of toad eggs was oviposited at the pond in one of my study years. Rough-skinned newts are also present at the pond. Jays (Corvidae) and mallard ducks (*Anas platyrhynchos*) regularly forage in the pond as it is melting.

A variety of invertebrates are present at the pond during the anuran breeding seasons. Caddis fly larvae (Limnephilidae) and leeches (Hirudinea) were seen attached to frog egg masses. Dragonflies (*Aeshna*), damselflies (Coenagrionidae), giant waterbugs (*Lethocerus americanus*), backswimmers (Notonectidae), and predacious diving beetles (*Dytiscus*) are also present. These invertebrates were not regularly seen at the other study sites during toad breeding.

LITERATURE CITED

Arnold, S.J. and M.J. Wade. 1984a. On the measurement of natural and sexual selection: theory. Evolution 38:709-719.

______. 1984b. On the measurement of natural and sexual selection: applications. Evolution 38:720-734.

Black, J.H. and R.B. Brunson. 1971. Breeding behavior of the boreal toad, *Bufo boreas boreas* (Baird and Girard), in Western Montana. Great Basin Nat. 31:109-113.

Blair, W.F. 1963. Evolutionary relationships of North American toads of the genus *Bufo*: A progress report. Evolution 17:1-16.

Blaustein, A.R. 1988. Ecological correlates and potential functions of kin recognition and kin association in anuran larvae. Behavior Genetics 18:449-464.

Borgia, G. 1979. Sexual selection and the evolution of mating systems. Pages 19-80. In: Sexual selection and reproductive competition in insects. M.S. Blum and N. A. Blum (eds.). Academic Press, New York.

Briggs, J.L. 1976. Breeding biology of the Cascade frog, *Rana cascadae*. Herp. Review 7:75.

______. 1987. Breeding biology of the Cascade frog, *Rana cascadae*, with comparison to *R. aurora* and *R. pretiosa*. Copeia 1987:241-245.

Briggs, J.L. and R.M. Storm. 1970. Growth and population structure of the Cascade frog, Rana cascadae Slater. Herpetologica 26:283-300.

Darwin, C. 1871. The descent of man and selection in relation to sex. Appleton, New York.

Emlen, S.T. and L.W. Oring. 1977. Ecology, sexual selection and the evolution of mating systems. Science 197:215-223.

Halliday, T. 1978. Sexual selection and mate choice. Pages 180-213. In: Behavioural ecology: an evolutionary approach. J.R. Krebs and N.B. Davies (eds.). Sinauer Assoc., Sunderland, Massachusetts.

Koenig, W.D. and S.S. Albano. 1986. On the measurement of sexual selection. Amer. Nat. 127:403-409.

Kluge, A.G. 1981. The life history, social organization, and parental behavior of Hyla rosenbergi Boulenger, a nest-building gladiator frog. Miscel. Public. Mus. Zool. Univ Mich. 160:1-170.

Nussbaum, R.A. E.D. Brodie, Jr., and R.M. Storm. 1983. Amphibians and reptiles of the Pacific Northwest. Univ. Press. Idaho, Moscow, Idaho.

O'Hara, R.K. and A.R. Blaustein. 1981. An investigation of sibling recognition in R. cascadae tadpoles. Anim. Behav. 29:1121-1126.

______. 1982. Kin preference behavior in Bufo boreas tadpoles. Behav. Ecol. Sociobiol. 11:43-49.

Orians, G.H. 1969. On the evolution of mating systems in birds and mammals. Amer. Nat. 103:589-603.

Partridge, L. and T. Halliday. 1984. Mating patterns and mate choice. Pages 222-250. In: Behavioral ecology: an evolutionary approach. Second edition. J.R. Krebs and N.B. Davies (eds.). Sinauer Assoc., Sunderland, Massachusetts.

Payne, R.B. 1979. Sexual selection and intersexual differences in variance of breeding success. Amer. Nat. 114:447-452.

Perrill, S.A. 1984. Male mating behavior in *Hyla regilla*. Copeia 1984:727-732.

Samollow, P.B. 1980. Selective mortality and reproduction in a natural population of *Bufo boreas*. Evolution 34:18-39.

Smits, A.W. 1984. Activity patterns and thermal biology of the toad *Bufo boreas halophilus*. Copeia 1984:689-696.

Snyder, W.F. and D.L. Jameson. 1965. Multivariate geographic variation of mating call in populations of the Pacific tree frog. Copeia 1965:129-142.

Trail, P.W. 1985. The intensity of selection: intersexual and interspecific comparisons require consistent measures. Amer. Nat. 126:434-439.

Trivers, R.L. 1972. Parental investment and sexual selection. In: Sexual selection and the descent of man, 1871-1971. B. Campbell (ed.). Aldine, Chicago.

Vehrencamp, S.L. and J.W. Bradbury. 1984. Mating systems and ecology. Pages 251-278. In: Behavioural ecology: an evolutionary approach. Second edition. J.R. Krebs and N.B. Davies (eds.). Sinauer Assoc., Sunderland, Massachusetts.

Wade, M.J. 1979. Sexual selection and variance in reproductive success. Amer. Nat. 114:742-747.

Wade, M.J. and S.J. Arnold. 1980. The intensity of sexual selection in relation to male sexual behavior, female choice, and sperm precedence. Anim. Behav. 28:446-461.

Whitney, C.L. and J.R. Krebs. 1975. Mate selection in Pacific tree frogs. Nature 255:325-326.

CHAPTER I

BREEDING ECOLOGY AND VARIABLE MATING PATTERNS IN THE WESTERN TOAD (Bufo boreas)

ABSTRACT

A long-term study of three western toad breeding populations uncovered extensive variability in the occurrences of two size-dependent mating patterns, a large male mating advantage and positive assortative mating by size. A third mating pattern, an early-arriving male pairing advantage, was found more consistently at the breeding aggregations. The relationships between the size-dependent mating patterns and several demographic, ecological, and behavioral components of breeding toads were examined by correlation and multiple regression analyses. Toad size variance and sexual size dimorphism explained much of the mating pattern variation. Mechanisms of sexual selection dependent on size variance and sexual size dimorphism may have produced both the mating patterns and the mating pattern variability. Several ecological parameters proposed to affect the intensity of sexual selection were not associated with the western toad mating patterns. These factors included population size, sex ratio, oviposition synchrony, and breeding season length. The correspondences of male pairing probability, male size, and male arrival day at the sites may have resulted in the mating patterns at some aggregations, but this mechanism is not a general cause of either mating patterns or mating pattern variability in the western toad. Predation also may have influenced western toad mating patterns.

INTRODUCTION

Animal mating systems and mating success can be affected by many aspects of ecology and behavior (e.g. Emlen and Oring 1977; Halliday 1978; Orians 1969; Trivers 1972; Vehrencamp and Bradbury 1984). The proximate components of sexual selection, mate choice and competition for mates (Darwin 1871), are perhaps the most commonly discussed behavioral aspects of animals having a direct affect on their mating success (e.g. papers in Bateson 1983; Blum and Blum 1978). The opportunity for (intensity of) sexual selection has been defined in relation to the variance in reproductive success (Arnold and Wade 1984a, 1984b; Trivers 1972; Wade 1979; Wade and Arnold 1980; but see Koenig and Albano 1986). The intensity of sexual selection may, in turn, be either influenced by or associated with demographic and ecological factors such as the breeding population density and sex ratio, spatial and temporal distribution of mates and resources, mate age-size distribution, breeding season length, and level of sexual dimorphism (e.g. Trivers 1972; Emlen and Oring 1977; Wells 1977; Howard 1978, 1981; Alexander et al. 1979).

Mating is not usually a purely random process in natural populations (Partridge and Halliday 1984) and patterns of nonrandom mating may be affected by demographic, ecological or behavioral aspects of animals in breeding populations. Nonrandom mating patterns have often been observed in anuran amphibians (e.g. Arak 1983; Howard and Kluge 1985; Olson et al. 1986). Two size-dependent mating patterns, a large male mating advantage and size assortment of mates have been reported to occur in several anuran species (e.g. Arak 1983; Berven 1981; Davies and Halliday 1977, 1979; Gatz 1981a, 1981b; Howard 1978, 1983; Howard and Kluge 1985; Kagarise Sherman 1980; Lee and Crump 1981; Robertson 1986; Ryan 1985; Sullivan 1982, 1983; Wells 1979; Wilbur et al. 1978; Woodward 1982a, 1982b). Anuran mating patterns may result from the proximate components of sexual selection, specifically female choice of mates and male-male competition for mates (Arak 1983; Berven 1981; Davies and Halliday 1977, 1979; Gatz 1981a, 1981b; Howard 1978, 1981; Howard and Kluge 1985; Lamb 1984; Licht 1976;

Robertson 1987; Ryan 1980a, 1985; Sullivan 1982, 1983; Whitney and Krebs 1975; Wilbur et al. 1978; Woodward 1982b). In anurans, the intensity of sexual selection, breeding behavior, and mating patterns may be affected by the breeding population size and sex ratio (Arak 1983; Berven 1981; Emlen 1976; Kagarise Sherman 1980; Sullivan 1986; Wells 1977), age/body size distribution (Berven 1981; Howard 1978, 1981; Sullivan 1987), breeding season length (e.g. Arak 1983; Lee and Crump 1981; Olson et al. 1986; Wells 1977), and breeding synchrony (Arak 1983; Emlen 1976; Howard and Kluge 1985; Kagarise Sherman 1980; Wells 1977).

Variable size-dependent mating patterns (i.e. the occurrences of both random and nonrandom mating) seems quite common within anuran species (Olson et al. 1986). In studies of natural breeding aggregations, nonrandom mating patterns occurred variably among breeding populations of a species, among breeding seasons within populations, or among days of breeding within breeding seasons (see discussion in Olson et al. 1986). The proximate causes of anuran mating pattern variability are unknown. Variability may be associated with breeding season length; variable patterns seem to occur more often in anurans with relatively short breeding seasons (Olson et al. 1986). Alternatively, variable degrees of the proximate components of sexual selection, and the interacting ecological factors of a breeding population may result in mating pattern variability (Arak 1983; Lawrence 1986; Olson et al. 1986).

This paper addresses the effects of several ecological components on size-dependent mating patterns in the western toad, *Bufo boreas*. The potential relationships between two variably expressed mating patterns, a large male mating advantage and positive assortative mating by size, and demographic conditions (breeding population size and sex ratio), aspects of toad size distribution (degree of sexual size dimorphism and toad size variance), and measures of the temporal distribution of mates (breeding season length and level of oviposition synchrony) were investigated. Additionally, the arrival day of toads at the breeding sites was examined with regard to toad size and mating success. Can western toad size-dependent mating patterns and mating pattern variability be explained by these aspects of breeding population ecology?

This long-term study represents an advance over many previous studies of anuran breeding which were conducted for a single season or at a single study site. Long-term studies conducted simultaneously at several sites can uncover the extent of intraspecific variability and yield a more complete understanding of the dynamics of breeding populations. Western toad breeding dynamics and mating patterns were examined for five years at three sites yielding a total of 15 breeding aggregations. The consistency of western toad breeding ecology and mating patterns were examined among populations, within populations among breeding seasons, and within seasons among days of breeding.

METHODS

Western toad breeding was monitored during five breeding seasons, 1982-1986, at three lakes in the Cascade Mountains of Oregon, USA: (1) Site A = Lost Lake (Linn County, elevation 1220 m), (2) Site B = Little Three Creeks Lake (Deschutes County, elevation 1950 m), and (3) Site C = Todd Lake (Deschutes County, elevation 1860 m). These three sites probably have distinct toad breeding populations; in the 5 years of the study, individually marked toads were never found at a lake different from the one at which they were first captured.

At the 15 breeding aggregations, adult toads were marked by toe-clipping. At all three sites in 1982-1984 and at sites B and C in 1985 and 1986, unique combinations of toes were clipped to allow individual identification of toads. Because of the limitations of the toe-clipping scheme used and the number of toads captured at site A, unique toe-clips were no longer possible for all toads in 1985 and 1986. At these two breeding aggregations, new captures were uniquely toe-clipped if they were captured paired, whereas unpaired toads were marked to indicate their date of arrival at the breeding site. Toe-clipping seems to be a permanent marking technique for western toads; toe-clips were easily discerned in recaptured toads year-to-year, with no visible toe-regeneration between years.

Toad size was assessed by one, two, or three measurements. The snout-urostyle length (SUL) of toads at all 15 breeding aggregations was measured to the nearest mm with a ruler. Male SUL was measured dorsally at the 15 breeding aggregations, as was female SUL in 1983-1986. Female SUL in 1982 was measured ventrally because toads captured in amplexus (pairs) during this year were not separated. Female dorsal lengths were estimated from ventral lengths by calculating a conversion factor from a sample of 14 females on which both ventral and dorsal SUL were measured ($y=0.97x+0.76$, $r^2=0.82$, Olson et al. 1986). In subsequent years, 1983-1986, pairs were separated for measurements and re-paired after handling. Dorsal lengths are reported in this paper.

The second size measure, toad mass (to the nearest g), was obtained using a Pesola scale. In 1983, mass was not measured. Mass was usually measured after SUL was determined or a few minutes after capture to minimize the amount of water on the skin of wet toads and to enhance the probability of an empty bladder. For females, only mass of gravid individuals are reported.

Fore-arm length (= arm length) was the third size measure collected from all toads captured in 1985 and 1986. These measurements were collected by measuring the radio-ulna section of a toad's arm to the nearest mm with a caliper.

Toads were captured along the lake shores near the breeding sites. New captures were marked, measured and returned to their approximate place of capture. Recaptures from previous years were recorded and measured but not toe-clipped. Within years, toads that were already captured were noted as still being present at the breeding site and were sometimes re-measured. This non-destructive sampling did not seem to affect toad breeding behavior; toads usually returned to their previous activity within minutes of release.

Censusing of toads spanned the breeding seasons at most breeding aggregations. However, breeding activity was monitored less thoroughly at site A in 1982, 1985 and 1986, and at site C in 1985. At these aggregations, either toads were sampled on all breeding days but only a subset of the toads present each day were captured (site A: 1985 and 1986) or a subset of the breeding days were censused. Because of the number of toads censused and the general mechanics of western toad mating behavior (Olson et al. 1986, Olson 1988b), data from these aggregations probably represent reliable samples for the purpose of this paper.

The three size measurements for each sex were compared between sites (Student's t-test, two-tailed; Snedecor and Cochran 1980). At each breeding aggregation, the mean SUL difference between males and females was calculated to estimate the degree of sexual size dimorphism. The mean sexual SUL difference at each site was determined and compared between sites (Student's t-test, two-tailed). Relationships within individuals between the three size measures (SUL, mass, and arm length) were examined by product-moment correlations.

Toad SUL was examined with respect to day of arrival at the breeding site for each sex. Regressions were conducted between mean toad size of new arrivals and arrival day. The first day of breeding activity recorded at a site each year was numbered as arrival-day "one", the second day was numbered "two", etc. Data from adjacent days were combined if fewer than 10 new toads were found at the breeding aggregation. A non-zero slope from this regression indicates that there is an overall relationship between toad size and arrival day at a breeding aggregation. A negative slope indicates early arrivals are larger toads, whereas a positive slope indicates late arrivals are larger.

Mating Patterns and Ecological Components

To address the extent of western toad nonrandom mating, two potential size-dependent mating patterns were examined at each breeding aggregation for the aggregation as a whole (= population analysis) and for the toads present at the sites each day of breeding (= daily analysis). Daily analyses were conducted because daily breeding dynamics may be different from the breeding dynamics summarized for the population as a whole. Also, individual toad breeding behavior is most likely a response to daily conditions. The daily analyses may also help our understanding of the proximate causes of population-level mating patterns. The two size-dependent mating patterns were examined with respect to SUL, mass, and arm length.

The two potential mating patterns investigated were a large male mating advantage (LMMA) and positive assortative mating by size (PAM). To examine the occurrences of a LMMA, the sizes of paired and unpaired males were compared (Student's t-test). PAM was examined by analyzing the sizes of males and females within pairs (product-moment correlation). A significant positive correlation of toad sizes within pairs indicates that mates are "assorted by size" (e.g. large males and females tend to mate, as do small males and females). In the population analyses, males were classified as either paired or unpaired; a male was considered paired if it was observed in amplexus with a female, whereas an unpaired male was never observed clasping a female. Males at a breeding aggregation were included in the population analysis only once. In the daily analyses, males found clasping the same female as on a previous day were not included in the subsequent-day's analysis because they were not part of the pool of "available" males searching for mates. A male was included in the analysis as being paired on each day examined if it was clasping a "new" female, one to which it was not clasped on a previous day. Thus, males could be included in daily analyses on more than one day. Data from adjacent days were combined to allow a sufficient sample size for comparison if fewer than 10 newly-paired males (both LMMA and PAM analyses) or 10 unpaired males (LMMA analyses only) were present on a day.

The relationships between the two size-dependent mating patterns and several ecological factors were investigated by correlation and multiple regression analysis. Correlation analysis was conducted to measure the pair-wise association between each ecological factor and mating pattern. Multiple regression was examined to address the possibility that a linear combination of ecological parameters may be produced to form a model to explain a significant proportion of the variation observed in each mating pattern. Correlation and multiple regression analyses were conducted with both population and daily data using the mating patterns with respect to all three size measurements, SUL, mass, and arm length.

In these analyses, the test-statistics of the mating patterns were used to indicate the degree to which the mating patterns were present in the breeding aggregations. For the mating pattern addressing a large male mating advantage, the t-statistic was modified (t^*) to remove the effect of sample size. For this modification, sample size was simply factored out of the equation for the Student's t. Thus, the t^*-statistic is essentially a measure of the size difference between paired and unpaired males. For positive assortative mating by size, the correlation coefficient (r) between male and female sizes within-pairs was used as the indicator variable against which the relationships with the ecological parameters was assessed.

The ecological parameters analyzed were those that could affect the mating patterns by potentially altering the demographic composition of breeding toads or their breeding behavior. These parameters included breeding season length (= no. days breeding activity), oviposition synchrony (explained below), size of the breeding population, number of males present, number of females present, sex ratio of breeding adults, variance in size of males and of females, difference in mean male and female size, study site, year of study, and calendar date of breeding (month and day).

Oviposition synchrony was defined as the ratio of the number of days oviposition occurred to the number of days breeding activity was observed. In western toads, highly synchronous oviposition usually indicated that pairs remained in amplexus for a longer time and spawned altogether at the same place and time, and that males had less opportunity to mate with more than one female (Emlen and Oring 1977). Asynchonous oviposition indicated the converse: pairs were in amplexus for a shorter time, on average, and males may have had the opportunity to re-enter the pool of "available " males searching for mates before all females were already clasped by males.

The degree of sexual size dimorphism was determined by the size (SUL) difference between the sexes. However, using the ratio of male to female size as the estimate of sexual dimorphism yielded similar results in the correlation and regression analyses. The value of each ecological component was determined separately for the population analyses and for each day of breeding in the daily analyses. Breeding season length and oviposition synchrony were included in population analyses but not daily analyses because these factors were measured for an entire breeding aggregation. Study site, year and calendar date of breeding were only included in daily analyses.

Product-moment correlations were conducted between the mating patterns, the r-value of PAM or the t* of LMMA, and the ecological parameters for both population and daily data. Inter-correlations between ecological parameters are also reported. Both population and daily data were analysed by stepwise multiple regression (Statpro: the statistics and graphics database workstation for use on Apple computers), using the r-value of PAM or the t* of LMMA as dependent variables and the ecological factors as independent variables. Stepwise inclusion of independent variables proceeded only with the maintenance of statistical significance (F-test, $p<0.05$). Partial regression coefficients (B) and the percentage of the variation in the mating pattern explained by the regression (R^2) are reported.

A third potential mating pattern was examined at the 15 breeding aggregations: the relationship between male mating success and male day of arrival. The proportion of newly-arriving males per day that were observed paired during the breeding season was regressed against arrival day. A negative slope of the regression line would indicate an early-male mating advantage and a positive slope would indicate a late-male pairing advantage. A binomial distribution was used to determine the relative expected frequency of receiving the resulting number of non-zero slopes.

RESULTS

POPULATION ANALYSES

Behavioral Ecology and Demography

Breeding was explosive at all 15 breeding aggregations; the breeding season ranged from 5 to 23 days (Table I.1). Toad activity at site A in 1984 was abruptly interrupted by a week of near-freezing weather accompanied by snow-storms, temporarily halting breeding and extending the breeding season to 23 days. Conversely, at site A in 1986, several warm days during breeding may have aided in producing a very short breeding season of 5 days.

Breeding occurred at the sites after the lakes and lake-shores were free of ice and snow. The date of the onset of breeding (Table I.1) became earlier each year of the study at most sites, reflecting earlier spring snow-melts. The calendar date of the breeding did not seem to affect the activity levels of the toads; breeding activity proceeded in the same manner each year at the three sites. The date of the onset of breeding was not associated with the length of the breeding season at the three study sites (Site A: $r=0.496$, $N=5$, $p>0.05$; Site B: $r=0.721$, $N=5$, $p>0.05$; Site C: $r=0.484$, $N=5$, $p>0.05$).

Variation among breeding aggregations was observed in oviposition synchrony, the ratio of the number of days oviposition occurred to the number of days toads were active at each breeding site. Oviposition was highly synchronous during four breeding seasons (1982-1985) at site A; egg-laying occurred on only a few of the days that breeding activity was apparent (Table I.1). Oviposition occurred on more days of toad breeding activity at the other breeding aggregations and oviposition occurred on all days of observed breeding activity (oviposition synchrony = 1.0) at one aggregation (site C, 1986). Oviposition was communal at all 15 breeding aggregations.

There was also considerable variation in the sex ratio of breeding adults among the 15 breeding aggregations. The breeding sex ratio (no. males/no. females) was male-biased in all years at sites A and B, and was female-biased during 2 of 5 years at site C (Table I.1).

The breeding behavior of male western toads differed in many respects from that of most anurans. Males did not produce an advertisement call to attract females at any time during breeding (Olson et al. 1986). Unlike other anurans with explosive breeding seasons (e.g. Davies and Halliday 1977, 1979; Lamb 1984), displacement of paired males from females by unpaired males was never observed and is probably not an important manner by which western toad males obtain mates (Olson et al. 1986, Olson 1988b). At most aggregations, paired individuals remained together through oviposition (Olson 1988b, 1989).

In all five years of the study, toads at site A were larger than those at site B and site B toads were larger than toads at site C (Fig. I.1, Students t-test, $p<0.05$ for all comparisons between sites A and B, and sites B and C). Females had consistently greater SUL, mass, and arm length than males at each of the 15 breeding aggregations (Fig. I.1; Student's t-test, $p<0.05$ for each of the 3 size comparisons). Females had consistently greater SUL, mass, and arm length than males at each of the 15 breeding aggregations (Fig. I.1; Student's t-test, $p<0.05$ for each of the 3 size comparisons between the sexes at the 15 aggregations). The number of breeding adults captured at each aggregation was large (Table I.1).

Sexual size dimorphism was variable among study sites. The toads were most dimorphic in size at site A and least dimorphic at site C. The dimorphism (mean female SUL minus mean male SUL) ranged from 1.5 to 3.0 cm (mean=1.94 cm, $N=5$) at the site A breeding aggregations, from 1.2 to 1.3 cm (mean=1.21 cm, $N=5$) at site B, and from 0.7 to 1.2 cm (mean=0.9 cm, $N=5$) at site C. These site-mean SUL differences were unequal (site A vs B, $t=2.74$, df=8, $p<0.05$; site A vs C, $t=3.73$, df=8, $p<0.01$, site B vs C, $t=3.43$, df=8, $p<0.01$). This trend of dimorphism among sites was also apparent for toad mass and arm length (mass difference between the sexes at site A: mean=79.8 g, $N=4$; site B: mean=39.0 g, $N=3$; site C: mean=23.3 g, $N=3$;

arm length difference at site A: mean=0.31 cm, N=2; site B: mean=0.16 cm, N=2; site C: mean=0.07 cm, N=2). Within individuals, the three size measurements (SUL, mass, and arm length) were highly correlated (Table I.2).

No consistent relationship between toad size (SUL) and arrival day was found when the slopes of the regression lines between these two factors were examined at the 15 breeding aggregations (Table I.1). For both males and females, there were many positive and negative slopes, none of which were significantly different from zero (t-test, $p > 0.05$). However, these slopes can represent significant changes in toad size over the course of breeding when the sample size of new arrivals each day is large and daily size variance small.

Mating Patterns and Demographic Components

A LMMA with regard to SUL was found at many breeding aggregations. In all 5 years of this study, paired males were larger in SUL than unpaired males at 6 of 15 (40%) breeding aggregations (Table I.1; site A: 1982, 1983; site B: 1982, 1983, 1984; site C: 1983). There was no LMMA with respect to mass at the 9 aggregations analyzed and there was no LMMA with respect to arm length at the 6 breeding aggregations at which arm lengths were collected (Table I.1).

The occurrence of PAM was more consistent among size measures (Table I.1). In all years, mates were positively assorted by: (1) SUL at 2 of 15 (13%) breeding aggregations (Site A: 1982, 1984), (2) mass at 1 of 10 (10%) aggregations (Site B: 1985), and (3) arm length at 2 of 6 (33%) aggregations (Site B: 1985, 1986).

An early male mating advantage was found at eleven of the 15 breeding aggregations (Table I.1, negative slopes in the regressions between male pairing success and arrival day at the sites). Only one slope was significantly different from zero (Site B in 1984), although the few number of days analyzed for each aggregation probably accounts for this. There is a very low probability that 11 of 15 slopes are negative by chance (binomial distribution, relative expected frequency=0.043).

Two correlations were found between the ecological parameters and the population size-dependent mating patterns (Table I.3). The degree of PAM by SUL at the breeding aggregations was positively correlated with male SUL variance and the sexual size dimorphism. No other correlations resulted from the comparisons of a LMMA and PAM with the ecological parameters (Table I.3).

Correlations among the ecological parameters included: male size variance vs. sexual size dimorphism (SUL: $r=0.88$, $df=13$, p 0.01; mass: $r=0.94$, $df=7$, $p<0.01$; arm length: $r=0.86$, $df=4$, $p<0.05$), female mass variance vs.

mass dimorphism between the sexes ($r=0.82$, $df=7$, $p<0.01$), male vs. female mass variance ($r=0.79$, $df=7$, $p<0.05$), breeding season length vs. population size of breeding adults ($r=-0.63$, $df=13$, $p<0.02$), and breeding season length vs. oviposition synchrony ($r=-0.54$, $df=13$, $p<0.05$).

Variation in some of the mating patterns was explained by toad breeding demography. Stepwise multiple regression using ecological parameters as independent variables and mating patterns as dependent variables yielded results reflecting the pairwise correlations obtained above (Table I.4). Male size variance explained 75% of the variation in PAM by SUL observed among breeding aggregations. Male size variance and the sexual size dimorphism explained 50% of the variation in a LMMA by SUL (Table I.4). No regression models were found to reliably explain the variation seen in the mass or arm length mating patterns (F-test, $p>0.05$); the sample sizes for these regressions were also smaller.

DAILY ANALYSES

Ecological Components and Mating Patterns

The values of daily ecological components were often very different from values in the population analyses, reflecting the sporadic arrival, departure, and activity of breeding toads. First, the sex ratios of breeding adults were often much more male-biased than that reflected by the overall sex ratios of the entire breeding populations (Fig. I.2). During 69 days or day-combinations, the male:female sex ratio ranged from 0.88 to 9.25 (Fig. I.2). On 23 of 69 days examined, the sex ratio was greater than 3.4, which was the highest recorded at the population level. On average, the daily sex ratios were 0.7 higher than the population sex ratios (average difference between mean daily and population sex ratios for site A = 0.71, site B = 1.21, site C = 0.23). At site C, the daily sex ratios were usually male-biased, whereas the sex ratio of the entire breeding population was 1.0 during one year and was female-biased in two years.

Second, the number of toads present on a daily basis was always lower than the total collected at the entire breeding aggregation throughout the breeding season. For example, the largest number of males captured at a breeding site on any one day was 155 (site B, 1983), which was less than half the number captured in the entire season.

The two size-dependent mating patterns, LMMA and PAM, were found on some days or day-combinations at all three study populations (Table I.1). A LMMA was observed for SUL on 9 of 58 days (15% of the days), on 2 of 23 days (9%) for mass, and on 0 of 19 days for arm length. PAM was observed on 7 of 60 days (12%) for SUL, on 3 of 23 days (13%) for mass, and on 2 of 19 (10.5%) for arm length. Both a LMMA and PAM occurred less frequently at site C.

Some correlations were found between the ecological factors and the daily mating patterns (Table I.3). Both a LMMA and PAM were correlated with female SUL variance. The degree of PAM by SUL was also correlated with the calendar date of breeding. No other correlations ($p > 0.05$) were found between the ecological factors and the SUL mating patterns, and no correlations were found for these factors with the mating patterns of mass and arm length.

Notable intercorrelations ($p < 0.05$) among the ecological parameters examined in the daily analyses for SUL, mass (=M), and arm length (=AL) included: (1) Male size variance vs: site (SUL, M, AL), female size variance (SUL, AL), population size (SUL), and the sexual size dimorphism (SUL, M, AL); (2) Female size variance vs: site (AL), sex ratio (AL), population size (SUL) and the sexual size dimorphism (SUL, AL); and (3) Sexual size dimorphism vs: site (SUL, M, AL), and population size (SUL).

Little of the daily mating pattern variation was explained by toad breeding demography (multiple regression analyses, Table I.4). Three factors (female size variance, site, and sexual size dimorphism) explained 28% of the variation in a LMMA by SUL. When site was removed from this analysis, the regression model was reduced to a single independent variable (female size variance) explaining

11.5% of the variation in a LMMA. Female size variance and calendar date explained 23.7% of the variation in PAM by SUL and 38.5% of the variation in PAM by arm length.

DISCUSSION

The two size-dependent mating patterns investigated, a LMMA and PAM by size, occurred variably among breeding populations, within populations among breeding seasons, and within breeding seasons among days of breeding. Overall, the most common size-dependent mating pattern observed was a LMMA by SUL at the population level. This mating pattern was seen at 6 of 15 (40%) breeding aggregations. On a daily basis, a LMMA by SUL was also most common, but it occurred only 15% of the time. The lower incidence of a LMMA on a daily basis suggests that the proximate mechanism resulting in a LMMA may differ between daily and population samples. A LMMA by mass and fore-arm length was never seen in the population analyses and only a LMMA by mass was seen in the daily analyses (on 2 of 23 days examined). The incidence of PAM was more consistent among all three size measures for both population and daily analyses. In the daily analyses, PAM occurred on 10-13% of the days for all size measures. In the population analyses, PAM by SUL was seen at 13% of the aggregations, PAM by mass occurred 10% of the time, and PAM by arm length was found at one-third of the aggregations.

Although the three size measures were highly correlated within individuals, the mating patterns with regard to the three measures were not always observed at the same aggregations or on the same days. At the population level, many of the SUL mating patterns were observed at aggregations monitored in the first few years of the study. Mass and arm length measurements were not collected from all toads in these years, precluding the possibility of equivalent patterns for these measures at the early-studied aggregations. This may explain the lower overall occurrences of nonrandom mating patterns with respect to mass and arm length.

The third mating pattern observed in the western toad, an early-arriving male pairing advantage, occurred more consistently among breeding aggregations (being found at 11 of the 15 aggregations). Early males probably have greater mating success because they spend more time at the breeding aggregations and are therefore more likely to find a mate (e.g. Gatz 1981b; Kagarise Sherman 1980; Ryan 1985; Woodward 1982a).

Why is there mating pattern variation in the western toad?

When addressing the cause of both the size-dependent mating patterns and the mating pattern variability in the western toad the role of chance should be considered. First, in a statistical sense, when so many tests of mating patterns are made, some significant results are expected due to chance alone. Also, because the patterns were not always consistent among size measures and occurred seldomly for some size measures, they could be merely chance occurrences. However, nonrandom mating patterns were found in more than 5% of the analyses. For all size measures and for both mating patterns, 12 of 60 (20%) population analyses and 21 of 202 (10%) daily analyses yielded significant results. In addition, the lack of pattern consistency among size measures may be explained by limited size variance among the toads. These factors, the pattern consistency that is present (i.e. the incidence of PAM) and the more common occurrences of a few patterns (i.e. LMMA for SUL at the population level) suggests that proximate mechanisms other than pure chance are resulting in the patterns.

Western toad arrival date at the breeding sites may have sometimes played a role in the occurrence of their size-dependent mating patterns (see also Gatz 1981b; Lee and Crump 1981). There was an early male pairing advantage at most (11 of 15) breeding aggregations and early-arriving males were larger (SUL) toads at 5 of the 15 aggregations. Early arrivals were both larger and paired more often at 3 aggregations (negative slopes of both regressions at site B in 1982, 1985 and 1986; Table I.1). One of these three had a LMMA, which could have resulted simply from this correspondence. The remaining 2 aggregations did not have a LMMA, however, indicating a problem with the generality of this explanation. This explanation fails again when the aggregations are examined for both a late-arriving male pairing advantage and larger males arriving more often late. The one aggregation with both conditions, site C in 1982, did not have a LMMA. The near-zero slopes of some of the regressions, between either pairing probability or size and toad arrival day, may explain why the correspondence between these aspects of toad breeding ecology do not always result in a nonrandom mating pattern. The proposed relationship may also be dependent on the daily sample size. A LMMA is more likely to be observed if many large males are captured on either an early or a late day, and arrival day and pairing are likewise associated. A day was included in the daily analyses if a minimum of 10 paired and 10 unpaired males were captured, yet up to 155 males were captured on a single day. The proposed relationship may also explain why a LMMA was more common at the population level than at a daily level. On a daily basis, any relationship between toad size, pairing success and arrival day cannot be affirmed. In any case, the correspondence of toad size, mating success, and arrival time at the breeding site cannot provide a general explanation for when a LMMA will occur in the western toad, but it may account for some appearances of the pattern in the population analyses.

In the population analyses, PAM may also result from size-dependent arrival times of toads. If toads pair soon after they arrive at the breeding site, and the sizes of males and females are related to arrival day, size assortative mating in the entire population may be observed. There was a correspondence in the sizes of newly arriving males and females at 4 of the 15 breeding aggregations (2 negative or 2 positive slopes between toad SUL and arrival day; Table I.1). PAM was seen at none of these 4 aggregations. Although this is a rough method of analysis for the correspondence of arrival time, size and mating, there is no evidence that this mechanism alone may account for either the mating patterns or the mating pattern variability in the western toad.

The Role of Breeding Ecology

Two measures of the size distribution of breeding toads, size variance and sexual size dimorphism, explained much of the variation in the occurrence of some mating patterns. Size variation is a trivial condition for these patterns. Specifically, male size variation is obviously necessary for a LMMA to occur, and both male and female size variation is required for PAM. Western toad female and male size variances are sometimes correlated (in the population analysis for mass and daily analyses for SUL and arm length). The associations between the mating patterns and size variance suggest that there may be insufficient variance in size at some aggregations for the patterns to develop. Limiting size variance in western toad populations may explain why the patterns are not present in some aggregations, and also the lack of mating pattern consistency among the three size measures, but it cannot explain why the patterns are sometimes observed.

In the western toad, increasing size variance and sexual dimorphism are probably morphological functions of increasing toad body size. Although Alexander et al. (1979) did not find a relation between body size and sexual dimorphism in their review of several mammal species, the differences between the determinate growth of mammals and anuran indeterminate growth may explain this discrepency. As in bullfrogs (Howard 1981), the degree of western toad size variation and sexual dimorphism in a breeding aggregation probably depends on the survivorship of older toads and the numbers and sizes of age classes, as well as the length of the toad season of growth. Western toads at the lower-elevation site A had the longest summer "active-season", and hence the greatest opportunity for growth. Site C toads had the shortest summer active season. Toad size, size variance and dimorphism were greatest at site A and smallest at site C, with site A breeding first each year and site C last. Study site and calendar date were two additional factors appearing in the correlation and multiple regression analyses of the daily mating patterns; their importance as variables useful in explaining variation in the mating patterns, however, is difficult to interpret beyond their associations with these other demographic parameters.

An association between sexual dimorphism and sexual selection in many animals was proposed by Darwin (1871). In particular, large male size may be a result of selection due to female choice of large males or male-male competition for mates where large males have a competitive advantage. In many anurans, large size of females is also selectively advantageous because size is directly related to reproductive output (e.g. clutch size, Salthe and Duellman 1973). In anurans where there is no selective advantage for large male size (i.e. large male size is unimportant for reproductive success), males should be smaller than females (Wells 1978), and thus the degree of sexual dimorphism would be greater in anurans with less sexual selection for large male size (i.e. "reverse" sexual dimorphism, Alexander et al. 1979; Woolbright 1983). Males are smaller than females in most anurans (Shine 1979). Wells (1978) found an association between the degree of sexual dimorphism and male mating behavior; three anuran species in which males have aggressive wrestling bouts for territory acquisition had less dimorphism (larger males with respect to females) than 5 species in which males showed less aggressive male-male interactions. If sexual selection was important in determining the degree of sexual size dimorphism in western toads, then the form or intensity of sexual selection would be expected to differ among my three study populations. The greatest intensity of sexual selection might be expected at site C, where toads were least dimorphic. However, site A males were larger. Among sites, western toad sexual size dimorphism differences may be more easily explained by developmental constraints than sexual selection. Scenarios (1) and (3) are probably not important as proximate mechanisms affecting mating patterns at my western toad study populations (Olson 1988b).

Regardless of the origin of the different levels of sexual dimorphism, the dynamics of male-male or male-female interactions in a breeding aggregation may vary with the degree of dimorphism and also the level of toad size variance. Mate choice and competition for mates may be more effective in a population with greater size variance and sexual size dimorphism and result in the observed size-dependent mating patterns. Howard (1981) found that male bullfrog mating behavior and size-specific mating probabilities are influenced by male age-size distributions. In a sexually dimorphic western toad population with great variance in toad size, small males may be ineffective in pairing because they (1) are less able to resist takeovers by larger males, especially when they are clasping large females, and thus lose when in direct aggressive competitive interactions with large males for mates (Arak 1983; Berven 1981; Davies and Halliday 1979; Halliday 1983; Howard and Kluge 1985; Lamb 1984; Lee and Crump 1981; Wells 1979), (2) inadequately clasp large females due to a mechanical limitation based on their size (for example, their small arms cannot grasp large females) and thus lose in an exploitative "scramble" competition for mates without direct male-male interactions (Olson 1988b), or (3) are not chosen by females if female choice of mates based on size or a size-related character is operating (e.g. Howard 1978; Ryan 1985; Wilbur et al. 1981; Woodward 1982b). All three of these scenarios may result in PAM and a LMMA, yet the three scenarios and their resulting mating patterns would not be found in a population without size variability.

Interestingly, western toad mating patterns were not associated with several other ecological parameters, including the breeding population size, sex ratio, breeding season length, and oviposition synchrony. Although previous studies have emphasized the effects of these demographic factors on the intensity of sexual selection, the occurrence of nonrandom mating, and mating systems in general (e.g. Arak 1983; Emlen and Oring 1977; Wells 1977), they did not seem to influence the western toad breeding dynamics leading to size-dependent mating patterns. If variable degrees of the proximate components of sexual selection resulted in the western toad mating pattern variability (Olson et al. 1986), it was probably not in response to changes in these aspects of toad breeding demography. The western toad mating system may be less structured by the proximate components of sexual selection proposed to be affected by these factors (i.e. mate choice and aggressive mate competition), and defined more by exploitative and opportunistic breeding behavior (Olson 1988b).

Lastly, differences in predation pressure may affect the behavior of anurans in breeding populations (e.g. Ryan 1980; Ryan et al. 1981; Ryan et al. 1982). Predation by ravens on breeding western toads was observed at 3 aggregations (site A in 1984, site C in 1985 and 1986) and was associated with changes in toad behavior affecting male pairing success (Olson 1989). The breeding dynamics leading to mating patterns may have been disrupted by predation at these 3 aggregations (Olson 1989).

In summary, this long-term, multi-site investigation of western toad breeding uncovered considerable variation in size-dependent mating patterns within and among both breeding populations and seasons. Nonrandom mating in the western toad was related to two aspects of their size distribution, toad size variance and sexual size dimorphism. Limiting size variance and a low degree of sexual size dimorphism may also preclude the development of nonrandom mating by size in other anurans, and variable size distributions among anuran breeding aggregations may explain the frequently observed differential occurrence of nonrandom mating (Olson et al. 1986). Chance, predation, and the size-dependent arrival of western toads at breeding sites may also have influenced the development of mating patterns. Contrary to expectation, several ecological factors (i.e. demographic conditions: population size and sex ratio; and aspects of the temporal distribution of mates: breeding season length and oviposition synchrony) were not associated with the size-dependent mating patterns. Western toad breeding dynamics may not change in response to variation in these ecological conditions. The variability reported among breeding aggregations in western toad ecological conditions and the occurrences of mating patterns illustrate the importance of long-term multi-site studies. Characterizations of populations from single site and season studies are more likely to report rare events and give a limited profile of the ecology and potential dynamics of the mating system. Understanding the extent of variation in natural systems, the cause of variation, and the role of variation in the structuring of ecological systems is an important direction for future work.

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Figure I.1: Mean (± SEM) male (●) and female (○) body lengths (SUL=snout-urostyle length, Fig. 1A), mass (1B), and arm lengths (1C) at the 15 western toad breeding aggregations.

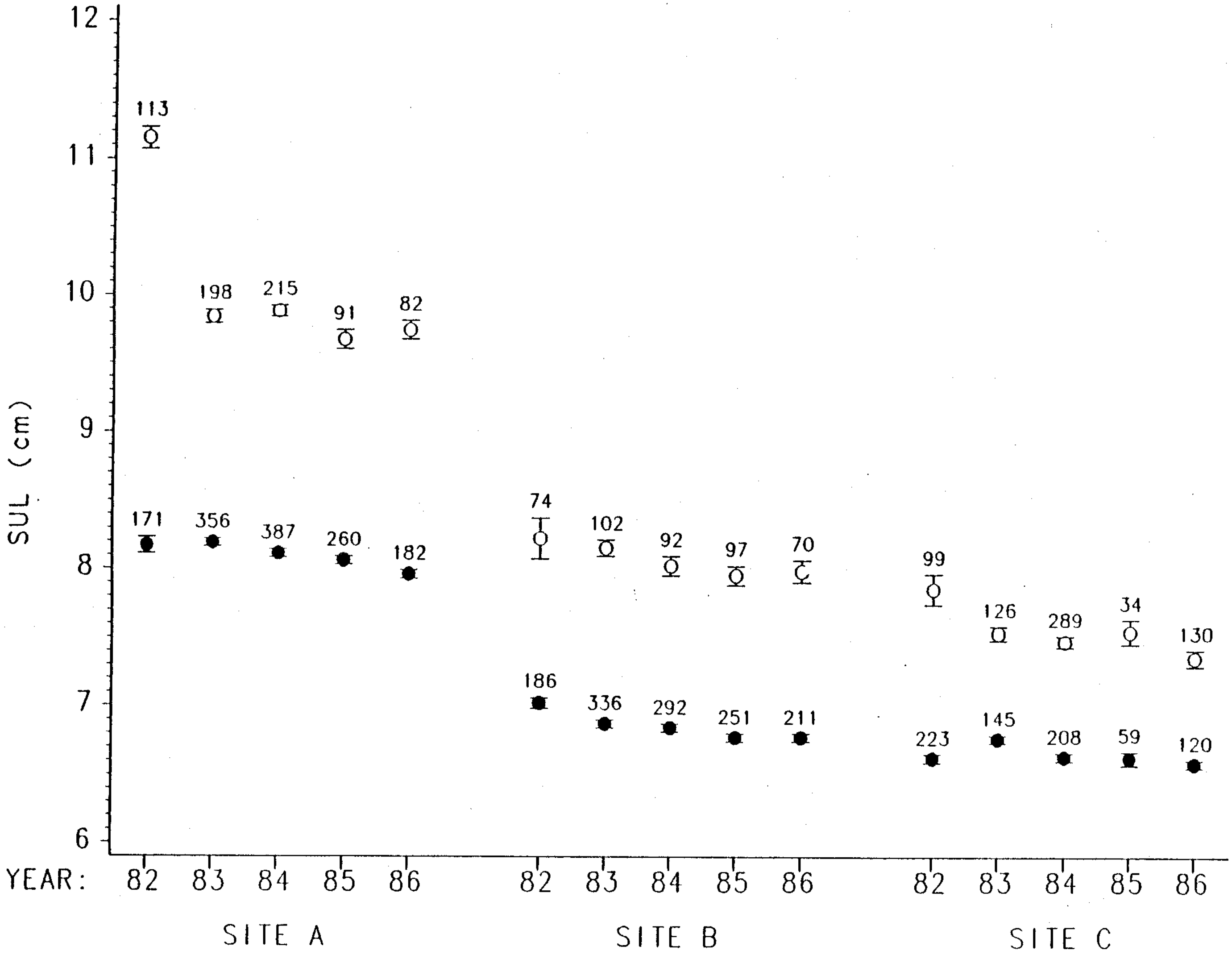
SUL (cm)
12
11
10
9
8
7
6
YEAR:
82
83
84
85
86
SITE A
SITE B
SITE C
113
198
215
91
82
171
356
387
260
182
74
102
92
97
70
186
336
292
251
211
99
126
289
34
130
223
145
208
59
120

Figure I.1A

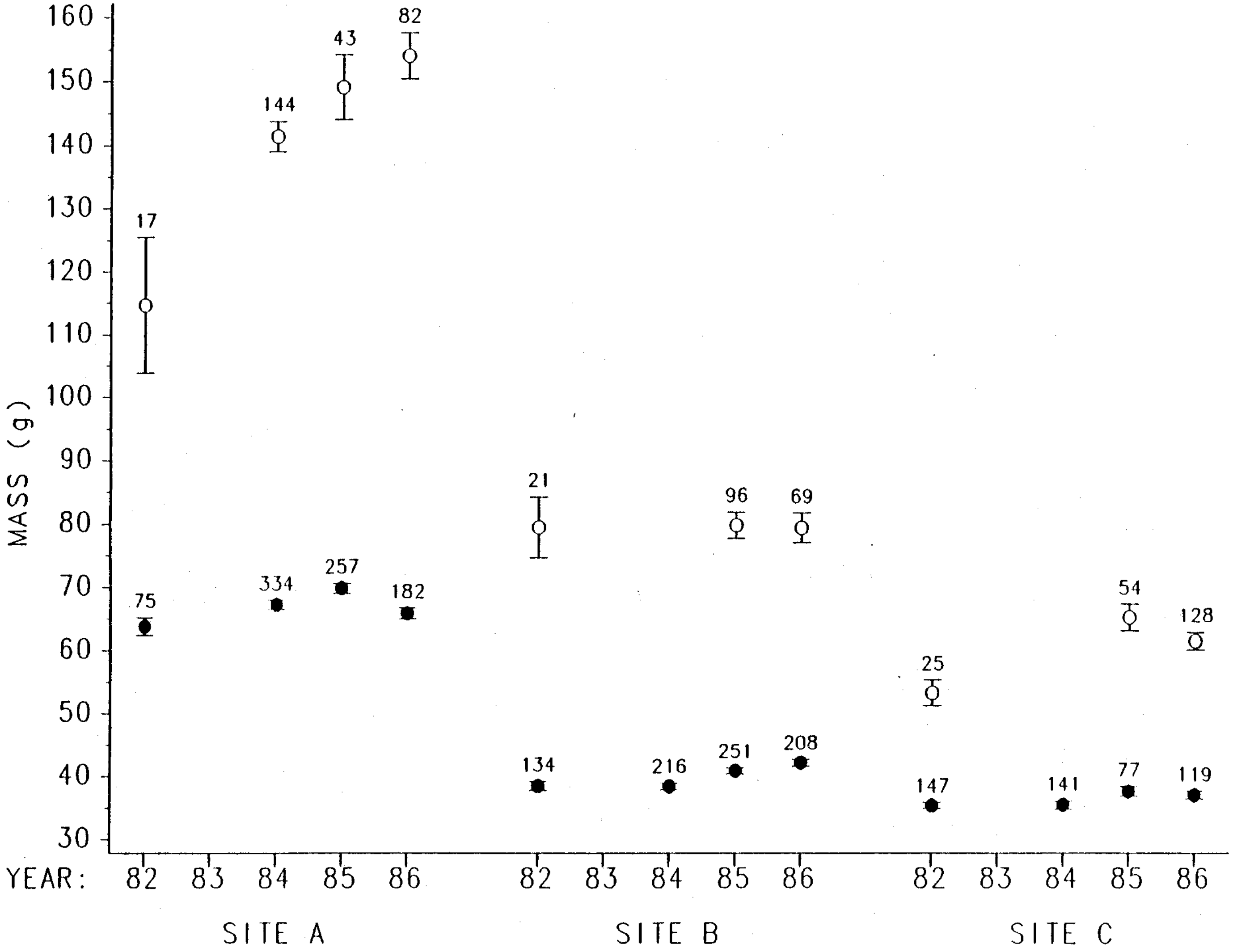
MASS (g)
160
150
140
130
120
110
100
90
80
70
60
50
40
30
YEAR:
82
83
84
85
86
SITE A
SITE B
SITE C
17
144
43
82
75
334
257
182
21
96
69
134
216
251
208
25
54
128
147
141
77
119

Figure I.1B

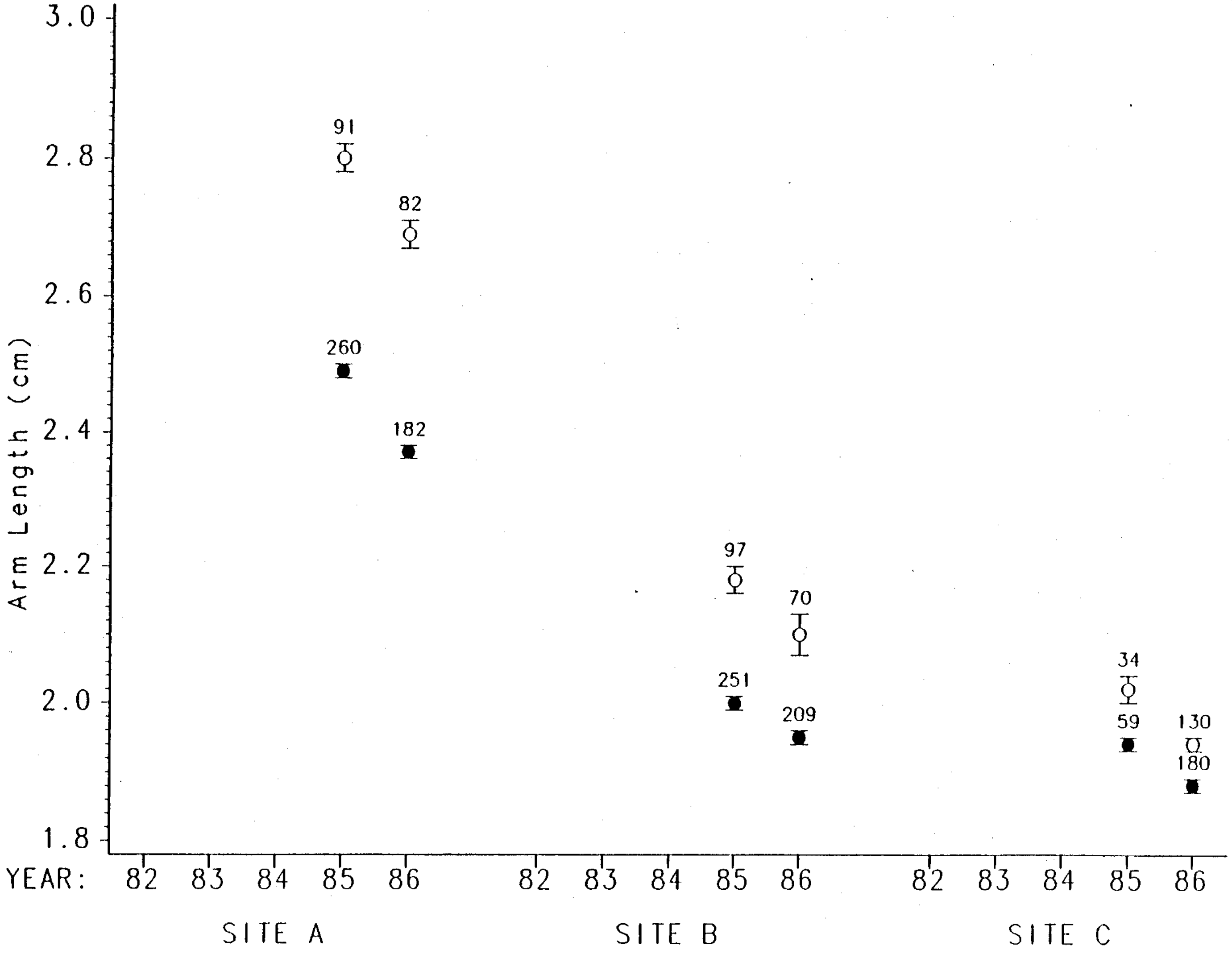
Arm Length (cm)
3.0
2.8
2.6
2.4
2.2
2.0
1.8
YEAR:
82
83
84
85
86
SITE A
SITE B
SITE C
91
82
260
182
97
70
251
209
34
59
130
180

Figure I.1C

Figure I.2: Daily sex ratios (male:female) at the 15 western toad breeding aggregations.

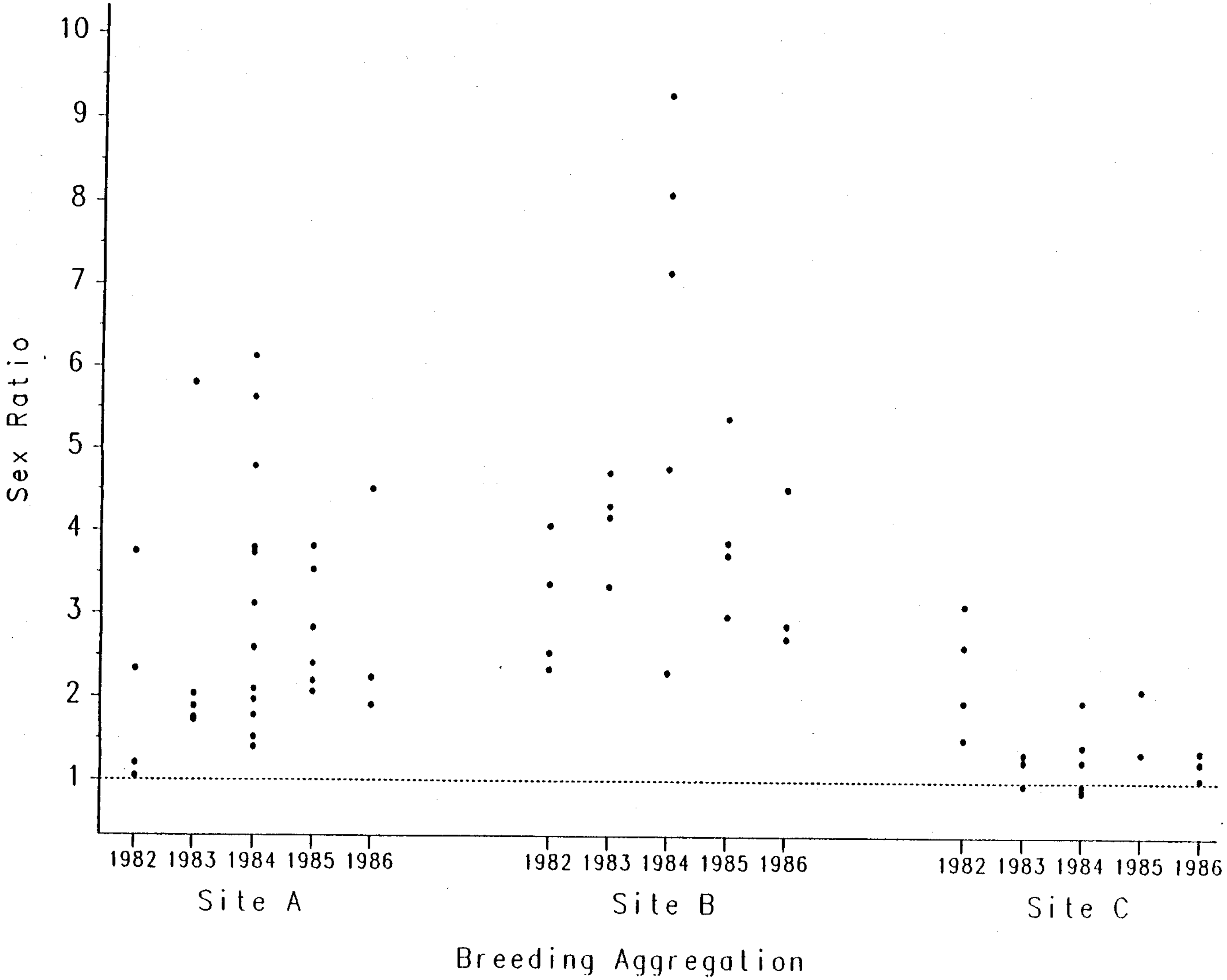
Sex Ratio
10
9
8
7
6
5
4
3
2
1
1982 1983 1984 1985 1986
Site A
1982 1983 1984 1985 1986
Site B
1982 1983 1984 1985 1986
Site C
Breeding Aggregation

Figure I.2

Table I.1: Summary of demographic factors and mating patterns (LMMA = large male mating advantage, PAM = positive assortative mating by size) at the 3 western toad breeding populations, Site A, Site B, and Site C.

Table I.1A

	Site A				
	1982	1983	1984	1985	1986
Ecological Factors					
Breeding season length (days)	13	11	23	9	5
Date of onset of breeding	5 June	19 May	26 May	21 May	16 May
Oviposition syncnrony	0.46	0.36	0.13	0.22	0.80
Sex ratio (male/female)	1.51	1.80	1.80	2.86	2.22
Breeding population size	284	554	602	352	264
Toad SUL vs. arrival day					
Male: Regression slopes					
(no. days analyzed)	0.03(4)	0.02(5)	0.00(13)	0.03(6)	0.05(3)
Female: Regression slopes					
(no. days analyzed)	-0.09(3)	0.00(5)	0.01(11)	0.07(6)	0.05(2)
Mating Patterns:					
Population Analyses					
LMMA, t(df):					
SUL	2.57(174)*	3.36(354)**	1.41(382)	1.16(258)	1.31(180)
Mass	1.44(73)	--	0.71(350)	0.69(255)	0.16(179)
Arm length	--	--	--	0.32(258)	0.09(180)
PAM, r(df):					
SUL	0.43(107)*	0.13(183)	0.15(219)*	0.04(91)	0.06(79)
Mass	-0.23(11)	--	0.16(134)	-0.25(37)	0.11(78)
Arm length	--	--	--	0.03(81)	0.09(79)*
Male pairing success vs. arrival day: Slope					
(no. days analyzed)	-0.23(4)	-0.09(5)*	0.03(13)	-0.06(6)	-0.14(3)
Daily Analyses:					
(no. days with pattern/ no. days analyzed):					
LMMA:					
SUL	1/3	2/5	1/9	0/5	0/2
Mass	--	--	1/7	0/2	0/2
Arm length	--	--	--	0/5	0/2
PAM with respect to:					
SUL	2/3	1/5	1/9	0/5	0/2
Mass	--	--	1/7	0/2	0/2
Arm length	--	--	--	0/5	0/2

*p <0.05

**p <0.005

Table I.1B

	Site 8				
	1982	1983	1984	1985	1986
Ecological Factors					
Breeding season length (days)	10	15	8	7	7
Date of onset of breeding	29 June	27 June	21 June	8 June	2 June
Oviposition synchrony	0.90	0.80	0.87	0.71	0.57
Sex ratio (male/female)	2.51	3.29	3.37	2.59	3.01
Breeding population size	260	438	384	348	281
Toad SUL vs. arrival day					
Male: Regression slopes (no. days analyzed)	-0.09(5)	0.00(6)	0.00(5)	-0.01(5)	-0.04(5)
Female: Regression slopes (no. days analyzed)	0.06(5)	-0.02(5)	-0.17(3)	-0.05(4)	-0.03(3)
Population Analyses					
LMMA, t(df):					
SUL	2.79(195)*	2.18(341)*	2.73(314)*	1.63(260)	1.11(206)
Mass	0.62(132)	--	--	1.19(260)	0.57(203)
Arm length	--	--	--	1.58(260)	0.26(204)
PAM, r(df):					
SUL	0.14(71)	0.13(93)	0.07(83)	0.16(95)	0.08(71)
Mass	-0.03(15)	--	--	0.23(94)*	-0.03(72)
Arm length	--	--	--	0.37(95)*	0.42(69)*
Male pairing success vs. arrival day: Slope (no. days analyzed)	0.03(5)	-0.06(6)	-0.10(5)*	-0.04(5)	-0.02(4)
Daily Analyses (no. days with pattern/ no. days analyzed):					
LMMA:					
SUL	1/4	1/4	0/3	1/4	0/3
Mass	--	--	--	1/4	0/3
Arm length	--	--	--	0/4	0/3
PAM:					
SUL	0/5	1/4	0/3	1/4	0/3
Mass	--	--	--	1/4	0/3
Arm length	--	--	--	1/4	1/3

*p <0.05

**p <0.005

Table I.1C

	Site C				
	1982	1983	1984	1985	1986
Ecological Factors					
Breeding season length (days)	10	8	8	7	8
Date of onset of breeding	7 July	9 July	11 July	18 June	16 June
Oviposition syncnrony	0.60	0.50	0.87	0.71	1.00
Sex ratio (male/female)	2.25	1.15	0.72	1.43	0.92
Breeding population size	322	271	497	131	250
Toad SUL vs. arrival day					
Male: Regression slopes					
(no. days analyzed)	0.06(4)	0.05(3)	-0.01(5)	0.00(2)	0.03(4)
Female: Regression slopes					
(no. days analyzed)	0.04(4)	0.19(3)	0.00(6)	0.02(2)	0.04(4)
Mating Patterns:					
Population Analyses					
LMMA, t(df), with respect to:					
SUL	1.14(227)	2.42(143)*	1.03(204)	0.25(57)	0.52(118)
Mass	--	--	--	0.73(75)	1.19(117)
Arm length	--	--	--	0.07(57)	0.46(118)
PAM, r(df):					
SUL	0.03(83)	0.12(126)	0.07(281)	-0.01(31)	-0.07(131)
Mass	--	--	--	0.12(47)	-0.05(100)
Arm length	--	--	--	0.13(31)	0.06(102)
Male pairing success vs. arrival day: Slope					
(no. days analyzed)	0.03(4)	0.00(3)	-0.10(5)	0.29(2)	-0.01(4)
Daily Analyses					
(no. days with pattern/ no. days analyzed):					
LMMA:					
SUL	0/4	0/1	0/6	0/2	0/3
Mass	--	--	--	0/2	0/3
Arm length	--	--	--	0/2	0/3
PAM:					
SUL	0/4	0/2	1/6	0/2	0/3
Mass	--	--	--	0/2	1/3
Arm length	--	--	--	0/2	0/3

*p <0.05

**p <0.005

Table I.2: Product-moment correlation coefficients between the three size measurements (SUL, mass, and fore-arm lengths) from toads captured at the three sites in 1986. $p < 0.01$ for all correlations.

	Site					
	A		B		C	
	r	df	r	df	r	df
Males						
SUL and Mass	0.801	179	0.839	207	0.736	117
SUL and Arm	0.725	180	0.641	207	0.784	118
Mass and Arm	0.797	179	0.636	206	0.610	117
Females						
SUL and Mass	0.776	80	0.937	57	0.486	110
SUL and Arm	0.828	80	0.604	57	0.579	112
Mass and Arm	0.702	80	0.580	57	0.683	110

Table I.3: Correlations (r) between several demographic parameters and the two size-dependent mating patterns, a large male mating advantage (LMMA) and positive assortative mating (PAM) with respect to all three size measures for both population, P(N), and daily, D(N), analyses.

Table I.3

DEMOGRAPHIC PARAMETER	Correlation Coefficient											
	LMMA(t*)						PAM(r)					
	SUL		Mass		Arm		SUL		Mass		Arm	
	P(15)	D(56)	P(9)	D(23)	P(6)	D(19)	P(15)	D(56)	P(9)	D(23)	P(6)	D(19)
Breeding season length	0.01	--	0.04	--	0.20	--	0.39	--	0.04	--	-0.23	--
Oviposition synchrony	0.00	--	0.27	--	0.30	--	-0.34	--	0.25	--	0.00	--
Population size	-0.08	-0.12	-0.30	0.00	0.26	-0.08	0.26	-0.04	0.17	-0.08	0.34	0.14
No. males present	0.04	-0.11	-0.47	-0.07	0.30	-0.10	0.21	-0.06	0.17	-0.07	0.33	0.15
No. females present	0.02	-0.09	0.06	0.14	0.61	-0.01	0.09	0.01	0.13	-0.07	-0.28	0.06
Sex ratio (male/female)	0.00	0.00	-0.65	-0.11	-0.06	0.08	0.02	-0.10	-0.01	-0.01	-0.51	-0.04
Male size variance	0.49	-0.10	-0.17	0.07	0.13	0.09	0.87*	0.06	-0.31	0.07	0.00	0.02
Female size variance	0.27	0.34*	0.28	-0.06	0.00	0.06	0.17	0.36*	-0.57	-0.33	0.55	0.30
Sexual size dimorphism	0.18	0.07	-0.27	-0.04	-0.28	0.21	0.80*	-0.18	0.29	0.02	-0.23	-0.19
Study site	--	0.18	--	0.09	--	-0.15	--	0.16	--	-0.07	--	0.21
Year	--	-0.21	--	-0.15	--	0.01	--	-0.15	--	-0.26	--	-0.04
Calendar date	--	0.15	--	0.16	--	-0.29	--	0.35*	--	0.15	--	0.39

*p <0.05

Table I.4: Multiple regression results of population and daily analyses of the three size measures using the two size-dependent mating patterns, LMMA (t*) and PAM (r), as dependent variables and the ecological factors (see Table I.3) as independent variables (F-M = size difference between the sexes, MVar = male size variation, FVar = female size variation, Date = calendar date).

Table I.4

Analysis Conducted	N	Dependent Variable	No. Indep. Var. Examined For Regression	Indep. Variables in Model 1	2	3	Regression Coefficient B_0	B_1	B_2	B_3	Variation Explained	F
Population:												
SUL	15	t*	9	MVar	F-M		0.23	1.47	-0.25		50.6	6.16^{1}
		r	9	MVar			-0.08	0.74			75.5	39.99^{2}
Mass	9	t*	9	--			--				--	ns
		r	9	--			--				--	ns
Arm	6	t*	9	--			--				--	ns
Daily:												
SUL	56	t*	10	FVar	Site	F-M	-25.86	11.31	5.18	9.25	28.5	6.90^{1}
			9^{a}	FVar			-3.75	11.40			11.5	7.03^{1}
		r	10	FVar	Date		-0.69	0.46	0.09		23.7	8.22^{2}
			9^{b}	FVar	F-M		0.09	0.57	-0.17		19.8	6.53^{1}
Mass	23	t*	10	--			--				--	ns
		r	10	--			--				--	--
Arm	19	t*	10	--			--				--	ns
		r	10	Date	FVar		-1.73	0.28	6.81		38.5	5.02^{1}
			9^{b}	--			--				--	ns

[a] Site removed as an independent variable

[b] Date removed as an independent variable

$^{1}p<0.05$

$^{2}p<0.005$

ns = $p>0.05$

LITERATURE CITED

Alexander, R.D., J.L. Hoogland, R.D. Howard, K.M. Noonan, and P.W. Sherman. 1979. Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates and humans. Pages 402-435 in N.A. Chagnon and W. Irons, editors. Evolutionary Biology and Human Social Behavior. Duxbury Press, North Scituate, Massachusetts, USA.

Arak, A. 1983. Male-male competition and mate choice in anuran amphibians. Pages 181-210 in P. Bateson, editor. Mate Choice. Cambridge University Press, Cambridge, Great Britain.

Arnold, S.J., and M.J. Wade. 1984a. On the measurement of natural and sexual selection: theory. Evolution 38:709-719.

_______. 1984b. On the measurement of natural and sexual selection: applications. Evolution 38:720-734.

Bateson, P. 1983. Mate Choice. Cambridge University Press, Cambridge, Great Britain.

Berven, K.A. 1981. Mate choice in the wood frog, *Rana sylvatica*. Evolution 35:707-722.

Blum, M.S., and N.A. Blum. 1979. Sexual Selection and Reproductive Competition in Insects. Academic Press, New York, USA.

Darwin, C. 1871. The Descent of Man and Selection in Relation to Sex. John Murray, London, Great Britain.

Davies, N.B., and T.R. Halliday. 1977. Optimal mate selection in the toad _Bufo_ _bufo_. Nature 269:56-58.

_______. 1979. Competitive mate searching in male common toads, _Bufo_ _bufo_. Animal Behaviour 27:1253-1267.

Emlen, S.T. 1976. Lek organization and mating strategies in the bullfrog. Behavioral Ecology and Sociobiology 1:283-313.

Emlen, S.T., and L.W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223.

Gatz, A.J. 1981a. Size selective mating in _Hyla_ _versicolor_ and _Hyla_ _crucifer_. Journal of Herpetology 15:114-116.

_______. 1981b. Non-random mating by size in American toads, _Bufo_ _americanus_. Animal Behaviour 29:1004-1012.

Halliday, T.R. 1978. Sexual selection and mate choice. Pages 180-213 _in_ J.R. Krebs and N.B. Davies, editors. Behavioral Ecology: An Evolutionary Approach, Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

Herreid, C.F., II, and S. Kinney. 1967. Temperature and development of the wood frog, _Rana_ _sylvatica_, in Alaska. Ecology 48:579-590.

Howard, R.D. 1978. The evolution of mating strategies in bullfrogs, _Rana_ _catesbeiana_. Evolution 32:850-871.

_______. 1981. Male age-size distribution and male mating success in bullfrogs. Pages 61-77 *in* R.D. Alexander and D.W. Tinkle, editors. Natural Selection and Social Behavior: Recent Research and New Theory, Chiron Press, New York, USA.

_______. 1983. Sexual selection and variation in reproductive success in a long-lived organism. American Naturalist 122:301-325.

Howard, R.D., and A.G. Kluge. 1985. Proximate mechanisms of sexual selection in wood frogs. Evolution 39:260-277.

Kagarise Sherman, C. 1980. A comparison of the natural history and mating system of two anurans: Yosemite toads (*Bufo canorus*) and black toads (*Bufo exsul*). Dissertation. University of Michigan, Ann Arbor, Michigan, USA.

Koenig, W.D., and S.S. Albano. 1986. On the measurement of sexual selection. American Naturalist 127:403-409.

Lamb, T. 1984. Amplexus displacement in the southern toad *Bufo terrestris*. Copeia 1984:1023-1025.

Lawrence, W.S. 1986. Male choice and competition in *Tetraopes tetraophthalmus*: effects of local sex ratio variation. Behavioral Ecology and Sociolbiology 18:289-296.

Lee, J.C., and M.L. Crump. 1981. Morphological correlates of male mating success in *Triprion petasatus* and *Hyla marmorata* (Anura: Hylidae). Oecologia 50:153-157.

Licht, L.E. 1976. Sexual selection in toads (Bufo americanus). Canadian Journal of Zoology 54:1277-1284.

Olson, D.H. 1988b. The role of mate choice and mate competition in western toad (Bufo boreas) nonrandom mating. Submitted.

______ 1989. Predation on breeding western toads (Bufo boreas). Copeia 1989 (in press).

Olson, D.H., A.R. Blaustein, and R.K. O'Hara. 1986. Mating pattern variability among western toad (Bufo boreas) populations. Oecologia 70:351-356.

Orians, G.H. 1969. On the evolution of mating systems in birds and mammals. American Naturalist 103:589-603.

Partridge, L., and T. Halliday. 1984. Mating patterns and mate choice. Pages 222-250 in J.R. Krebs and N.B. Davies, editors. Behavioral Ecology: An Evolutionary Approach, Second Edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Robertson, J.G.M. 1986. Female choice, male strategies and the role of vocalizations in the Australian frog Uperoleia rugosa. Animal Behaviour 34:773-784.

Ryan, M.J. 1980a. Female mate choice in a neotropical frog. Science 209:523-525.

______. 1980b. The reproductive behavior of the bullfrog (Rana catesbeiana). Copeia 1980:108-114.

_______. 1985. The Tungara Frog: a study in sexual selection and communication. University of Chicago Press, Chicago, Illinois, USA.

Ryan, M.J., M.D. Tuttle, and A.S. Rand. 1982. Bat predation and sexual advertisement in a neotropical anuran. American Naturalist 119:136-139.

Ryan, M.J., M.D. Tuttle, and L.K. Taft. 1981. The costs and benefits of frog chorusing behavior. Behavioral Ecology and Sociobiology 8:273-278.

Salthe, S.N., and W.E. Duellman. 1973. Quantitative constraints associated with reproductive mode in anurans. Pages 229-249 _in_ J.L. Bial, editor. Evolutionary Biology of the Anurans. University of Missouri Press, Columbia, Missouri, USA.

Shine, R. 1979. Sexual selection and sexual dimorphism in the Amphibia. Copeia 1979:297-306.

Snedecor, G.W., and W.G. Cochran. 1980. Statistical methods. The Iowa State University Press, Ames, Iowa.

Sullivan, B.K. 1982. Sexual selection in Woodhouse's toad (_Bufo woodhousei_) I. Chorus organization. Animal Behaviour 30:680-686.

_______. 1983. Sexual selection in Woodhouse's toad (_Bufo woodhousei_) II. Female choice. Animal Behaviour 31:1011-1017.

_______. 1984. Size dimorphism in Anurans: a comment. American Naturalist 123:721-724.

_______. 1986. Intra-populational variation in the intensity of sexual selection in breeding aggregations of Woodhouse's toad (Bufo woodhousei). Journal of Herpetology 20:88-90.

_______. 1987. Sexual selection in Woodhouse's toad (Bufo woodhousei). III. Seasonal variation in male mating success. Animal Behaviour 35:912-919.

Trivers, R.L. 1972. Parental ivnvestment and sexual selection. In B. Campbell, editor. Sexual Selection and the Descent of Man. Aldine Publishing Co., Chicago , Illinois, USA.

Vehrencamp, S.L., and J.W. Bradbury. 1984. Mating systems and ecology. Pages 251-278 in J.R. Krebs and N.B. Davies, editors. Sinauer Associates, Sunderland, Massachusetts, USA.

Wade, M.J. 1979. Sexual selection and variance in reproductive success. American Naturalist 114:742-747.

Wade, M.J., and S.J. Arnold. 1980. The intensity of sexual selection in relation to male sexual behavior, female choice, and sperm precedence. Animal Behaviour 28:446-461.

Wells, K.D. 1977. The social behaviour of Anuran Amphibians. Animal Behaviour 25:666-693.

_______. 1978. Territoriality in the green frog (Rana clamitans): vocalisations and agonistic behaviour. Animal Behaviour 26:1051-1063.

______. 1979. Reproductive behavior and male mating success in a neotropical toad, _Bufo typhonius_. Biotropica 11:301-307.

Whitney, C.L., and J.R. Krebs. 1975. Mate selection in Pacific tree frogs. Nature 255:325-326.

Wilbur, H.M., D.I. Rubenstein, and L. Fairchild. 1978. Sexual selection in toads: the roles of female choice and male body size. Evolution 32:264-270.

Woodward, B.D. 1982a. Male persistence and mating success in Woodhouse's toad (_Bufo woodhousei_). Ecology 63:583-585.

______. 1982b. Sexual selection and nonrandom mating patterns in desert anurans (_Bufo woodhousei_, _Scaphiopus couchi_, _S_. _multiplicatus_ and _S_. _bombifrons_). Copeia 1982:351-355.

Woolbright, L.L. 1983. Sexual selection and size dimorphism in Anuran Amphibia. American Naturalist 121:110-119.

CHAPTER II

THE ROLE OF MATE CHOICE AND MATE COMPETITION IN WESTERN TOAD (*Bufo boreas*) NONRANDOM MATING

ABSTRACT

Western toad mating behavior was monitored at 15 explosively breeding aggregations and in field enclosure experiments where the effects of density, sex ratio and the toad size distribution were controlled. Male mating success seemed to be affected by both female choice of mates and male-male competition, however both of these aspects of sexual selection were indirectly manifested. There was no evidence for either the direct displacement of already-clasped males by unpaired males or direct choice of specific males by females. Females exhibited a suite of "coy" behaviors in response to male clasp attempts and these behaviors were not equally associated with either the type of male clasp or the size of the clasping male. Larger males paired in less time and were more successful at clasping when females responded with their more vigorous attempts to apparently avoid the male. Time-to-pairing was

less for pairs with less sexual size dimorphism. Density and sex ratio seemed to have few effects on mating behaviour. The female and male pairing behaviors can result in the variable occurrences of two size-dependent mating patterns, a large male mating advantage and positive assortative mating by size, observed at the 15 western toad breeding aggregations.

INTRODUCTION

The proximate mechanisms of sexual selection, mate choice and mate competition (Darwin 1871), are important components of animal mating systems (e.g. Blum & Blum 1979; Bateson 1983; Trivers 1972; Emlen and Oring 1977; Orians 1969). Patterns of nonrandom mating often result from sexual selection (e.g. Partridge and Halliday 1984). The intensity of sexual selection and the dynamics of mating are potentially influenced by breeding population density and sex ratio (Emlen and Oring 1977; Wells 1977), although few empirical studies have been conducted (but see Lawrence 1986).

Mate choice and mate competition affect the mating success of many anuran amphibians (e.g. Howard and Kluge 1985; Wells 1977; Arak 1983; Ryan 1985; Sullivan 1983; Woodward 1982a). Although anurans often exhibit size-dependent nonrandom mating patterns (Arak 1983; Howard

& Kluge 1985; Olson et al. 1986), such patterns occur variably among breeding aggregations of many species (Olson et al. 1986). Because of the potentially important roles of mate choice and competition in the structuring of anuran mating systems and in the determination of many mating patterns (Wells 1977; Arak 1983), it is likely that anuran mating pattern variability also results from these types of behavioral interactions. Additionally, breeding population density and sex ratio are associated with anuran mating success and the opportunity for sexual selection in some species (Sullivan 1987; Olson 1988d). However, definitive empirical studies determining the effects of density and sex ratio on mate choice and mate competition have not been conducted with anurans.

The western toad (Bufo boreas) is an ideal species in which to investigate the integral roles of the proximate components of sexual selection, nonrandom mating patterns, and population demography because mating dynamics may vary with breeding conditions. Size-dependent mating patterns occurred variably among western toad breeding aggregations at three different populations over a five year period (Olson et al. 1986; Olson 1988a).

The occurrences of two mating patterns were positively associated with toad size variability and the degree of sexual size dimorphism of the breeding populations, but not population density or sex ratio (Olson 1988a).

In addition, sex ratio was associated with male mating success (no. mates/male), and both density and sex ratio were associated with the opportunity for sexual selection in the western toad (Olson 1988d).

This paper addresses the following questions: Do western toads exhibit mate choice or mate competition? Can the mating behavior of western toads explain the observed variable occurrences of nonrandom mating? Can western toad breeding behaviors explain the associations between their mating patterns and toad size variability and sexual size dimorphism? Does western toad mating behavior vary with density and sex ratio? These questions were addressed by observations of breeding toads at their natural breeding aggregations and through the use of field experimental enclosures, in which the effects of toad density, sex ratio, and the toad size distribution were controlled.

METHODS

Field Observations

Observations of western toad breeding aggregations were conducted at three high elevation lakes in the Oregon Cascade Mountains (Lost Lake = site A, elevation 1220 m, Linn Co.; Little Three Creeks Lake = site B, elevation 1950 m, Deschutes Co.; Todd Lake = site C, elevation 1860 m, Deschutes Co.) during five breeding seasons, 1982-1986. I censused toads several times daily by collecting and identifying individuals along the lake-shores at breeding sites. Few toads were found on land or in the open water of the lakes. Toads were individually marked by clipping unique combinations of toes, and measured for snout-urostyle length (SUL). Paired toads were separated for measuring in 1983-1986, then re-paired before release at the breeding site. Displacements of paired males by unpaired males and interactions between unpaired males and females were noted when seen during censuses. Toads were easily captured and usually resumed their pre-capture activity immediately upon release; capture and handling of toads thus had little apparent effect on their breeding activity.

Field Enclosure Experiments

Field experiments were conducted to examine potential mate choice and mate competition in the western toad because interactions between unpaired males and females, including the event of a female becoming paired by a male, were rarely seen at natural breeding sites. In field experimental enclosures, the behavior of unpaired toads and the behavioral sequences during intersexual encounters were recorded for both sexes. Potential behavioural differences were examined between: (1) toads of different body size classes, (2) toads of each sex during successful and unsuccessful clasping attempts, and (3) toads under different density and sex ratio regimes.

Field experiments were conducted only at site A in 1984-1986 because the same individuals were rarely captured at this site for more than one year and because the breeding population at this site was extremely large (Olson et al. 1986). The preliminary results of 1984 tests were used in determining the experimental design and protocol of 1985 tests. Because the 1985 breeding season was very short and resulted in few test replications, many tests were repeated in 1986. Results of 1985 and 1986 tests, and some preliminary 1984 results are reported.

The experimental enclosure was a 2.5 m diameter circular arena with nylon mesh sides and bottom. The enclosure was positioned within 20 m of the traditional oviposition sites used by toads year-to-year in 50-70 cm water. At this site, breeding activity occurred on the water surface in water up to 2.5 m deep and toads were rarely found in more shallow water (Olson 1989). Thus, the enclosure location was in a typical area of the lake used by breeding toads. Tests were begun at the onset of the breeding season and ended when numbers of breeding toads were too few for the experiments. Tests were conducted during the peak hours of toad breeding activity between 1000 and 1800 hours.

Females used in enclosure tests in 1985 and 1986 were captured paired and gravid at the breeding site. The clasping pairs were separated, marked, measured, and sorted by sex into separate holding pens in 5-10 cm water. Unpaired males were put into a third holding pen after marking and measuring. The time a toad spent in a holding pen was minimized by collecting test animals just prior to testing. For visual identification of toads during enclosure tests, colored plastic dots were glued to the dorsal regions of their heads, posterior to their eyes. After testing, toads were released into the breeding site. Toads remaining in holding pens at the end of a day, and thus not used in a test, were released and not used in tests on subsequent days. Toads were used in tests once.

Tests were conducted using a series of toad densities and sex ratios (Table II.1). A total of 310 toads were used in 1985 and 206 toads in 1986 tests. In the low density (N=6) test-treatments, males of different sizes were used. Specifically, in the sex ratio 2:1 treatments, two large (SUL $>$ 8.2 cm) and two small (SUL $<$ 7.6 cm) males were used per test. In sex ratio 1:1 tests, males of all sizes were used. Males were matched for size in other tests and extremely large (SUL $>$ 9.0 cm) and small (SUL $<$ 7.2 cm) males were not used. Because paired gravid females were not always abundant at the sites, female sizes were recorded but not matched in tests.

Within experimental treatments, males were usually matched for field pairing status (either captured paired or unpaired). However, during six tests, there were not enough males of one pairing-category and both previously paired and unpaired males were used. These included: two tests of density 12/sex ratio 5:1, one of density 6/sex ratio 1:1, one of density 6/sex ratio 2:1, one of density 6/sex ratio 5:1, and one of density 24/sex ratio 11:1.

Test Protocol

Males were introduced to an enclosure before females and allowed to acclimate for 5 min., then females were introduced. Females were placed in the center of the arena away from males. The observer stood motionless outside the enclosure and kept a written record of all behavioral encounters between males and females, including: (1) sex of toad initiating encounter, (2) male response to encounter (unsuccessful clasp attempt, successful clasp, or no clasp), (3) female response to encounter (dive underwater, retraction, swim away, kick, other response, or no response), and (4) time to successful clasp.
The observer did not appear to disturb toad activity. Observations continued until all females were paired or 30 min. had elapsed. If a female had not paired within 30 min. (which occurred when females spent much time underwater), the test was continued for another 30 min.

unobserved and the males clasping the females at the end of this time were recorded. Most (85%) females became paired within the first 10 minutes of a test. In 1986, pairs were separated after the first run of a test and a second run was conducted. In 1985, only one run was conducted.

Behavioral Analyses

In density 6/sex ratio 2:1 tests, potential behavioral differences were examined between pairing and unpairing males, males and females of small (male SUL $<$ 7.6 cm, female SUL $<$ 9.6 cm) and large (male SUL $>$ 8.2 cm, female SUL $>$ 10.2 cm) sizes, and pairs with low (SUL difference between the sexes $<$ 1.3 cm) and high (SUL difference $>$ 2.2 cm) levels of sexual size dimorphism using Mann-Whitney U-tests, Wilcoxon rank sum tests, and contingency table analyses (Chi-square tests). Table II.2 shows the specific behavioral questions addressed and the methods used for each. Additionally, potential pairwise associations between measures of toad size and enclosure behaviors were addressed with data from all density and sex ratio tests using analyses of variance and regression analyses.

Analyses of variance were used to assess the potential effects of toad density and sex ratio on four toad behaviors in enclosures, including: the number of unsuccessful clasps per successful clasp by pairing males, time-to-pairing, average number of clasping attempts (unsuccessful and successful) per male in a test, and female response to an encounter. Female responses were assigned numeric values corresponding to the extent to which females remained in the vicinity of the encounter: diving removed females quickest and furthest from encounters, followed by swim-behaviors, kicks, retractions, and no response. In addition, pairwise associations between these four enclosure behaviors and male field pairing status (previously paired or unpaired) were examined (analyses of variance).

Square root transformations were used for all behaviors in analyses of variance, except when examining the effects of time-to-pairing. To assess the validity of combining data from tests conducted in different years and of considering the 1986 runs as independent tests, density and sex ratio analyses 1-3 (Table II.4) were conducted for 1985 and 1986 separately, separately for the 1986 runs, and for the combined-years. Analysis 4 (Table II.4) was examined with only 1985 data because density=24 tests were not conducted in 1986. Thus, 16 analyses were conducted with regard to each of the four behaviors and their potential associations with density and sex ratio. Analyses of variance were conducted using the SAS computer package (GLM procedure, SAS User's Guide: Statistics, Version 5 Edition, SAS Institute Inc., 1985).

Product-moment correlation coefficients and Student's t-tests were used in comparisons of toad sizes.

RESULTS

Field Observations

At each of the 15 breeding aggregations (5 yrs x 3 sites), breeding was explosive; all breeding activity occurred between 5 and 23 days at a site in a year (Olson et al. 1986; Olson 1988a). Communal oviposition occurred synchronously by pairs in traditional locations, used by toads from year-to-year.

Males actively searched the surface of the water for females near the traditional oviposition sites (Olson et al. 1986). While males searched for females, they neither oriented themselves in any particular direction (i.e. toward the shore or the open water of the lake) nor remained in any location that could be construed as a "territory". Males clasped any toad or pair in amplexus they encountered and unclasped when a release call was given by a male (unpaired or paired). Western toad males did not give advertisement calls.

Active displacements (takeovers) of paired males by unpaired males were never observed during the censusing of over 5000 toads in over 100 days of my attendance at the lakes during breeding. Two or more males were seen clasping the same female prior to oviposition on only 10 occasions at all 15 breeding aggregations (Table II.5). In these multiple-male pairings, the male clasping in the dorsal axillary position usually remained clasped while the other male(s) unclasped.

Two types of separations of mating pairs before oviposition were occasionally seen. At breeding aggregations where I separated pairs for measuring, it was sometimes difficult to entice a male to reclasp. It was recorded if a male did not immediately reclasp his mate after being returned to the breeding site (Table II.5, separations). These separations were observed more often at breeding aggregations with high predation rates on adult toads by ravens (site A in 1984, site C in 1985 and 1986; Olson 1989). Second, when I recaptured a paired female before or during oviposition, replacement of the previously-clasping male with another male was sometimes found (Table II.5, replacements). These replacements may have resulted from unobserved displacement behavior by unpaired males, or the previously-paired males may have unclasped with no interaction with unpaired males. Separation and replacement data are not given for site A in 1985 and 1986 (Table II.5) because field-paired toads used in enclosure experiments conducted at these aggregations were always removed from their mates.

Replacements of clasping males before oviposition was uncommon at most breeding aggregations, but occurred at higher rates at site A in 1984 and site B in 1986. The higher number of replacements at site A in 1984 may be attributed to the extended length of the breeding period; toad breeding seasons usually lasted one week, but breeding activity continued for 23 days at this aggregation, possibly due to an iinterruption by a snowstorm and cold weather conditions (Olson 1988a). Many of the replaced males were those found clasping females in the first week of breeding activity, whereas synchronous oviposition occurred in the last few days of breeding two weeks later.

In both breeding aggregations with high replacement rates, replacement males were larger than replaced males, but not significantly so (site A in 1984: replaced male SUL $\bar{x}=8.157$, var=0.205, n=21, replacement male SUL $\bar{x}=8.314$, var=0.380, n=21; Student's t-test: t=0.94, df=40, $p>0.05$; site B in 1986: replaced male SUL $\bar{x}=6.775$, var=0.129, n=12, replacement male sul $\bar{x}=6.925$, var=0.134, n=12; t=1.01, df=22, $p>0.05$). There were no large male mating advantages at these two breeding aggregations (Table II.5).

Additionally, size assortative mating was observed for the entire breeding aggregation at site A in 1984, but not at site B in 1986 (Olson 1988a, Table II.5). At site A in 1984, there was no correlation of sizes (SUL) within pairs with male replacements (r=0.06, df=19, $p>0.05$), yet there was a size-relationship of mates in replaced-male pairs (r=0.48, df=19, $p<0.05$). This trend was not found at site

B in 1986 (correlation of sizes of replacement-male pairs: $r=0.317$, $df=10$, $p>0.05$; and of replaced-male pairs: $r=0.138$, $df=10$, $p>0.05$). Removing the pairs involving replacements from the population analysis for size assortment at site A in 1984, however, did not change the degree of positive assortative mating (the level of significance of the correlation coefficient after removal: $r=0.16$, $df=197$, $p<0.05$; before removal: $r=0.15$, $df=218$, $p<0.05$; Olson 1988a). Thus replacements probably did not result in the observed positive assortative mating at site A in 1984.

To address the possibility that both size-dependent mating patterns resulted from inadequate clasping abilities of small males, the mating patterns were re-analysed at breeding aggregations showing nonrandom mating without the inclusion of extremely small males. At three of the six aggregations with a large male advantage (Table II.5, Olson 1988a), the removal of the smallest males, comprising 3-9% of the males at an aggregation, from comparisons between the sizes of pairing and unpairing males resulted in random mating (site A in 1982: $t=0.52$, $df=164$, $p>0.05$, removal of 10 males from analysis; site B in 1982: $t=1.18$, $df=178$, $p>0.05$, removal of 17 males from analysis; site C in 1983: $t=1.15$, $df=138$, $p>0.05$, removal of five males from analysis; nonrandom mating was still observed at the remaining three aggregations, $p<0.05$). Thus, the inability of extremely small males to mate resulted in a large male advantage at half of the aggregations, supporting the hypothesis that this mating pattern can result solely from the activities of small males at a site.

The removal of pairs with small males also sometimes affected the occurrence of positive assortative mating. At site A in 1984, the removal of only four pairs, with the four smallest pairing males (of 220 pairs censused), resulted in random mating ($r=0.122$, $N=216$, $p>0.05$). Thus, size assortment at this aggregation can be atributed to the pairing of these few individuals. At the other aggregation with size assortment, site A in 1982, the removal of both five (4%) and 17 (15%) pairs with the smallest males had no influence on the mating pattern ($r=0.346$, $N=108$, $p<0.05$; $r=0.294$, $N=96$, $p<0.05$). In this case, size assortment does not seem to be the result of small male pairing activity.

Female behavior in the 15 breeding aggregations was very different from male behavior. All females at the breeding sites obtained a mate. Unpaired females were observed floating on the water surface, resting on vegetation in the water along the lake-shore, or if no longer gravid, were seen leaving the oviposition site. The few interactions between unpaired females and males observed at the breeding sites were similar to interactions seen in the experimental observation enclosures (see below). Females did not usually approach males and used the same suite of behaviors described in the enclosure tests. A female direct-approach to a male was seen only once by an unpaired gravid toad at an oviposition site two days after synchronous oviposition by most pairs. This female repeatedly approached and bumped other toads, mostly a few ovipositing pairs, until she encountered an unpaired male, was clasped, and soon began oviposition.

Paired females appeared to entirely control the movements of clasping males, who either remained motionless on the females' backs or would synchronize their hind-limb swimming movements with the females. Paired females were never seen to directly approach other toads and always avoided encounters with other toads by diving, swimming away, or kicking. Paired male defense against clasping attempts by unpaired males was by kicking, holding the female tighter, and giving a release call.

Although breeding population sizes and sex ratios varied at the natural breeding aggregations (Olson 1988a), no striking behavioral differences were notable in correspondence to these changes.

In summary, field observations do not support male-male aggressive competition for mates or mate choice as important components affecting western toad mating success. At half the breeding aggregations with size-dependent mating patterns, nonrandom mating could have resulted from the pairing activities of a few of the smallest males at the aggregations.

Field Enclosure Experiments

Results of field enclosure tests conducted in 1984 suggested that whether or not a toad was paired during collection from the breeding site (=field pairing status) may affect its behavior in the enclosure. Female field pairing status affected the tendency of females to approach other toads in the observation enclosure (Chi-square analysis, $N=60$, $p<0.01$); previously paired females approached males more often than unpaired females. However, males approached females much more often and male approaches were usually quickly-executed direct approaches. Females never appeared to have a vigorous directed approach to a male or other toad. Rather, female approaches appeared as slow random swimming movements on the water surface, or if the female was underwater she would slowly come to the water surface near another toad. In contrast to male approaches, physical contact between toads did not always occur during female approaches. Female approaches could have been largely the result of the area-limitations of the enclosure. Additionally, male field pairing status influenced male pairing success in the test enclosure (Contingency Table, Chi-square analysis, $N=96$, $p<0.01$);

previously unpaired males were more likely to remain unpaired in the enclosure. Thus, the readiness of both the male and female to pair in enclosure tests seemed to be affected by their field pairing status. In 1985 and 1986, only previously paired females were tested and males were usually matched for field pairing status within tests.

During 1984 tests, four female behaviors were identified during encounters: dive, retraction, swim and kick. Females responded to another toad by diving underwater in 96 of 174 (55%) encounters. A retraction was recorded during 18% of encounters when a female pulled all four limbs in close to her body and exhaled. This behavior usually resulted in the female moving backwards and down, underwater. Alternatively, females would swim away from the encountered-toad (9% of encounters), kick the encountered-toad (sometimes causing the kicked toad to fly over-water and land 0.5 m away, 14% of encounters), or have no visible behavioral response (4% of encounters). Dives, retractions, swims and kicks usually removed the female from the site of the encounter. Of the four behaviors, dives were most quickly executed and resulted in the female being furthest from the encountered-toad, followed by swim-behaviors, kicks and retractions. All behaviors were used during both male- and female-intiated encounters.

Table II.2 shows the results of tests conducted to address the effects of toad size on pairing behavior, and behavioral differences between unsuccessful and successfully pairing males. Toad pairing behavior was sometimes dependent on toad size. First, the number of successful clasps were not equal between large and small males in the combined-runs test in 1986 (Q1B). In this test, small males made more successful clasps. Second, female behavior during an encounter was dependent on male size (Q4). Inspection of the contingency table analyses showed that small male successful clasps were more frequently associated with female retractions, whereas large males were more successful at clasping females than small males when females responded to the encounter by diving, swimming away, or kicking (1985, 1985 + 1986). Additionally, when no clasp was made by a large male during an encounter, females more often swam away (1985) and kicked (1986, 1985 + 1986) than they did during small-male no-clasp encounters.

Female behavior during an encounter with a male was independent of female size (SUL, Q9) and the degree of sexual size dimorphism (Q12), and male clasping success with regard to the different female behaviors was independent of sexual size dimorphism (Q8). There were no differences between the number of unsuccessful clasping attempts made by pairing and nonpairing males (Q2), or by small and large males (Q1A).

Time to successful clasping and number of clasp attempts per successfully clasping male were dependent on the degree of sexual dimorphism in combined-years analyses (Q6, Q7). Pairs with a large degree of sexual dimorphism took less time to clasp than pairs with a low degree of dimorphism (Q6). For example, 16 of 19 pairs with great dimorphism paired within 5 min., whereas only seven of 16 pairs with low dimorphism paired within 5 min. Males of pairs with low dimorphism made more unsuccessful clasping attempts before pairing than males of pairs with great dimorphism (Q7, Figure I.1).

Female behavior and male clasping behavior was associated (Q5). When male behavior during an encounter was classified as either "clasp" (unsuccessful and successful) or "no clasp", female swim behavior was more often associated with no clasp (1985, 1985 +1986), and female kick and clasp were associated more frequently (1985). When female behaviors were analysed with respect to male clasping success (male behavior = unsuccessful or successful clasp), female dives were seen more often with unsuccessful clasps and retractions with successful clasps (Figure II.2; 1985, 1986, 1985+1986).

The 12 pairwise analyses between measures of toad size and enclosure behavior using results of all density and sex ratio tests yielded three significant results (Table II.3). Male size (SUL) was positively associated with time-to-pairing (regression analysis, F-test, $p<0.05$), and sexual size dimorphism was positively associated with both time-to-pairing (regression analysis, F-test, $p<0.05$) and male clasping behavior (successful or unsuccessful clasp, analysis of variance, F-test, $N=375$, $p<0.02$). Female behavior and recorded mechanical difficulties in clasping were not associated with male or female size, or the level of sexual size dimorphism.

These last results were surprising because during enclosure tests many small males had very obvious mechanical difficulties clasping huge females. It appeared that many unsuccessful small male clasps were the result of their arms not being able to reach across female backs, whereas larger males more often merely missed their clasp by either "overshooting" the females and clasping their heads or clasping "half-heartedly". Because enclosure observers were recording the activities of all toads in a test, the precise behavioral sequences of unsuccessful clasps could rarely be fully noted. However, when time permitted, more precise recordings of toad encounters were made. The sporadic nature of these recordings may inadequately represent the "mechanical difficulty" categorization in the previous analyses (Table II.3), and account for the insignificant results with regard to male size and sexual dimorphism.

Male field pairing status had no effect on toad pairing behaviors: number of unsuccessful clasps per successful clasp, time-to-pairing, mean number of clasps per male in a test, and female behavior (F-tests, $p>0.05$).

In summary, in enclosure experiments, there were several effects of toad size on pairing behavior. For example, large males were more successful at clasping during "vigorous" female responses and paired in less time than small males. Additionally, small males sometimes had mechanical problems clasping large females. These pairing behaviors could easily result in size-dependent pairing patterns.

Density and Sex Ratio Effects on Pairing Behavior

Density and sex ratio had few effects on the four enclosure behaviors analysed (female response, time-to-pairing, no. clasps per male, no. male unsuccessful clasps per successful clasp). Female behavior was associated with density and sex ratio in only two of 16 analyses (Table II.4, analysis 1, 1986 run 2, F-test, $p<0.05$; analysis 4, 1986 run 2, F-test, $p<0.05$). Time-to-pairing was associated (F-test, $p<0.05$) primarily with sex ratio in four of 16 analyses (analysis 1: 1986 combined-runs; analysis 3: 1986 combined-runs, 1986 run 1; analysis 4: 1985+1986 combined-years). The mean number of clasps per male in a test was inversely associated with density and sex ratio in 11 of 16 analyses. The number of male unsuccessful clasps per successful clasp was not associated with either density or sex ratio (analyses 1-4, all separate and combined runs and years tests: 16 F-tests, $p > 0.05$). No associations (F-tests, $p > 0.05$) were found for 1985 data (analyses 1-4) or for analysis 2, 1986 run 2.

Multiple-male Pairings

In the experimental enclosures, prolonged clasping (>10 sec) of a female by more than one male was seen during six of 193 observed pairings (three in 1985, three in 1986). Two of these six multi-male pairings resulted in the displacement of the first-paired male. One male (SUL=7.9 cm) released his grasp on the female after 5 min. of clasping by a second male (SUL=8.1 cm). The other displacement involved 3 males (SUL=8.3, 7.7, 8.3 cm) and one female. This foursome remained together for over 30 min. and after being left in the enclosure for several hours, the second-clasping male (SUL=7.7 cm) remained clasped whereas the other two males released the female. All six multi-male pairings occurred during higher density tests: four occurred in density=12/sex ratio=2:1 tests, one occurred in a density=12/sex ratio=11:1 test, and one occurred in a density=24/sex ratio=11:1 test. The number of multi-male pairings might have increased in enclosure experiments if tests were not ended after all females were paired.

DISCUSSION

Mate Choice

Female choice of mates has been most often reported for anurans in which territorial males produce advertisement calls that differentially attract mates (e.g. Ryan 1980, 1985; Howard 1978; Gerhardt 1982, Sullivan 1983). The opportunity for mate choice in explosively breeding anurans with male "scramble competition" for mates is probably constrained by male searching and clasping activities (Wells 1977). Indeed, in the western toad, it is unlikely that females could have their unobstructed choice of any male in the breeding population because of male behavior.

However, the suite of female behaviors exhibited during encounters with other toads suggests that western toad females did not simply accept all male pairing attempts and often appeared to be avoiding encounters with males. Females may have been behaving coyly, with the result that successfully clasping males were those that were most vigorous or persistent in their clasping attempts, or perhaps those that had less mechanical problems reaching around the expanse of the gravid females' backs (and thus were also perhaps somewhat size-matched with the female).

Female coyness was supported by the experimental results. Females did not respond to all male encounters equally. During no-clasp encounters, females kicked or swam away from large males more often than small males. Retractions were seen more often during male pairings, whereas dives were more frequently associated with unsuccessful clasps. Retractions seemed to be the least "vigorous" of female responses, whereas dives, swims, and kicks were more quickly executed and usually resulted in the female being entirely removed from the encountered-male. Small males that paired in enclosure tests were most successful when females retracted. In contrast, large males that paired were much more successful at clasping than small males during the more vigorous female dives, kicks, and swim-responses.

Passive choice of large males by females could have been implemented by their predominant usage of vigorous behaviors, in response to which large males were better claspers. However, female choice of large males may have been obstructed by other toad mating behaviors. For example, many results suggested that large males were not better than small males at clasping females. Large and small males made equal numbers of clasps (Q1C), were equally unsuccessful at clasping (Q1A), and clasped within the same time period (Q3). Sometimes, small males were more successful at pairing than large males (Q1B). In some analyses, pairs with greater dimorphism (hence, smaller male size with respect to female size) took less time to pair (Q6), and had fewer unsuccessful clasping attempts before pairing (Q7). The inconsistency of these results between years probably indicate their transitory nature.

A potential fitness advantage to females of passively choosing large males has not been determined for the western toad. The fertilization efficiency of western toad males does not vary with their body size (Olson 1988d). Large males may be favored by females because they may confer a size-advantage to offspring or because they exemplify superior survival ability. Alternatively, the western toad female responses to encounters may have been misdirected anti-predator mechanisms or responses to inhibit interspecific claspings.

Paired females may choose mates by inciting displacements by unpaired males (Arak 1983). However, in the western toad, there was no evidence that females did this; there were few replacements at most aggregations and paired females avoided contact with other toads during observations in enclosures and at natural breeding aggregations.

There was little evidence for male mate choice during pairing attempts in both field and enclosure observations. Males clasped any toad encountered. However, male mate choice may have occurred at site A in 1984. At this aggregation, separations during handling occurred more commonly than at most aggregations and paired males that released their mates were found to be clasping significantly smaller females than males that remained in amplexus (Olson 1989). Anuran female fecundity is proportional to female size in many anurans (e.g. clutch size, Salthe & Duellman 1973). If this relationship holds for western toads, male annual reproductive success would be less with smaller females. The threat of predation by ravens was also higher at this aggregation. Males releasing mates during handling may have been balancing the cost of predation and loss of mating success with small females (Olson 1989).

Male-male Competition

Explosively-breeding male anurans may compete directly for mates by aggressive interactions or indirectly by their differential abilities to find and clasp females (i.e. exploitative competition). Direct aggression resulting in displacements of paired males by unpaired males has been observed in a few species (e.g. Davies and Halliday 1977, 1979; Lamb 1984). In western toads, displacements were never seen at natural breeding aggregations and rarely occurred in observation enclosures. Replacements, where it was unknown why a male stopped clasping his mate, were also infrequent at most aggregations and multiple-male pairings of a female were uncommon, supporting the lack of overt aggression among males contending for mates (Table II.5).

In enclosure tests and at breeding sites, males that clasped each other readily released their grasps after release calls were given. In western toads, it is unlikely that direct aggressive interactions among males greatly affects male mating success.

Indirect competition among western toad males can be manifested in several ways. For example, early arrival or persistence at the breeding sites may influence pairing success (e.g. Lee & Crump 1981; Gatz 1981; Woodward 1982b); an early male pairing advantage was seen at 11 of the 15 western toad breeding aggregations (Olson 1988a). Alternatively, clasping ability may vary among males and pairing males may exhibit a behavioral advantage in clasping.

In enclosure tests, some behavioral differences were observed between males in response to the different female behaviors. Recall that large males were more successful at pairing when females exhibited "vigorous" responses to an encounter. In addition, larger males and pairs with less sexual dimorphism took less time to pair, when data from all tests were analysed. Less dimorphism and male clasping success were also associated. These results may have influenced the occurrence of nonrandom mating by male size.

A mechanical limitation of small males when clasping large females was observed in many enclosure tests and may have resulted in their predominant pairing success during the more benign female response, retraction, and their overall longer time-to-pairing (Table II.3). A mechanical clasp-limitation would be most severe for the smallest males in a population. The removal of very few of the smallest males from mating pattern analyses sometimes changed mating from being size-dependent to random. Thus, the activities of extremely small males can have a great contribution to the occurrence of nonrandom mating and a clasping limitation is a likely proximate mechanism.

Density and sex ratio had few interesting effects on western toad pairing behavior. Time-to-pairing sometimes increased with sex ratio. This is probably a simple result of greater number of encounters of males with females as the proportion of males in the enclosure increased. A similar result would probably have been obtained with density if more tests with density=24 were conducted. The result that the average number of clasps made per male in a test decreased with increasing density and sex ratio reflects the lower mating opportunities of individual males in high density and sex ratio conditions. Under these conditions, individual males probably have less chance finding and clasping females because most encounters are with other males. The inconsistencies of the relationships between female behaviors and density and sex ratio among analyses (1-4) and years make that association difficult to interpret.

Western Toad Behavior and Nonrandom Mating Patterns

The two variably-expressed nonrandom mating patterns, a large male mating advantage and positive assortative mating by size, were probably the result of the differential pairing ability of males with regard to their size and their size dimorphism with an encountered female. Large males and pairs with less sexual dimorphism probably had a pairing advantage because they could become paired in less time. This result may be due to the enhanced large male clasping ability in response to the female behavioral repertoire and the lack of mechanical-clasping problems in pairs with less sexual dimorphism.

These behaviors can explain the occurrence of a large male mating advantage and positive assortative mating, as well as the observed associations of the patterns with the degree of size variance and sexual size dimorphism in a population. Size-dependent behavior would be less expressed in populations having less size variance and dimorphism.

Mating pattern variability may also result if other pairing behaviors sometimes override the effects of size-dependent behaviors. For example, in many respects large and small males were equal in their pairing behaviors. If these behavioral components were more important in the determination of male pairing success then size-dependent nonrandom mating may not be observed. In addition, in enclosures, small males had a pairing advantage in 1985. This type of sporadic result could have been just a random occurrence and may override size-dependent pairing behaviors.

In conclusion, the western toad appears to be an unusual explosively-breeding anuran. The lack of overt aggression among males while seeking mates and the implication of passive female choice of mates via their coy behaviors are unique aspects of their mating system. As predicted by Sullivan (1987), both demographic and behavioral factors are important as proximate factors resulting in nonrandom mating. The variably expressed size-dependent mating patterns observed at the 15 breeding aggregations I monitored seem to be the result of size-dependent pairing behaviors (where both female mate choice and exploitative competition among males play predominant roles) in aggregations with higher levels of body size variance and sexual size dimorphism (Olson 1988a). Interestingly, two demographic aspects of breeding aggregations that have been predicted to affect anuran mating systems, density and sex ratio (e.g. Wells 1977), seemed to affect only western toad encounter-frequency during enclosure tests and had no apparent influence on mating behaviors at natural breeding aggregations where these conditions varied.

The breeding dynamics that have been revealed for the western toad illustrate the importance of long-term, multi-site, longitudinal studies of several aspects of breeding biology (behavior, ecology, population demography). Additionally, the use of both controlled experiments and observations at undisturbed natural breeding aggregations can most effectively uncover the roles of the diverse factors affecting mating success. Future research on mating systems would be most productive with longitudinal studies utilizing both experimental and observational techniques.

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Figure II.1: Frequency distribution of the number of clasping attempts made by males of pairs with low (open bars) and high (hatched bars) levels sexual dimorphism.

Figure II.1

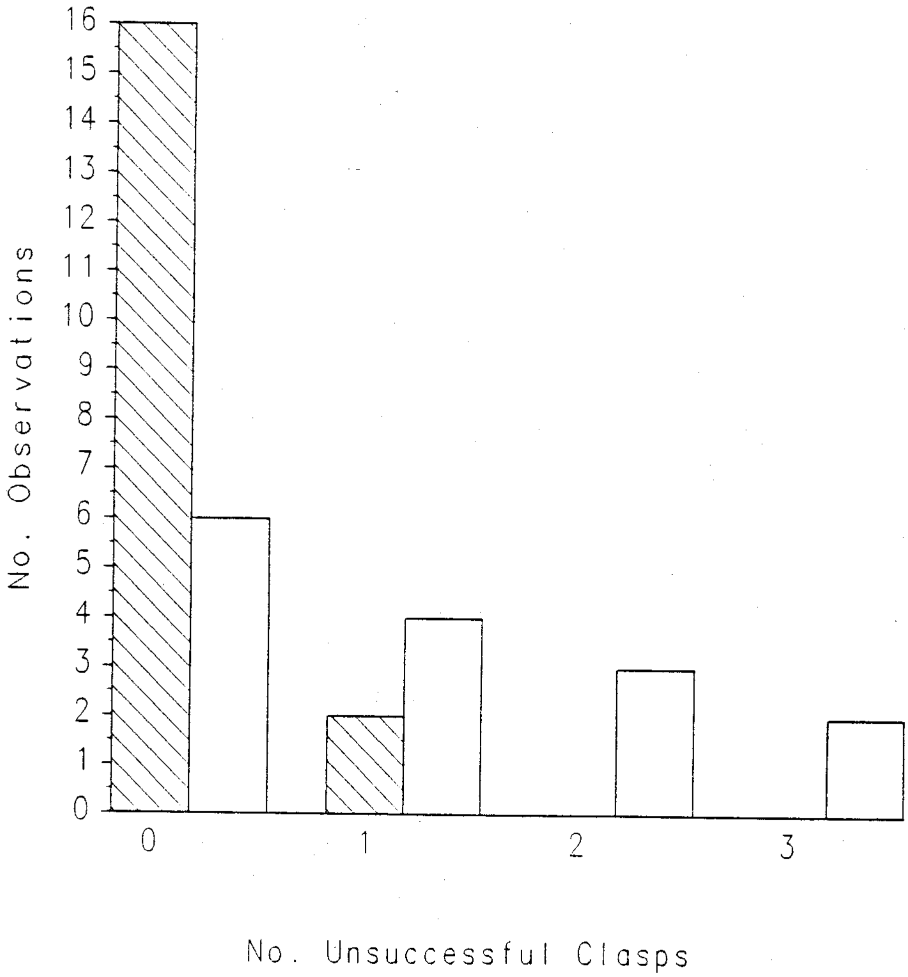
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
No. Observations
0
1
2
3
No. Unsuccessful Clasps

Figure II.2: Frequency distribution of the number of successful (open bars) and unsuccessful (hatched bars) clasps made in association with the different female behaviours.

Figure II.2

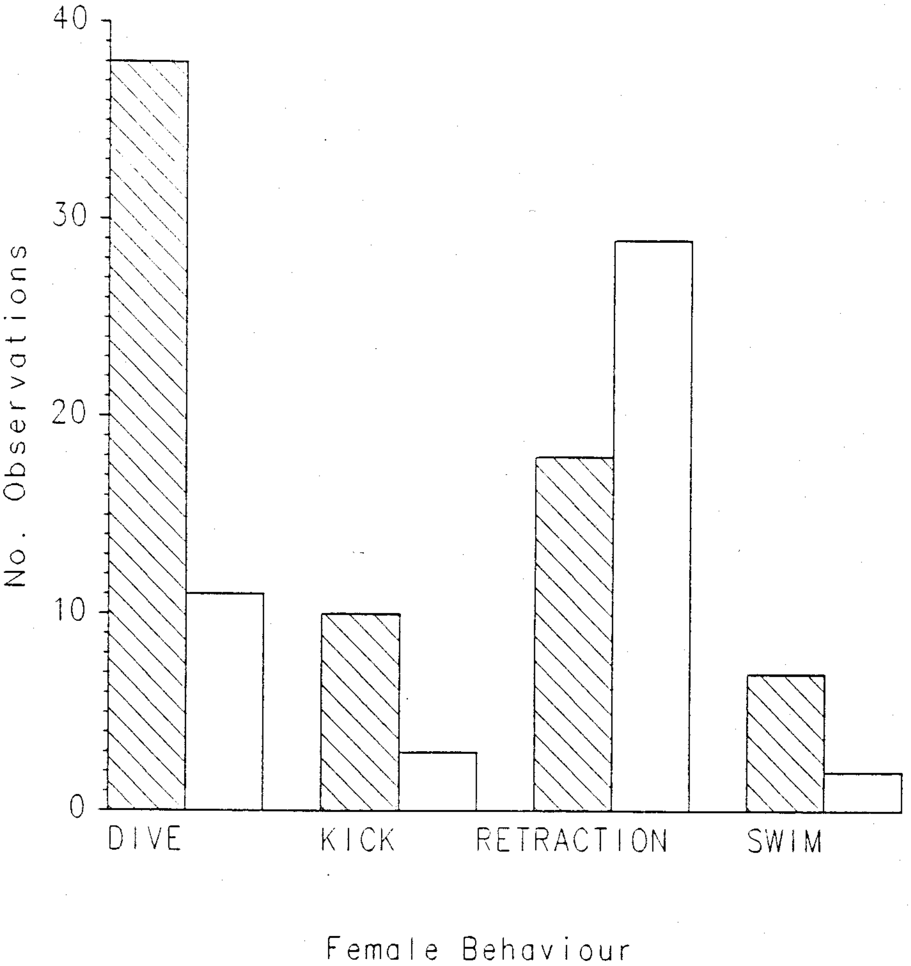
40
30
20
10
0
No. Observations
DIVE
KICK
RETRACTION
SWIM
Female Behaviour

Table II.1: Toad densities and sex ratios (male:female) used in field observation enclosure experiments.

		Number of Replicates		
Density	Sex Ratio	1985	1986	1985 & 1986
6	1:1	11		11
	2:1	11	20	31
	5:1	3	6	9
12	2:1	3	12	15
	5:1	3	10	13
	11:1	3		3
24	11:1	2		2

Table II.2: Questions addressed concerning toad behaviour during pairing, statistical methods, and results.

Table II.2

Question Addressed	Statistical Test Used	1985	1986 Run 1	1986 Run 2	1986 Run 1&2	1985+1986
Q1A: Do large and small males make equal nos. unsuccessful clasps? YES	Mann-Whitney	ns	ns	ns	ns	ns
B: Do large and small males make equal nos. successful clasps? YES/NO	Wilcoxon Rank Sum	ns	ns	ns	T=10,n=13 $p<0.01$	ns
C: Do large and small males make equal nos. successful and unsuccessful clasps? YES	Mann-Whitney	ns	ns	ns	ns	ns
Q2: Do successful and unsuccessful males make equal nos. unsuccessful clasps? YES	Wilcoxon Rank Sum	ns	ns	ns	ns	ns
Q3: Is the time to pairing equal between large and small males? YES	Mann-Whitney	ns	ns	ns	ns	ns
Q4A: Are large and small male behaviors equally associated with female behaviors? NO	Contingency Table	$X^2=11.9$,df=4 $p<0.05$	-	-	$X^2=17.1$,df=2 $p<0.001$	$X^2=9.6$,df=4 $p<0.05$
B: Are large and small male successful clasps equally associated with female behaviors? NO/YES	Contingency Table	$X^2=15.2$,df=4 $p<0.005$	-	-	ns	$X^2=15.4$,df=5 $p<0.01$
Q5A: Are female behaviors equally associated with male successful and unsuccessful clasps? NO	Contingency Table	$X^2=22.4$,df=2 $p<0.001$	-	-	$X^2=25.0$,df=1 $p<0.001$	$X^2=39.5$,df=3 $p<0.001$
B: Are female behaviors equally associated with male clasp and no clasp behaviors? NO	Contingency Table	$X^2=14.0$,df=4 $p<0.01$	-	-	-	$X^2=19.1$,df=4 $p<0.001$
Q6: Is the time to pairing independent of the degree of sexual size dimorphism within pairs? YES/NO	Mann-Whitney	ns	ns	ns	ns	U=227,$p<0.05$ n1=15,n2=19
Q7: Is the no. clasping attempts a successful male makes independent of the degree of sexual size dimorphism? YES/NO	Mann-Whitney	ns	ns	ns	U=82,$p<0.05$ n1=8,n2=13	U=206,$p<0.01$ n1=15,n2=18
Q8: Are female behaviors used independently of the degree of sexual dimorphism? YES	Contingency Table	ns	-	-	ns	ns
Q9: Are female behaviors used equally by small and large females? YES	Contingency Table	ns	-	-	ns	ns

ns = $p>0.05$, * data not analysed because there were few no-clasps

Table II.3: Pairwise analyses of the associations between measures of toad size (SUL) and pairing behaviours: male clasp = successful or unsuccessful clasp attempt; female behaviour = dive, retraction, swim away, kick, none; mechanical problem = recorded difficulty of male clasp because of small male arms grasping a very large female; time-to-pairing= time to successful clasp in enclosure. N = no. observations in analysis. F-test results given.

	Size Measure		
Behaviour	Male Size	Female Size	Sexual Dimorphism
Male Clasp	ns (N=369)	ns (N=373)	p<0.02 (N=370)
Female Behaviour	ns (N=305)	ns (N=309)	ns (N=306)
Mechanical Problem	ns (N=623)	ns (N=374)	ns (N=629)
Time-to-Pairing	p<0.05 (N=178)	ns (N=178)	p<0.05 (N=178)

ns = p>0.05

Table II.4: Densities and sex ratios (male:female) used in analyses of enclosure tests.

Analysis Number	Density	Sex Ratio
1	6, 12	2:1, 5:1
2	12, 24	11:1
3	6	1:1, 2:1, 5:1
4	12	2:1, 5:1, 11:1

Table II.5: Field observations of the number of pairs captured, the number of pairs in which the first-clasped male was replaced by another male before oviposition (="replacements"), the number of pairs separating during observer-handling, the number of pairs in which more than one male was found clasping a female, and the occurrences (yes) of nonrandom mating (Olson 1988a) at 15 natural breeding aggregations.

Table II.5

Field Observation	Site A					Site B					Site C				
	1982	1983	1984	1985	1986	1982	1983	1984	1985	1986	1982	1983	1984	1985	1986
No. Pairs Captured	113	185	221	93	81	76	96	88	98	80	85	130	280	33	133
No. Replacements	1	0	21	-	-	1	5	0	1	12	1	3	5	1	5
No. Separations	6	1	23	-	-	3	2	0	3	0	2	3	5	6	27
No. Multi-male Pairs	0	2	1	0	0	1	0	2	1	2	0	0	0	1	0
Size Assortment	yes	no	yes	no	no	no	no	no	no	no	no	no	no	no	no
Large Male Advantage	yes	yes	no	no	no	yes	yes	yes	no	no	no	yes	no	no	no

LITERATURE CITED

Arak, A. 1983. Male-male competition and mate choice in anuran amphibians. In: Mate choice. (Ed. by P. Bateson), pp.181-210.Cambridge: Cambridge University Press.

Bateson, P. 1983. Mate choice. Cambridge: Cambridge University Press.

Blum, M.S. & Blum, N.A. 1979. Sexual Selection and Reproductive Competition in Insects. New York: Academic Press.

Darwin, C. 1871. The Descent of Man and Selection in Relation to Sex. London: John Murray.

Davies, N.B. & Halliday, T.R. 1977. Optimal mate selection in the toad _Bufo bufo_. Nature 269:56-58.

_____. 1979. Competitive mate searching in male common toads, _Bufo bufo_. Animal Behaviour 27:1253-1267.

Gatz, A.J. 1981. Non-random mating by size in American toads, _Bufo americanus_. Animal Behaviour 29:1004-1012.

Howard, R.D. 1978. The evolution of mating strategies in bullfrogs, _Rana catesbeiana_. _Evolution_ 32:850-871.

Howard, R.D. & Kluge, A.G. 1985. Proximate mechanisms of sexual selection in wood frogs. Evolution 39:260-277.

Lamb, T. 1984. Amplexus displacement in the southern toad _Bufo terrestris_. Copeia 1984:1023-1025.

Lawrence, W.S. 1986. Male choice and competition in *Tetraopes tetraophthalmus*: effects of local sex ratio variation. Behav. Ecol. Sociobiol. 18:289-296.

Lee, J.C. & Crump, M.L. 1981. Morphological correlates of male mating success in *Triprion petasatus* and *Hyla marmorata* (Anura: Hylidae). Oecologia 50:153-157.

Olson, D.H. 1988a. Breeding ecology and variable mating patterns in the western toad (*Bufo boreas*). Submitted.

______ 1988d. Reproductive success and the opportunity for selection in the western toad (*Bufo boreas*). Submitted.

______ 1989. Predation on breeding western toads (*Bufo boreas*). Copeia 1989 (in press).

Olson, D.H., Blaustein, A.R. & O'Hara, R.K. 1986. Mating pattern variability among western toad (*Bufo boreas*) populations. Oecologia 70:351-356.

Orians, G.H. 1969. On the evolution of mating systems in birds and mammals. Amer. Nat. 103:589-603.

Partridge, L. & T. Halliday. 1984. Mating patterns and mate choice. In: Behavioral ecology: an evolutionary approach. Second edition. (Ed. by J.R. Krebs & N.B. Davies), pp.222-250. Sunderland, Massachusetts: Sinauer Assoc.

Ryan, M.J. 1980. Female mate choice in a neotropical frog. Science 209:523-525.

_____. 1985. The Tungara Frog: a Study in Sexual Selection and Communication. Chicago: University of Chicago Press.

Salthe, S.N. & Duellman, W.E. 1973. Quantitative constraints associated with reproductive mode in anurans. In: Evolutionary biology of the anurans. (Ed. by J.L. Vial), pp.229-249. Columbia: University of Missouri Press.

Sullivan, B.K. 1983. Sexual selection in Woodhouse's toad (Bufo woodhousei). II. Female choice. Animal Behaviour 31:1011-1017.

______. 1987. Sexual selection in Woodhouse's toad (Bufo woodhousei). III. Seasonal variation in male mating success. Animal Behaviour 35:912-919.

Trivers, R.L. 1972. Parental investment and sexual selection. In: Sexual selection and the Descent of Man. B. Campbell (ed.). Aldine Publ. Co., Chicago.

Wells, K.D. 1977. The social behaviour of anuran amphibians. Animal Behaviour 25:666-693.

Wilbur, H.M., Rubenstein, D.I. & Fairchild, L. 1978. Sexual selection in toads: the roles of female choice and male body size. Evolution 32:264-270.

Woodward, B.D. 1982a. Sexual selection and nonrandom mating patterns in desert anurans (*Bufo woodhousei*, *Scaphiopus couchi*, *S. multiplicatus* and *S. bombifrons*). Copeia 1982:351-355.

______. 1982b. Male persistence and mating success in Woodhouse's toad (*Bufo woodhousei*). Ecology 63:583-585.

CHAPTER III

MULTIYEAR BREEDING SCHEDULES AND ADULT SURVIVAL IN THE WESTERN TOAD (_Bufo boreas_)

ABSTRACT

The breeding population turnover rates (no. new captures/no. recaptures), individual breeding schedules, and adult survival of western toads, _Bufo boreas_, was examined at three large populations during five years. Sex and population differences were found for most aspects of breeding demography addressed. Males at one population rarely returned to the breeding site among years (turnover rate 85-98%), whereas male site-fidelity and return rates among years were relatively high at two populations (turnover rates 23-76%). Only 88 of over 1700 females bred at the sites more than once. Returning females usually skipped one or more years between breeding bouts whereas returning males most often attended breeding aggregations in consecutive years. At most, females attended breeding aggregations for two years, and some males attended a site in all five study-years. Male breeding longevity averaged

1-2.5 years, and lifespans of males reaching reproductive age are estimated to range from 3 to 11 years. The many sex, site, and between-year differences found in western toad demography emphasize the importance of long-term, multi-site ecological studies, especially when conducted on relatively long-lived organisms.

INTRODUCTION

Multi-year investigations of individual reproduction and survival have been conducted with few long-lived amphibians (e.g. newts: Gill 1978; Gill et al. 1983; frogs: Howard 1978, 1981, 1983; Daugherty and Sheldon 1982). Research on reproductive demography conducted simultaneously at several large, distinct populations over many years for a long-lived amphibian have not been reported. Short term studies or studies conducted at only one site may overlook the extent of intraspecific variability and give a misleading profile of demographic and ecological conditions during breeding. This paper reports intraspecific variability in reproductive ecology during a five year study of three western toad (*Bufo boreas*) populations in the Oregon Cascade Mountains. Western toad population turnover rates, multiyear breeding schedules of individuals, and estimates of adult survival and breeding longevity varied dramatically between the sexes and between study-populations.

METHODS

Breeding populations were monitored in the Oregon Cascade Mountains at three sites in five years (= 15 breeding aggregations). In 1982-1986, toads attending the spring-summer explosive breeding aggregations at Lost Lake (site A, Linn Co., elevation 1220m), Little Three Creeks Lake (site B, Deschutes Co., elevation 1950m), and Todd Lake (site C, Deschutes Co., elevation 1860m) were captured and individually marked by toe clipping. Toads captured at site A in 1985 and 1986 were not uniquely marked, as they were at the other 13 aggregations, because of the large population at site A and the limitations of the toe-clipping scheme. Toads at site A in these two years were marked only to indicate their capture date and breeding status.

Toads were easily captured during the bbreeding season and thus an entire breeding aggregation coould be easily censused. However, at four of the 15 aggregations, some breeding adults may not have been captured because breeding was monitored less carefully: toads were not censused on all breeding days at site A in 1982 and site C in 1985, and toads were captured daily but the entire breeding population present each day was not ascertained at site A in 1985 and 1986.

Between-year turnover and survival rates of toads were determined for each sex from recaptures of marked individuals. Turnover rate was assessed as the ratio of the number of newly-captured toads (unmarked) to the total number of toads at an aggregation. Survival rate among years was determined directly by the proportion of marked individuals captured in later years at each site.

The return-behavior of each sex was assessed to address the question of whether males and females have the same breeding frequencies among years. The breeding longevity of each sex was determined from the mean and variance in the number of years toads attended breeding aggregations.

RESULTS

The return of toads to the breeding sites among years varied with site and sex (Table III.1). Females rarely returned among years (turnover close to 100%), although there was a 69% turnover of females at site C in 1986. Males showed higher degrees of site-fidelity among years and generally had decreasing turnover rates in subsequent years of the study. In the last 2-3 years of the study at sites B and C, males attending the breeding aggregations were primarily recaptures from previous years. Some toads with uncertain toe-clip numbers, because either a toe had been partially-lost by accident or a toe had been poorly clipped, could not be assigned a year of first-capture and are included in the category "unknown toe-clip" (Table III.1).

The breeding history of individuals also reveals site and sex differences. Of the 88 females breeding twice at all sites, 14 (16%) bred two years in a row, 48 (54.5%) skipped one year, 19 (21.6%) skipped two years, and 7 (7.9%) skipped three years between breeding bouts. No female was captured at a site in more than two of the five study years. In contrast, males generally returned to sites in consecutive years. At site B for example, 263 males (77% of recaptures) attended the site two years in a row, 64 (19%) returned after missing one year of breeding activity, 11 (3%) skipped two years and 4 (1%) males skipped three years between breeding bouts. This trend of male breeding frequency also held for sites A and C. Some site B and C males first-captured in 1982 and 1983 attended the site both in consecutive years and also skipped years between breeding bouts (they attended the site in more than two years and are considered in each pertinent category above). Most males returning to sites B and C attended two of the five monitored breeding years. However, many were captured at three and four breeding aggregations and some attended all five of the annual aggregations (Table III.2). The few returning site A males did not attend the site in more than two years.

Sites B and C had different survival rates (Table III.2). At site B, 44-57% of males first-captured in one year were known to be alive the following year, and 19% of the males first-captured in 1982 survived to 4 later breeding years. In contrast, only 17-35% of site C males survived to the next year and 4% of 1982-males survived to 4 later years. Because males sometimes skipped years between attending breeding aggregations, the return rates of males captured in the first two study years may most accurately estimate survival. For 1982 and 1983 males at site B, there was an average of 69% survival of recaptures between each subsequent year (e.g. 57.5% of 1982 and 1983 males survived one year and 39% survived two years: 39/57.5=68%, etc.). Projection of this rate after 1986 suggests it would be four more years (year 1990) until the site B male survival became as low as site C in 1986.

Breeding longevity of toads also showed site and sex differences (Table III.3). Breeding toads lived longest at site B, and adult males generally survived more years than females.

DISCUSSION

The sex differences in western toad breeding schedules may reflect the energetic costs of breeding for the two sexes (Gittins et al. 1980). Females bred in up to two years and those breeding twice usually skipped one or two years between reproductive efforts. In contrast, some males were found at all 5 breeding aggregations at a site and recaptured males were found most often in consecutive years. Other female amphibians are reported to skip breeding years, whereas males generally do not (e.g. newts: Gill et al. 1983; anurans: Gittins et al. 1980; Daugherty and Sheldon 1982). Western toad females deposited several thousand eggs in each breeding bout (Samollow 1980; Olson 1988d). Females may require more than one summer active season (lasting 3-6 mo. at these sites) to restore the necessary energy reserves for reproduction. The energy males expend finding and mating with females in a breeding season probably does not approach the tremendous energy expenditure of females. At the 15 breeding aggregations, I found that females can lose up to 60% of their body weight (e.g. over 150g) during oviposition whereas males lost a maximum of only 20% of their body weight (e.g. 18g) during the most prolonged breeding season (personal observations). The huge female energy expenditure with reproduction could easily increase their mortality and account for the higher longevity estimates of breeding males (Table III.3; Gittins et al. 1980).

The survival estimates of breeding toads were determined from the number of marked toads known to be alive because they bred at the sites in subsequent years of this study. These are necessarily minimum estimates because emigration of nonreturning toads cannot be distinguished from mortality. However, several factors suggest their dispersal may be limited. First, site B and C males had strong site-fidelity among years and other studies also report _B_. _boreas_ to have a high degree of site-fidelity: toads displaced from their breeding sites showed a strong tendency to return to their place of capture even though other areas were available for dispersal (Tracy and Dole 1969), and toads maintained "home burrows" to which they returned throughout a year (Smits 1984).

Additionally, in my study, the topography of sites B and C may inhibit migration because these lakes are nestled in "bowls" with steep ridges on 50-80% of their boundaries. At site A, there is a potential barrier to dispersal only along the south border of the lake where there is a steep ridge. Emigration at these sites among years also may be inhibited because the nearest potential breeding locations are several kilometers away over mountainous terrain. Marked toads were not found away from the sites.

The higher survival estimates of site B males probably represents a realistic difference between the sites. At site C, the toad summer active season is very short, lasting only from about July to September. A shorter summer would drastically reduce their chances for replenishing energy reserves needed for overwintering, increasing winter mortality. In addition, predation on adult toads may be higher at site C (Olson 1989).

The low site A toad recapture rates are somewhat enigmatic. The large size of the breeding aggregations suggests high migration to and from this site, although marked toads have not been captured elsewhere. Alternatively, annual toad mortality may be enormous at this location, with almost no toads surviving to breed in two years. Site A toad mortality could be affected by the considerable drop in lake level at this site from spring to late fall; there was little variation in lake level at sites B and C. For example, if toads overwinter in burrows within about 40 m of the water's edge when the site A lake is at its lowest level at the onset of winter, they would get flooded under the snowpack before spring, which may increase toad mortality. At the onset of breeding in the spring, the snow-pack is just beginning to melt around the lake and the lake level is near the highest it will reach in the year. At this time only 10-20 m of the lake shore from this high level is free of snow. Additionally, it is possible that the site A annual breeding population consists only of toads overwintering in this narrow strip of melted shore that is free of snow during breeding, and that the actual population size is extremely large. In support of this contention, toads were only rarely observed crossing snow as they approached the breeding area, unlike other high-elevation bufonids (Kagarise Sherman 1980). The dispersal and overwintering locations of western toads at all three sites in the Oregon Cascade Mountains warrants further investigation.

The survival rates that I have reported provide the first documentation that the western toad is a relatively long-lived animal in nature. Toads in their first and second years past metamorphosis are of distinct size-classes and prereproductive (personal observations). Thus, the earliest a toad may breed is probably in its third year, although age-size relationships of breeding adults are not obvious and have not yet been determined for these breeding populations. Recaptures of breeding toads in five years suggests some individuals may be at least seven years past metamorphosis, and using the survival projection of site B males, some breeding toads could be eleven years old.

The western toad longevity estimates are similar to those of other temperate zone anurans. On average, site B and C adults survived 1-2.5 breeding years, a breeding longevity similar to some ranids and other bufonids (e.g. Ryan 1953; Raney and Ingram 1941; Hillis et al. 1984; Frazer 1966). Breeding western toads probably have average life spans of 3-6 years, providing they become reproductively active in their third or fourth year. *B. terrestris* may also live 3-5 years in nature (Raney and Lachner 1947), and _R_. _catesbeiana_ may live 5-8 years (Howard 1978). A maximal longevity of 11 years for western toads may be high for anurans at natural populations. Turner (1962) reports the maximal longevity of North American anurans to range 3-12 years in nature, although _Ascaphus truei_ may live 14 years (Daugherty and Sheldon 1982).

The stability of montane toad populations in the Oregon Cascade Mountains may depend on their longevity because tremendous annual mortality is not unusual. Entire larval or juvenile cohorts may die at these high elevation sites because of either drought or early winter conditions (personal observations). Also, sporadic occurrences of mass-predation on breeding aggregations (Olson 1989) may greatly affect the composition of adult breeding populations. The fluctuations in sex ratio and breeding population size (Olson 1988a) at site C over the five study years may reflect differential mortality of cohorts, annual breeding populations, and the sexes.

The variation between populations and sexes in western toad turnover rates, breeding schedules, survival and longevity illustrates the importance of multi-site and year studies of long-lived animals. Intraspecific variability in other aspects of western toad breeding behavior and ecology have also been found (Olson et al. 1986, Olson 1988a, 1988d, 1989). Further investigations of intraspecific variability in breeding ecology may contribute to the understanding of patterns of population dynamics and life history evolution more readily than the use of potentially misleading single-site and year studies.

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Table III.1: Recapture-composition of each breeding aggregation for each sex (F = female, M = male) and turnover rates (= no. new captures/no. captures).

Table III.1

Aggregation			No. Captures From					Unknown	Turnover
Site	Year	Sex	1982	1983	1984	1985	1986	Toe-Clip	Rate
A	1982	F	113						--
		M	171						--
	1983	F	0	198					100.0
		M	8	348					97.7
	1984	F	4	1	210				97.7
		M	6	15	363			(3)	93.8
	1985	F	0	1	0	90			98.9
		M	0	1	3	256			98.5
	1986	F	1	3	0	0	78		95.1
		M	4	3	7	10	154	(4)	84.6
B	1982	F	74						--
		M	186						--
	1983	F	1	101					99.0
		M	79	257					76.5
	1984	F	6	1	85				98.3
		M	62	115	108			(7)	37.0
	1985	F	3	2	0	92			94.8
		M	48	88	36	78		(1)	31.1
	1986	F	3	6	4	3	54		77.1
		M	35	64	24	39	49	(4)	23.2
C	1982	F	99						--
		M	229						--
	1983	F	0	126					100.0
		M	39	106					73.1
	1984	F	2	3	284				98.3
		M	38	34	132			(4)	63.5
	1985	F	2	0	1	51			94.4
		M	17	8	29	23			29.9
	1986	F	3	5	28	4	90		69.2
		M	8	11	19	4	76	(2)	63.3

Table III.2: Male breeding site attendance and survival rates among years at sites B and C.

Table III.2

Site	Year of First Capture	No. Males Attending Site in					Male Rate of Survival to			
		1 yr	2 yrs	3 yrs	4 yrs	5 yrs	1983	1984	1985	1986
B	1982	90	44	31	23	9	58	41	34	19
	1983	117	66	39	39	--	--	57	37	25
	1984	66	36	10	--	--	--	--	44	22
	1985	227	37	--	--	--	--	--	--	50
C	1982	165	41	18	4	1	26	20	8	4
	1983	109	22	8	2	--	--	35	13	10
	1984	176	33	4	--	--	--	--	30	14
	1985	19	4	--	--	--	--	--	--	17

Table III.3: Breeding longevity of toads captured in the first two years of the study at sites B and C.

Sex	Site	Year of First Capture	Survival (yrs)		
			$\bar{x}$	Var	N
Males	A	1982	1.11	0.10	171
		1983	1.05	0.05	348
Males	B	1982	2.52	6.34	197
		1983	2.19	2.32	261
Males	C	1982	1.58	1.20	229
		1983	1.57	0.90	173
Females	A	1982	1.04	0.04	113
		1983	1.02	0.02	198
Females	B	1982	1.18	0.15	74
		1983	1.09	0.08	101.
Females	C	1982	1.07	0.07	99
		1983	1.06	0.06	126

LITERATURE CITED

Daugherty, C.H., and A.L. Sheldon. 1982. Age-determination, growth, and life history of a Montana population of the tailed frog (*Ascaphus truei*). Herpetologica 38: 461-468.

Frazer, J.F.D. 1966. A breeding colony of toads (*Bufo bufo* L.) in Kent. British J. Herpetol. 3:236-252.

Gill, D.E. 1978. The metapopulation ecology of the Red-spotted newt, *Notophthalmus viridescdens* (Rafinesque). Ecol. Monogr. 48:145-166.

Gill, D.E., K.A. Berven, and B.A. Mock. 1983. The environmental component of evolutionary biology. Pages 1-36 *in* Population biology: retrospect and prospect. C.E. King and P.S. Dawson (eds.). Columbia Univ. Press, New York.

Gittins, S.P., A.G. Parker, and F.M. Slater. 1980. Population characteristics of the common toad (*Bufo bufo*) visiting a breeding site in mid-Wales. J. Anim. Ecol. 49:161-173.

Hillis, D.M., A.M. Hillis, and R.F. Martin. 1984. Reproductive ecology and hybridization of the endangered Houston toad (*Bufo houstonensis*). J. Herpetol. 18:56-72.

Howard, R.D. 1978. The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. Evolution 32:850-871.

______ 1981. Male age-size distribution and male mating success in bullfrogs. Pages 61-77 *in* R.D. Alexander and D.W. Tinkle, eds. Natural selection and social behavior: recent research and new theory. Chiron Press, New York.

______ 1983. Sexual selection and variation in reproductive success in a long-lived organism. Amer. Nat. 122:301-325.

Kagarise Sherman, C. 1980. A comparison of the natural history and mating system of two anurans: Yosemite toads (*Bufo canorus*) and black toads (*Bufo exsul*). Dissertation. University of Michigan, Ann Arbor.

Olson, D.H. 1988a. Breeding ecology and variable mating patterns in the western toad (*Bufo boreas*). Submitted.

______ 1988b. The role of mate choice and mate competition in western toad (*Bufo boreas*) nonrandom mating. Submitted.

______ 1989. Predation on breeding western toads (*Bufo boreas*). Copeia 1989 (in press).

Olson, D.H., A.R. Blaustein, and R.K. O'Hara. 1986. Mating pattern variability among western toad (*Bufo boreas*) populations. Oecologia 70:351-356.

Raney, E.C., and W.M. Ingram. 1941. Growth of tagged frogs (Rana catesbeiana Shaw and Rana clamitans Daudin) under natural conditions. Amer. Midl. Nat. 26:201-206.

Raney, E.C., and E.A. Lachner. 1947. Studies on the growth of tagged toads (Bufo terrestris americanus Holbrook). Copeia 1947:113-116.

Ryan, R.A. 1953. Growth rates of some ranids under natural conditions. Copeia 1953:73-80.

Samollow, P.B. 1980. Selective mortality and reproduction in a natural population of Bufo boreas. Evolution 34:18-39.

Smits, A.W. 1984. Activity patterns and thermal biology of the toad Bufo bufo halophilus. Copeia 1984: 689-696.

Tracy, C.R., and J.W. Dole. 1969. Orientation of displaced California toads, Bufo boreas, to their breeding sites. Copeia 1969:693-700.

Turner, F.B. 1962. The demography of frogs and toads. Quart. Rev. Biol. 37:303-314.

CHAPTER IV

REPRODUCTIVE SUCCESS AND THE OPPORTUNITY FOR SELECTION IN THE WESTERN TOAD (*Bufo boreas*)

ABSTRACT

A multi-site longitudinal study of western toad, *Bufo boreas*, breeding dynamics was conducted by following individual toads through five breeding years at three populations. Toad mating success, fertility, and opportunity for selection were assessed.

Mating success variation was much greater for males than females. At each aggregation, females mated once, whereas males mated from 0-4 times. Yearly male mating success was associated with the breeding aggregation sex ratio, and was sometimes influenced by male body size and prior experience at the breeding sites. Cumulatively, males at two sites mated once, on average, after two years of site-attendance, and males mated once after three breeding years in the third population studied.

Male cumulative mating success did not increase significantly after attending a breeding aggregation for three years. Site differences in male multiyear and

lifetime cumulative mating success are attributed to the differential survival and site-fidelity of males among years and the site-specific sex ratio variation among breeding aggregations.

Two aspects of toad fertility were examined with respect to toad body size: clutch size and fertilization efficiency. No relationships were found between female size and clutch size, or between fertilization success and either male size or the ratio of male to female size.

Yearly mating success data provided an operational index of the opportunity for (intensity of) sexual selection. At some aggregations, males had the lowest opportunities for sexual selection recorded for any species of anuran. The western toad mating system can be very opportunistic and may be structured by random events and individual behaviors not involving interactions with other toads. Greater opportunities for sexual selection found at some western toad aggregations were comparable to those reported in other anurans with both explosive and prolonged breeding seasons.

The opportunities for both natural and sexual selection were addressed by partitioning western toad reproductive success into three basic selection episodes: survival of breeding adults, mating success, and fertility. The total opportunity for selection, including the effects of all three episodes was much greater for males than females, and male measures of selection opportunity varied among sites. For males, mating success (i.e. sexual selection) was the major contributor to the opportunity for selection. Clutch size, an aspect of fertility, was the primary fitness component affecting the opportunity for selection on females. The "total" opportunity for selection over the lifetime of toads would be more completely addressed with the addition of the influence of the opportunity for viability selection, the episode of selection on prereproductive survival.

This study is the first to provide direct lifetime measures of the variation in reproductive success among individuals for several populations of a long-lived anuran. The sex and site differences observed for most aspects of survival, mating success, and the opportunity for selection support the importance of multi-site longitudinal studies when addressing questions with evolutionary implications. Intraspecific variation in mating dynamics and opportunity for selection in western toads may also be useful in the development of anuran mating system theory based on selection indices.

INTRODUCTION

Variation in lifetime reproductive success is the basis of evolutionary change (e.g. Arnold and Wade 1984a, 1984b). Lifetime reproductive success of several relatively short-lived animals has been investigated (e.g. Fincke 1982; McCauley 1983; Koenig and Albano 1987), but there are few multi-year studies for longer-living animals (e.g. Clutton-Brock et al. 1982). Multiyear studies of animals breeding in many years are essential to accurately assess lifetime reproductive success because of the potential variation in between-year survival and mating success (e.g. Olson et al. 1986, Olson 1988a, 1988c). Estimates of lifetime reproductive success in animals living and breeding for many years have been provided by short-term studies and models of lifetime success based on yearly data (Howard 1983; Hausfater et al. 1981; Trivers 1976; McGregor 1981). Additionally, estimates of the opportunity for selection (=intensity of) have been obtained from some of these studies (Arnold and Wade 1984b, Howard 1983).

Anuran amphibians are excellent animals in which questions concerning reproductive success and the opportunity for selection can be effectively addressed. Anuran breeding aggregations are often conspicuous, individuals can be easily monitored, and their external fertilization allows for accurate paternity assessments.

Several important studies of mating systems and sexual selection have been conducted with anurans (e.g. Arak 1983; Howard 1978, 1983; Howard and Kluge 1985; Kluge 1981; Sullivan 1982, 1983, 1986, 1987; Ryan 1980, 1985; Wells 1977; Woodward 1982). Of the few long-term investigations of anuran reproductive success (Howard 1983; Sullivan 1986, 1987; Kluge 1981), none have reported multiyear or lifetime reproductive success from direct observations of the survival and mating success of individuals breeding in many years. In this paper, I report the yearly and multiyear cumulative mating success of individual western toads (Bufo boreas) over five years at three large breeding populations. Two measures of their fertility are assessed: annual clutch size and fertilization efficiency. Opportunities for natural and sexual selection are compared between sexes, between populations, and with other species.

METHODS

Breeding aggregations of the western toad were monitored for five years, 1982-1986, at each of three high-elevation sites in the Oregon Cascade Mountains: Lost Lake (=site A, Linn Co., elevation 1220m), Little Three Creeks Lake (=site B, Deschutes Co., elevation 1950m), and Todd Lake (=site C, Deschutes Co., elevation 1860m). Adults were captured along the lake shores near the breeding areas, marked by toe-clipping, measured for snout-urostyle length (SUL, ± 1mm), and returned to the site. Weights (spring scale, ± 1g) were also obtained at many aggregations.

During censusing, actively breeding toads were easily captured. At four aggregations, however, some adults may not have been captured because breeding was monitored less thoroughly: either toads were not censused on all breeding days, although censusing was conducted on both early and late breeding days (site A in 1982, site C in 1985), or toads were censused on a daily basis during breeding but the entire breeding population present at a site in a day was not thoroughly assessed (site A in 1985 and 1986).

Mating success was defined as the number of mates each individual acquired. Because pair displacements before oviposition were uncommon (Olson 1988b), accurate mating success estimates were easily obtained.

Yearly male mating success may be affected by male body size, previous experience at the site, and several demographic factors. At aggregations with high frequencies of multiple matings by males, the body sizes of males mating once, twice, three times, etc., and not at all were compared (Student's t-tests). Previous experience at the sites was partitioned into three components of known male breeding history: year a male was first-captured, number of years of previous site-attendence, and previous cumulative mating success among years. Potential differences in the mating success between males of different experience-classes were examined (Student's t-tests). The association between male mating success (both mean and variance for an aggregation) and four demographic components of breeding populations (male breeding population size, aggregation sex ratio, breeding season length, oviposition synchrony = no. days oviposition occurred/breeding season length) were addressed by product-moment correlation analyses. The last two aspects were analyzed because they could constrain multiple mating opportunities for males.

Multi-year cumulative mating success was determined for recaptures at the sites among years. The cumulative number of mates per individual was analyzed by the number of years (1-5) the toads attended the aggregations and by their year of first-capture (1982-1986). Potential cumulative mating success differences between toads were examined with the Student's t-test.

Two aspects of western toad fertility were addressed with respect to body size. First, the potential association between female body size and clutch size was examined by linear regression and product-moment correlation. Eggs were counted in clutches oviposited by pairs in 1 m^2 field enclosures adjacent to natural oviposition sites at site A in 1986 (N=10) and site C in 1985 (N=18). Second, fertilization efficiency (no.

fertilized eggs/no. eggs in clutch) was determined for each clutch oviposited in the site C field enclosures. Fertilization was assessed 1-2 days after oviposition by counting developing eggs (gastrula-neurula stages). Potential relationships were examined between fertilization efficiency and (1) male body size, and (2) the ratio of male to female size (linear regression and correlation analyses).

The opportunity for selection was determined by using the selection index, I = variance/mean-squared (Crow 1958; Wade 1979; Wade and Arnold 1980; Arnold and Wade 1984a, 1984b), for each fitness component addressed, including: yearly mating success, multi-year mating success, survival of breeding adults (breeding-longevity), and fertility (clutch size and fertilization efficiency). Potential associations were examined (product-moment correlation coefficients) between the opportunity for selection on yearly mating success (i.e. the opportunity for sexual selection) and five demographic components of the breeding aggregations: male population size, aggregation sex ratio, breeding season length, oviposition synchrony, and male body size variance. Sex and site differences in selection indices were compared, and the opportunities for natural and sexual selection were compared between these western toad aggregations and other anuran amphibians.

RESULTS

Yearly Reproductive Success

The number of mates per toad per aggregation was used as a measure of annual toad mating success and as an initial measure of annual reproductive success.

Males mated from 0 to 4 times in a year and mean male mating success ranged from 0.30 to 1.36 matings/male (Table IV.1). Within some sites, between-year mean male mating success differed. Of the 10 possible comparisons of mean male success between the five years at each site, significant differences (Student's t-test, $p<0.05$) were apparent in six comparisons at site A (1982 vs 1983, 1982 vs 1985, 1982 vs 1986, 1983 vs 1985, 1984 vs 1985, 1984 vs 1986), and in nine comparisons at site C (for comparison 1983 vs 1985, $p>0.05$). No differences ($p>0.05$) resulted from the other within-site, between years comparisons of mean male mating success, including all 10 comparisons at site B. Additionally, 12 of 15 within-year, between-site comparisons yielded significant differences (Student's t-test, $p<0.05$) between mean male mating success. Only the comparisons of 1982-site B vs C, 1985-site A vs B, and 1986-site A vs B showed no difference ($p>0.05$) in mean male success. Summing male mating success over all four years within sites and determining their overall average yearly mating success resulted in males at site C having the greatest overall average yearly mating success

($\bar{x}$=0.88 mates/male, s^2=0.61, N=784), site A-males having intermediate success ($\bar{x}$=0.51, s^2=0.27, N=1354), and site B-males having the lowest overall mating success ($\bar{x}$=0.34, s^2=0.27, N=1299). These overall averages were significantly different between sites (Student's t-tests, $p<0.001$).

In contrast to the highly variable male mating success both within and between sites, mating success of females at the breeding sites was constant each year. At the 15 breeding aggregations, over 1700 gravid females were captured and in a breeding season each female produced a single clutch and oviposited with one male.

I measured two other factors that can contribute to variation in reproductive success. First, the number of eggs produced per female was measured during oviposition in pair-enclosures at the natural breeding sites. Overall, larger females produced more eggs (Figure IV.1; $y=2978x - 1763$; $r=0.83$, N=28, $p<0.05$). However, within sites, the variability of egg number by female size was high and there was no significant relationship between number of eggs per clutch and female size (site C: $r=0.40$, N=18, $p>0.05$; site A: $r=0.52$, N=10, $P>0.05$). Second, the fertilization efficiency of males of different sizes relative to females was examined. Fertilization was assessed during the gastrula-early neurula stages of egg development. Thus, eggs that I have considered infertile include fertile eggs that died during the earliest stages of development. From 83.3-99.7% of the eggs shed in pair-enclosures at the natural breeding sites were fertilized and developed to gastrula-neurula stages (Figure IV.2). There was no association between fertilization success and the relative sizes of males and females within pairs (Figure IV.2; $y=3.8x + 92.4$; $r=0.07$, $N=18$, $p>0.05$). Additionally, male size was not correlated with fertilization success ($r=0.16$, $N=18$, $p>0.05$). In the natural communal egg masses of western toads, eggs were rarely seen unfertilized or not developing.

Population Demography and Yearly Male Mating Success

Several demographic aspects of breeding were investigated with respect to their association with male mating success (mean and variance of number of mates per male): 1) the number of males present at the breeding aggregation (range 77-385), 2) the sex ratio of the breeding adults (male/female, range 0.7-3.3), 3) the length of the breeding season (= no. days males and females were active at the sites, range 6-23 days), 4) the synchrony with which pairs oviposited (= no. days during which approximately 90% of the eggs were shed/breeding season length, range 0.13-1.0). The sex ratio of breeding adults at an aggregation was correlated with both the mean ($r=-0.904$, $df=13$, $p<0.01$) and the variance ($r=-0.522$, df=13, $p < 0.05$) of male mating success. Thus, the mean and variance of male mating success decreased as sex ratios became more male-biased. Male mating success was not associated with the other factors examined ($p > 0.05$).

Male Body Size and Yearly Mating Success

At site C in 1984, the body sizes (SUL) of males were examined with respect to their mating success because of the unusually large number of males with multiple mates (Table IV.1). Males mating twice were larger than unpaired males and males mating one time (Figure IV.3; Student's t-tests, $p < 0.05$). Additionally, males that paired one or more times were larger than unpaired males at this and five other of the 15 breeding aggregations censused (Olson et al. 1986, Olson 1988a).

Male Breeding History and Yearly Mating Success

Male mating success within a year was analyzed with respect to breeding history. First, the relationship between yearly male mating success and year of first capture was examined: in each of the last 4 years of the study, male mating success at a breeding aggregation was compared between males first-captured in different years. Only seven of the 60 comparisons yielded significant differences in mating success (Figure IV.4). In six of these seven cases, male experience at the breeding site in previous years (i.e. previous site attendance) was associated with enhanced later breeding success.

Second, the yearly mating success of males attending the breeding site for the first time and those present in 1-4 previous years were compared at sites B and C in 1985 and 1986. At site B, males with less site experience often had lower mating success. In 1985, males with two years of previous experience at site B had greater success than both new males (Student's t-test, $t=2.71$, $df=149$, $p<0.01$) and males with one year of experience ($t=2.05$, $df=128$, $p<0.05$). In 1986, newly captured site B males had less mating success than males with four years ($t=2.48$, $df=56$, $p<0.05$), three years ($t=3.14$, $df=95$, $p<0.05$), or one year ($t=2.115$, $df=102$, $p<0.05$) of previous site-attendance. All other comparisons resulted in no difference ($p>0.05$) in the mating success of males with 0-4 years of previous experience at site B. At site C, some more experienced males had lower mating success than less experienced males. In 1985, males with 2 years of experience at site C had significantly less mating success than new males ($t=3.24$, $df=35$, $p<0.005$), males with one year of experience ($t=2.39$, $df=41$, $p<0.025$), and males with 3 years of experience ($t=2.54$, $df=14$, $p<0.05$). There were no differences in the annual mating success of site C males in 1986 with regard to their number of years of site-experience.

Male mating success in a year was also examined with respect to previous mating success rather than just previous breeding site attendance. In this analysis, the cumulative mating success of recaptured males in previous years was compared between successful and unsuccessful males in each subsequent year, 1983-1986 at sites B and C (again, site A was not examined because of the small number of recaptured males). These comparisons were conducted separately for males by their year of first-capture. For example, at site B in 1986, the previous cumulative mating success of males first-captured in 1982 was compared between those mating and not-mating in 1986 (and likewise for 1983, 1984, and 1985-males). At both sites B and C, previous mating success of recaptured males was never associated with the mating success of those males in later years (Student's t-tests, $p > 0.05$ in all comparisons).

Cumulative Mating Success Among Years

Cumulative male mating success generally increased with the number of years males attended the breeding sites, and tended to double with each additional year a male was present, up to 3 years (Table IV.2: No. Years at Site). Within these sites, male mating success was significantly different between males present 1, 2, and 3 years (Student's t-tests, $p < 0.05$), but there were no differences between males present 3, 4, or 5 years ($p > 0.05$). At site C, this result may be due to the few males caught in 4 or 5 years. Additionally, there were striking differences in cumulative male mating success among sites. Males at site B mated only once, on average, after being present at the site 3 or more years, whereas site A and C males obtained more than one mate after 2 years of site-attendance (Table IV.2: No. Years at Site).

Cumulative mating success was also determined for both males and females with regard to their year of first capture (Table IV.2: Year First Capture). At sites A and B, males first-captured in 1985 and 1986 had lower cumulative mating success than males from all previous years (1982-1984, Student's t-tests, $p<0.05$), probably because of their fewer mating opportunities. At site A, 1982-males had greater cumulative mating success than males from each other year ($p<0.05$), whereas at site B, mating success did not differ between males first-captured in 1982, 1983, and 1984 ($p>0.05$). Male success at site C was generally greater than sites A and B. Site C males first-captured in 1985 had greater mating success than 1986-males, and 1984-males had greater success than males from all other years ($p<0.05$; Table IV.2: Year First Capture). For females, there was no consistent relationship between year of first-capture and cumulative mating success. Females with two mates attended breeding aggregations in two years (Table IV.2). Overall, females mated essentially once and there were no differences between females first-captured in different years or at different sites (Student's t-tests, $p > 0.05$).

Lifetime Estimates of Mating Success

Conservative lifetime measures of mating success can be made for marked adults known to survive and breed at the sites among years. A first measure of male lifetime mating success can be made directly from the cumulative mating success of males first-captured in the early years of the study (Table IV.2: Year First Capture). This measure may be most accurate for site A and C males first-captured in 1982 because few were known to survive to 1986, and if any bred in subsequent years they would probably be few and have little effect on the average success of males at the site.

A second estimate of site B male lifetime mating success was made by assigning projected survivors in subsequent years mating success, and including their projected success in the lifetime mating success estimate. For this estimate, a projected survival rate of 69% was used between years because this was the average survival of 1982 and 1983-marked and recaptured males (Olson 1988c). In each year, 34% of the survivors were estimated to mate once because this was the average mating success of site B males in a year and site B males rarely had multiple mates at a single aggregation (Table IV.1). Each projected year, survivors and mating males were chosen randomly from individuals present the previous year. The projected cumulative lifetime mating success of males first-captured in 1982 increased slightly with each subsequent year (Table IV.2: Projection of 1982 Males in-). By 1990, the projected survival rate of 1982-marked males at site B matched the site C survival of 1982-marked males through 1986. Thus, western toad male survival and reproduction were roughly equivalent between sites B and C only with great temporal disparity; rates of male survival and reproduction during 9 years at site B matched that of males during only 5 years at site C. Additionally, the lifetime mating success of these two year-classes of adult breeders were very similar (i.e. the 1982-marked males at: site B in 1990 vs. site C in 1986).

Female lifetime mating success was measured only by direct observations of multiyear breeding (Table IV.2). Projections of their survival and reproduction were not calculated because at most only 4% of the females first-captured in 1982 were known to be alive in 1986 (Olson 1988c).

Opportunity for Selection

The opportunity for selection was calculated from data on mating success, survival estimates of breeding adults, and fertility. Selection indices were determined from the mating success of toads at the annual breeding aggregations (I2, Table IV.1), from the cumulative mating success of males attending the sites in different numbers of years and males first-captured in different years (Table IV.2), and from lifetime estimates of toad mating success (Table IV.2). The yearly opportunity for selection on males varied both within and among sites (range 0.26-2.89, Table IV.1), as did the selection opportunity calculated from multiyear mating success determinations (Table IV.2, range 0.147-4.52). For males, the opportunity for selection on a yearly basis was associated with the sex ratio of the breeding aggregations ($r=0.92$, $df=13$, $p<0.01$) and the male population size ($r=0.63$, $df=13$, $p<0.05$), but not with the breeding season length, oviposition synchrony, or the male body size (SUL) variance at the breeding aggregations ($p>0.05$).

The opportunity for selection was determined from survival estimates (mean and variance in breeding longevity of adults) for toads first-captured in 1982 and 1983 (I1, Table IV.3, longevity data from Olson 1988c). The opportunity for selection was generally greater on males (range 0.04-1.0) than females (range 0.02-0.11), and within each sex, the selection opportunity was greatest at site B.

The selection index was calculated for the two aspects of toad fertility examined: clutch size (I3) and fertilization efficiency (I4). The selection index for clutch size varied little between sites (site A: I3 = 0.14, and site C: I3 = 0.13). The opportunity for selection on fertilization efficiency of pairs by size (Figure IV.2) was essentially zero (I4 = 0.003).

The total opportunity for selection (IT) can be estimated from the separate selection episodes addressed: survival of adults (I1), yearly mating success (I2), and fertility (I3 and I4). The addition of the selection indices from each episode assumes their independence (Table IV.4). For I1, the average values of 1982 and 1983-captured toads were used in the calculations of IT, and for I2, the mean value from all five aggregations at a site was determined (Table IV.4). The opportunity for selection on yearly mating success does not account for the multiyear mating success of most males (adult longevity one year, Olson 1988c). To adjust for multiyear mating chances, the mean I2 was also weighted by the mean number of breeding years (I2' = I2 x mean longevity, Olson 1988c), however, this reduces the independence of I1 and I2'. The opportunity for selection on fertility was assumed to be similar among sites: the site A and C clutch size indices were averaged to estimate I3 for site B, and the value of I4 from site C was also used for sites A and B (Table IV.4). The total opportunity for selection on male toads varied considerably between the sexes and among sites, due primarily to the site-differences in I2 and I2'.

DISCUSSION

Reproductive success and the opportunity for selection are most effectively addressed with longitudinal data, in which individuals are followed through time (e.g. Arnold and Wade 1984b). Additionally, the site and year differences in western toad mating success and the opportunity for selection illustrate the importance of multi-site longitudinal studies when addressing ecological, behavioral, and evolutionary questions in natural populations. The extent of between-population and between-year variation in reproductive demography in the western toad emphasizes the point that conclusions drawn from single site or short-term studies can be misleading.

Mating Success

Sex and site differences were most dramatic for toad mating success. At a breeding aggregation in a year, females mated once with one male. Males mated from 0-4 times at an aggregation, with site A males generally mating either once or not at all, most site B males not mating, and site C males often having multiple mates.

I assessed the influence of a variety of factors on yearly male mating success, including: population size, sex ratio, breeding season length, temporal synchronization of oviposition, male body size, year of first-capture (a possible indicator of male age in the latter years of the study), previous breeding site attendance, and previous mating success at the sites. Four of these factors (sex ratio, body size, year of capture, and previous site attendance) showed some relationship with male mating success.

Yearly male success was most strongly associated with the sex ratio of a breeding aggregation. In the aggregations with the most male-biased ratios (i.e. site B, male:female ratio about 3.0, Olson 1988a), the average success was the lowest achieved (mean success of site B males = 0.34 mates per male), whereas in aggregations with female-biased ratios (site C in 1984 and 1986, ratios = 0.71 and 0.92 respectively), generally all males mated (mean success $\geqslant$ 1.0).

At site C in 1984, where multiple mating by males was most commonly observed, the potential relationship between body size (SUL) and mating success was examined, and males mating twice were found to be larger than males with less success. The lower sample sizes of males mating 3 and 4 times may have precluded the observation of a size relationship for males with these classes of mating success. Also, male body size of paired males, those males pairing one or more times, was greater than unpaired males at this aggregation (Olson 1988a). At all 15 aggregations monitored, a large male pairing advantage was found at only six aggregations. Although male mating success (= no. mates/male) was associated with the aggregation sex ratio, the occurrence of a large male mating advantage was not associated with the sex ratios of the breeding populations. Size-dependent pairing patterns were associated with the body size variance of the aggregations, suggesting that some aggregations had insufficient size variation for the observation of this mating pattern (Olson 1988a).

Western toad lifetime mating success seems to vary with site and sex primarily because of the differential recapture (survival) rates of the toads and sex ratio differences among aggregations. Females and site A males rarely returned for a second breeding effort, and had the lowest lifetime measurements of mating success, whereas many site B and C males attended 4 and 5 breeding aggregations and some site B males may have attended the site in 9 years (Olson 1988c). However, lifetime mating success of site B and C males did not significantly increase past three years of site-attendance. Overall, site C males had the greatest mean and variance in lifetime mating success, probaby because the sex ratios of site C aggregations were the least male-biased of the three study sites (range of male:female ratio 2.25-0.71). The sex ratio of breeding adults at site C in 1984 was the most extremely female-biased ratio observed at any aggregation (male/female ratio = 0.71) and probably enhanced the mating opportunities of males attending the 1984 breeding aggregation. At site B, the number of male mating opportunities probably was more influenced by the year of first-capture and, hence, the number of years of site attendance, than sex ratio. The sex ratios of the five site B breeding aggregations differed very little, while site B males captured in the first three years of the study had greater cumulative mating success than later-arriving males first-captured in later years.

Reproductive Success

The reproductive success (fitness) of an organism depends on its survival, mating success and fertility. The lifetime mating success estimates I have reported for the western toad include measures of adult survival and annual mating success, and are probably representative of lifetime reproductive success. Differences in individual mating success within years for males and among years for both sexes seem to be the greatest contributors to variation in reproductive success. The annual mating success of western toads at these sites could be accurately assessed because mating pairs and unpaired males were easily censused at the breeding aggregations and pair displacements were uncommon (Olson 1988b).

The site-attendance of toads among years probably reflect between-year survival (Olson 1988c).

Fertility does not appear to contribute significantly to variation in western toad lifetime reproductive success because consistent patterns of fertility variation were not found. Male ability to fertilize eggs was not associated with male size or the ratio of male to female size. These results are contrary to predictions that there is an optimal size ratio for anuran pairs to maximize fertilization success (Licht 1976; Davies and Halliday 1977). Within sites, female clutch size was not associated with body size. However, at site A, some of the largest females examined had clutches twice the size of the smallest females, a potential doubling of their annual reproductive success. Site A males would also benefit by pairing with these large females, although consistent patterns of nonrandom mating of males with regard to female size have not been found. Size assortative mating was found at only two of the 15 aggregations (site A in 1982 and 1984, Olson et al. 1986, Olson 1988a). If there was a more consistent fertility advantage of large females and more consistent patterns of size assortative mating, then fertility differences could be an important contributor to variation in lifetime reproductive success for both western toad males and females.

Opportunity for Selection

The opportunity for selection can be operationally defined as the ratio of the variance to mean-squared of fitness components (=I, Crow 1958; Wade 1979; Wade and Arnold 1980; Arnold and Wade 1984a, 1984b). Over the lifetime of an individual, this selection index (I) will be a measure of the opportunity for both natural and sexual selection (e.g. Arnold and Wade 1984a, 1984b; Koenig and Albano 1986). Within breeding seasons where differential survival is negligible, "I" from mating success data can be an operational measurement of the opportunity for sexual selection (Wade 1979; Wade and Arnold 1980). However, this definition may overestimate the role of sexual selection if natural selection episodes are important factors affecting mating success variation (Koenig and Albano 1986).

Few investigations have provided information from multi-year studies of natural populations of long-lived organisms that could be used to directly partition the effects of natural and sexual selection (e.g. Arnold and Wade 1984a, 1984b; Koenig and Albano 1987). Comparisons of the opportunities for natural and sexual selection can be obtained from my data on survival, mating success, and fertility of western toads.

Sexual Selection

The opportunity for sexual selection, determined from the differential mating success of individuals, may be useful in comparisons of mating systems among diverse organisms (e.g. Payne and Payne 1977; Payne 1979, 1984; Kluge 1981; Trail 1985; Wade and Arnold 1980). A first step for the development of a mating system theory based on the opportunity for sexual selection is the observation of patterns within taxa, especially in organisms with similar breeding habits.

Anuran mating systems usually are categorized on the basis of breeding season length and the dominant proximate components of sexual selection, mate competition and mate choice (e.g. Wells 1977, Arak 1984). The mating behavior of explosive breeders is generally dominated by male scramble competition for mates, whereas in prolonged breeders, male territoriality and female choice of mates have been observed most often (Arak 1984). The western toad is an explosive breeder with male search and scramble competition for mates, however, western toad males do not aggressively compete for females (Olson 1988b) as in other explosive breeders (e.g. _B_. _bufo_, Davies and Halliday 1977, 1979). The western toad appears to have a more opportunistic mating system, where chance can play a large role in male mating success. However, other important aspects of their mating dynamics include size-dependent behaviors of both males and females: size-dependent exploitative competition among males for mates, and potential passive female choice of mates by their size-dependent coy-like responses to male pairing attempts (Olson 1988b). These behaviors have not been reported for other anurans, thus the western toad may have an unusual mating system among anurans.

Comparisons of sexual selection indices between the western toad and other anurans may provide further insight for the development of patterns useful for mating system classifications. The opportunity for sexual selection on western toads was estimated from their yearly mating success (Table IV.1). The sexual selection opportunity on western toad males varied both within and among sites (range 0.26-2.89). The value of 0.26 for site C in 1983 is the lowest reported for a male anuran. Kluge (1981) determined similar sexual selection indices for males of 15 species, range 0.5-13.6, and Sullivan (1986) found the opportunity for sexual selection to vary from 1.6-15.6 for _B_. _woodhousei_ breeding aggregations.

The low indices of the western toad suggest that sexual selection in these aggregations has little affect on male mating success. The breeding aggregations with these low indices are ones in which size-dependent mating patterns were generally not found, and in which male body size variances were the lowest observed. The correlation between variation in body size and size-dependent mating, and the size-dependent sexual behaviors observed suggest that the intensity of sexual selection may also be somewhat dependent on the toad body size distribution within a breeding aggregation (Olson 1988a, 1988b). However, there was no direct association between the sexual selection indices and male body size variance. The lowest western toad sexual selection indices probably indicate aggregations at which male opportunism and chance are large determinants of male success. Examples of western toad male opportunism affecting mating success include: the finding that male success is dependent on the aggregation sex ratio and the toad body size distribution, and that early arriving males at the sites usually had a greater chance of pairing (Olson 1988a).

Sexual selection via both exploitative male-male competition and female choice may play a larger role in western toad aggregations with greater size variance and greater sexual selection indices. The levels of the higher indices in the western toad are comparable to indices of other anurans with both explosive and prolonged breeding seasons (Kluge 1981; Sullivan 1986). The intensities of sexual selection may be similar in these anurans, despite the differences in the dominant behavioral components of sexual selection which structure their mating dynamics. The intensity of sexual selection seems to be potentially much greater in anurans with aggressive male scramble competition for mates (e.g. *B. bufo*, I=5.0; and perhaps *B. canorus*, $I \leqslant 13.6$, and *B. exsul*, $I \leqslant 5.2$; Kluge 1981).

Demographic correlates with the opportunity for sexual selection can reveal some of the intricacies of the dynamics of anuran mating systems. The opportunity for sexual selection was related to the sex ratio and size of the breeding aggregation, but not breeding season length in the western toad. Sullivan (1986) also found these three results for *B. woodhousei*. These findings support the significance of population size and sex ratio as important components for the operation of sexual selection and as factors potentially affecting mating system variation (in anurans, Wells 1977; Howard and Kluge 1985; in general, Emlen and Oring 1977).

Total Opportunity for Selection

The total lifetime opportunity for selection (IT) has not been reported from multiyear data of long-lived individual anurans. However, Howard (1983) estimated the total selection opportunity on bullfrogs, *Rana catesbeiana*, using simulation techniques and Arnold and Wade (1984b) used Howard's bullfrog data in an additional selection analysis. In western toads, I partitioned IT into three major episodes: survival of adults, mating success, and fertility. Yearly mating success was the major component of IT at all three sites for males, comprising 57-86% of the selection index (I2/IT). Using the weighted index of mating success to account for male multiyear mating, the total opportunity for selection became almost entirely a function of mating success (I2'/IT' range 0.68-0.87). Selection on the number of breeding years was the second largest contributor to male IT at sites B and C, suggesting that between-year survival of breeding adults is of much less importance than yearly mating success for male fitness. The bullfrog results (Howard 1983; Arnold and Wade 1984b) also predict that mating success is of prime importance for total selection opportunity on males.

The opportunity for selection on western toad females was sometimes an order of magnitude less than on males (IT males/IT females range 6.9-13.9, IT' males/IT females range 9.1-27.6). Clutch size was the most important female fitness component assessed for the opportunity for selection (I3/IT range 0.59-0.69). The result that clutch size is a more important component to variation in reproductive success in females than males is consistent with Howard's (1983) bullfrog study, but his simulation of lifetime reproductive success predicts similar total opportunities for selection for the two sexes (I ratio close to 1.0). The many life history and mating system differences between bullfrogs and western toads (Howard 1978, 1981, 1983; Olson et al. 1986) probably account for this difference.

The opportunities for selection in the fitness episodes presented in Table IV.4 were sometimes quite different from selection indices calculated using direct multiyear mating success data (I5, Table IV.2). The I5 selection indices incorporated known survival and mating success of individuals among breeding years, but not fertility estimates. From the lifetime mating success of site B males first-captured in 1982, I5 was approximately 1.2, whereas I1+I2 = 3.04 and I1+I2' = 6.16 for site B males. At site A, I5 was also about half the level of I1+I2. The more moderate I5 values from actual multiyear recaptures may have provided more realistic values of the opportunity for selection on male survival and mating success at sites A and B. I1 and I2 based on between-year survival rates and averages of mating success among years could have inflated the selection estimates. However, at site C the selection indices did not differ greatly (I5 vs I1+I2), suggesting that the survival and mating success determinations used for each measure were more consistent.

One fitness component that I have not addressed is viability, the probability that an individual will survive through larval and juvenile life stages to reproductive age. Prereproductive mortality is tremendous in the western toad. At site A, for example, over 200 pairs can breed in a year producing over 2 million eggs (mean clutch size of site A females is approximately 11800 eggs). Samollow (1980) reported differential survival of larval and juvenile western toads at site A. Although viability is an important component of fitness, the relative importance of viability selection to the total opportunity for selection and lifetime fitness variation among individuals is not known for western toads.

The importance of different selection episodes to the total opportunity for selection appears to vary with taxa, although selection on multiple fitness episodes has been analyzed in few species. For example, survivorship seems to be of primary importance to variance in reproductive success and lifetime selection opportunity in some insects (Koenig and Albano 1987; Fincke 1982; McCauley 1983). In contrast, the opportunity for selection was much greater with regard to mating success than survivorship in lizards (Arnold and Wade 1984b, data from Trivers 1976) and anurans (this study). In western toads, survivorship may become a much more important contributor to lifetime selection opportunity with the inclusion of the effects of larval and juvenile mortality. Comparisons of selection opportunities between taxa are difficult because of the diverse methods used to ascertain fitness episodes. In various studies, inconsistent measures of lifetime fitness have been analyzed (Trail 1985), natural and sexual selection episode partitioning presents several problems (Koenig and Albano 1986), and ordering of selection episodes can affect results (Koenig and Albano 1987). In studies of anuran sexual selection opportunity, many of these difficulties are not apparent because consistent measures of mating success have been reported.

In this paper, I have given a general presentation of the opportunity for selection in the western toad without regard to a specific trait. Consistent patterns for potential trait-selection have not been uncovered for all selection episodes in this species. Occasional size-dependent nonrandom mating patterns were observed in the 15 breeding aggregations, but their occurrences were variable within sites both among years and among days of breeding within-years (Olson et al. 1986, Olson 1988a). Consistent size-dependent fertility has also not been demonstrated within breeding populations. Potential selection on a phenotypic trait such as size also would be influenced by the effects of sex ratio on variation in male reproductive success within breeding aggregations (Howard and Kluge 1985).

Given phenotypic (e.g. size) mating and fertility patterns in the western toad, discussions of evolutionary changes are conditional upon the phenotype heritability.

Studies of trait inheritance have not been conducted with western toads. Intracohort genetic (allozyme) differences have been shown between tadpole, newly metamorphosed toadlets, and toadlets one year after metamorphosis, and differential allozyme variation was also shown in breeding adults, demonstrating differential survival among life stages (Samollow 1980). However, differential mating success and fertility by allozyme genotypes has not been studied.

Future research on the opportunity for selection in the western toad might include models of the fitness effects of sporadic mating and fertility patterns by body size, or studies of fertility and mating patterns associated with allozyme variation. Additional studies of anuran lifetime survival and reproduction are needed to more effectively address the opportunity for selection within and among populations. The potential use of selection indices in the development of mating system theory may be most effectively examined within taxa with similar breeding habits, and more directly within species with variations in breeding behavior and ecology among years or populations. Western toad site and year variations in mating dynamics and opportunity for selection has provided an opportunity for both intraspecific comparisons and comparisons with other anurans.

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Figure IV.1: Female clutch size in relationship to body size at site A (open circles) and site C (solid circles).

Figure IV.1

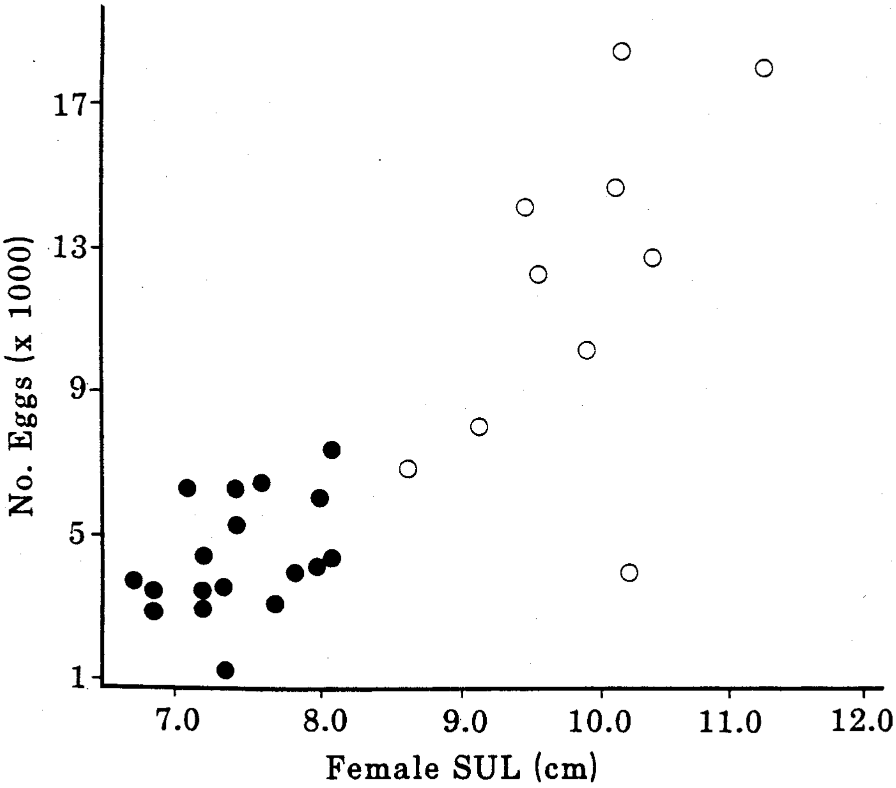

Figure IV.2: Fertilization efficiency of clutches with regard to the ratio of male to female body size within pairs.

Figure IV.2

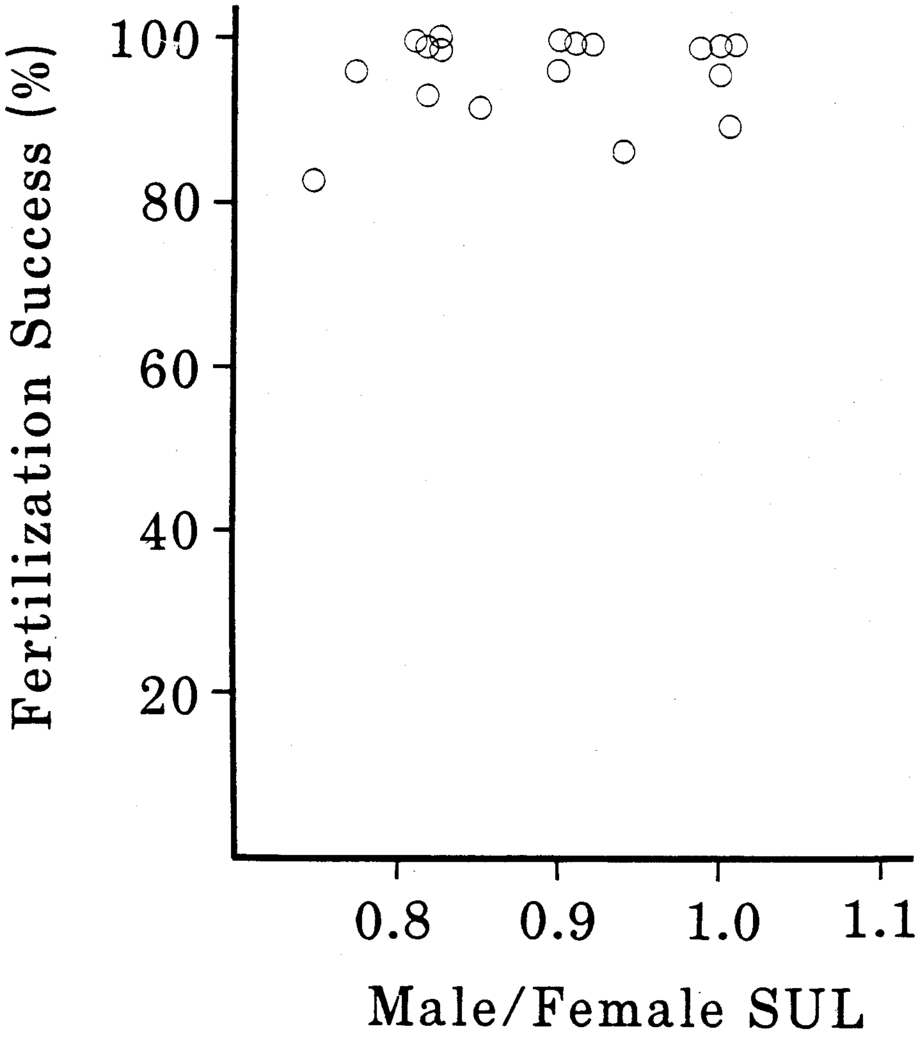
Fertilization Success (%)
100
80
60
40
20
0.8
0.9
1.0
1.1
Male/Female SUL

Figure IV.3: Male size (mean ± SEM, N) and mating success at site C in 1984.

Figure IV.3

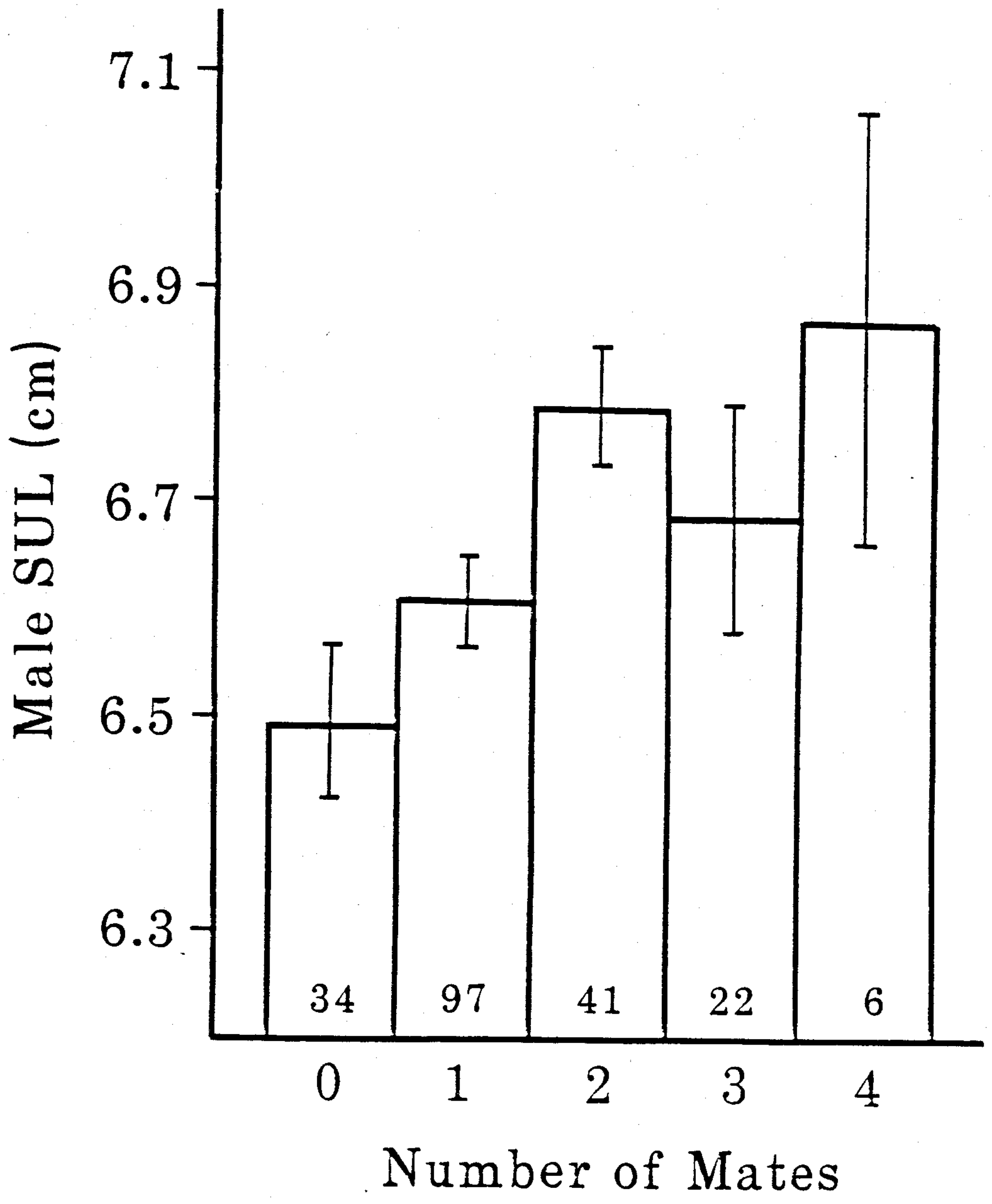

Figure IV.4: Mating success (mean ± SEM, N) of males by year of first-capture at site B and C aggregations in 1983-1986. Sample sizes are within bars and lines connecting bars indicate male size differences (Student's t-tests, $p<0.05$).

Figure IV.4

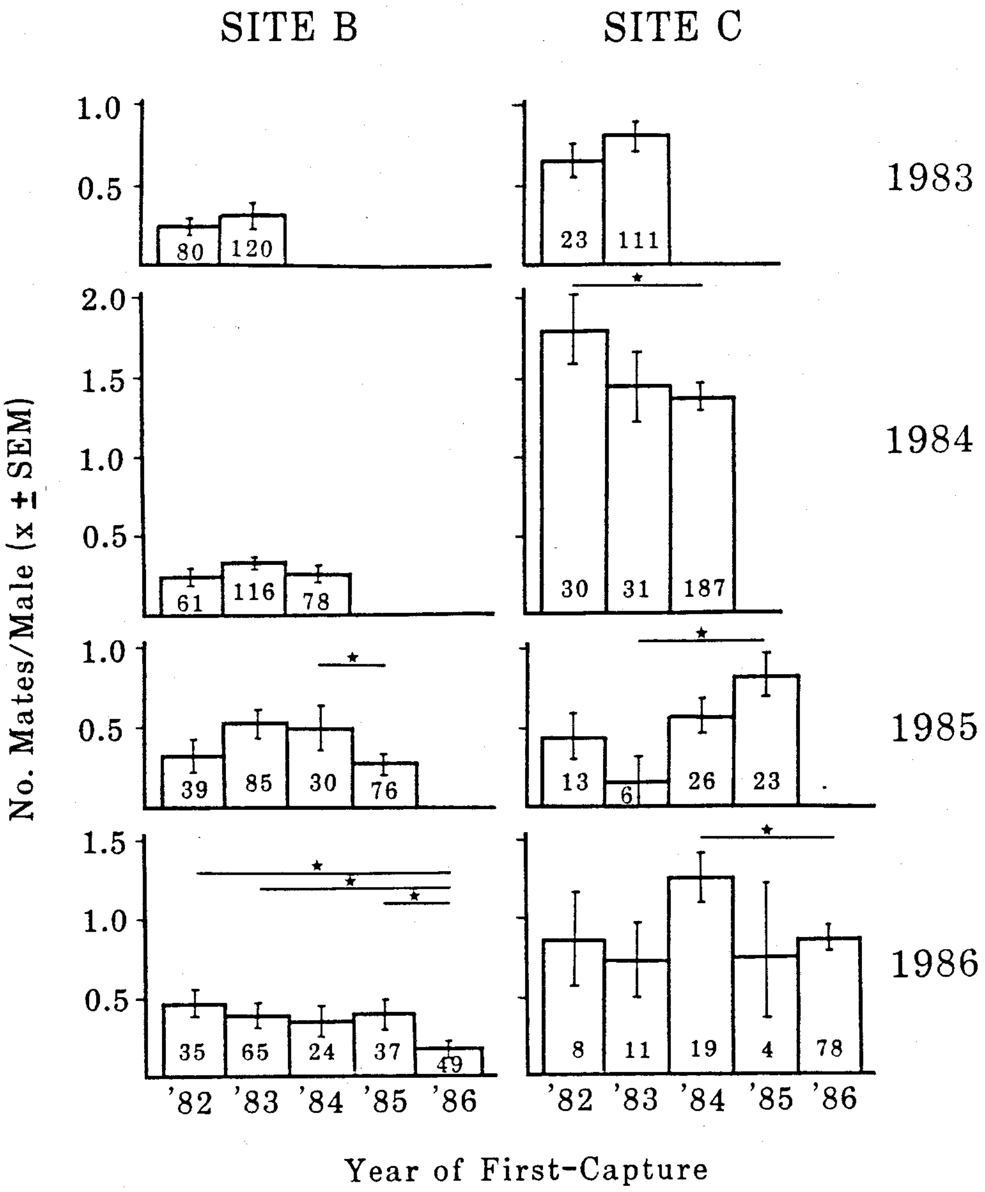
SITE B
SITE C
1983
1984
1985
1986
No. Mates/Male (x ± SEM)
1.0
0.5
2.0
1.5
1.0
0.5
1.0
0.5
1.5
1.0
0.5
80
120
23
111
61
116
78
30
31
187
39
85
30
76
13
6
26
23
35
65
24
37
49
8
11
19
4
78
★
'82 '83 '84 '85 '86
'82 '83 '84 '85 '86
Year of First-Capture

Table IV.1: Yearly male mating success and opportunity for selection (I2 = variance/mean^2 no. mates per male) at each of the western toad breeding aggregations.

Aggregation		No. Mates								
Site	Year	0	1	2	3	4	N	$\bar{x}$	Var	I2
A	1982	63	111	1	0	0	175	0.65	0.24	0.57
	1983	171	179	3	0	0	353	0.52	0.27	1.00
	1984	169	208	7	0	0	384	0.58	0.28	1.83
	1985	167	93	0	0	0	260	0.36	0.23	1.77
	1986	101	81	0	0	0	182	0.44	0.25	1.28
B	1982	124	72	1	0	0	197	0.38	0.25	1.73
	1983	241	89	5	1	0	336	0.30	0.26	2.89
	1984	207	81	2	2	0	292	0.31	0.27	2.81
	1985	174	88	7	0	0	269	0.38	0.29	2.01
	1986	135	68	5	0	0	208	0.37	0.28	2.04
C	1982	144	84	1	0	0	229	0.37	0.24	1.75
	1983	25	115	5	0	0	145	0.86	0.19	0.26
	1984	34	103	47	23	6	213	1.36	0.96	0.52
	1985	27	43	7	0	0	77	0.74	0.38	0.69
	1986	16	79	22	3	0	120	1.10	0.41	0.50

Table IV.2: Cumulative mating success (mean and variance of no. mates per toad) and selection indices (I5) determined for males attending breeding aggregations in 1-5 years and for males and females first-captured in each of the five study years at sites B and C.

Table IV.2

			No. Mates										
Sex	Site	Analysis	0	1	2	3	4	5	6	N	$\bar{x}$	Var	I_5
		No. Years At Site											
Males	A	1	642	628	11	0	0	0	0	1281	0.507	0.267	1.04
		2	8	27	17	0	0	0	0	52	1.173	0.46	0.33
Males	B	1	375	160	12	2	0	0	0	549	0.346	0.292	2.44
		2	87	69	25	2	0	0	0	183	0.683	0.558	1.20
		3	19	36	25	9	3	0	0	92	1.359	1.046	0.57
		4	11	22	19	8	3	0	0	63	1.524	1.116	0.50
		5	3	1	3	2	0	0	0	9	1.444	1.403	0.67
Males	C	1	173	310	40	18	6	0	0	577	0.811	0.605	0.920
		2	7	30	40	13	5	2	0	97	1.845	1.111	0.326
		3	1	6	5	10	6	2	0	30	2.667	1.678	0.236
		4	0	0	1	2	1	1	1	6	3.833	2.167	0.147
		5	0	0	0	0	1	0	0	1	4.00	0	--
		Year First Capture											
Males	A	1982	63	112	10	0	0	0	0	185	0.713	0.314	0.62
		1983	162	184	7	0	0	0	0	353	0.561	0.287	0.91
		1984	167	208	9	0	0	0	0	384	0.588	0.290	0.84
		1985	163	95	2	0	0	0	0	260	0.381	0.252	1.74
		1986	95	66	0	0	0	0	0	161	0.410	0.243	1.45
Males	B	1982	94	74	24	5	0	0	0	197	0.695	0.611	1.26
		1983	134	87	27	10	3	0	0	261	0.701	0.453	0.92
		1984	63	37	10	1	1	0	0	112	0.571	0.589	1.81
		1985	171	79	13	1	1	0	0	264	0.409	0.364	2.18
		1986	40	9	0	0	0	0	0	49	0.184	0.153	4.52
Males	C	1982	109	85	17	8	7	2	1	229	0.817	1.185	1.776
		1983	21	89	18	6	4	3	0	141	0.750	0.916	1.629
		1984	25	102	50	28	8	0	0	213	1.493	0.977	0.438
		1985	4	17	1	1	0	0	0	23	0.956	0.407	0.445
		1986	25	53	0	0	0	0	0	78	0.679	0.221	0.478
		Projection of 1982 Males in											
Males	B	1987	91	74	26	6	0	0	0	197	0.73	0.65	1.22
		1988	89	75	25	8	0	0	0	197	0.76	0.69	1.19
		1989	88	74	26	9	0	0	0	197	0.78	0.72	1.18
		1990	88	72	28	9	0	0	0	197	0.79	0.73	1.17
		Yr. First Capture											
Females	A	1982	0	108	5	0	0	0	0	113	1.04	0.04	0.04
		1983	0	193	5	0	0	0	0	198	1.03	0.02	0.02
		1984	0	210	0	0	0	0	0	210	1.0	--	--
		1985	0	90	0	0	0	0	0	90	1.0	--	--
		1986	0	78	0	0	0	0	0	78	1.0	--	--
Females	B	1982	0	61	13	0	0	0	0	74	1.18	0.15	0.11
		1983	0	92	9	0	0	0	0	101	1.09	0.08	0.07
		1984	0	81	4	0	0	0	0	85	1.05	0.05	0.04
		1985	0	89	3	0	0	0	0	92	1.04	0.01	0.01
		1986	0	54	0	0	0	0	0	54	1.0	--	--
Females	C	1982	0	92	7	0	0	0	0	99	1.07	0.07	0.06
		1983	0	118	8	0	0	0	0	126	1.06	0.06	0.05
		1984	0	255	29	0	0	0	0	284	1.10	0.09	0.08
		1985	0	47	4	0	0	0	0	51	1.08	0.07	0.06
		1986	0	90	0	0	0	0	0	90	1.0	--	--

Table IV.3: Opportunity for selection (I1=variance/x^2 no. breeding yrs.) on adult survival for breeding toads captured in the first two study-years at sites B and C.

Site	Year of First Capture	I1 Males	I1 Females
A	1982	0.08	0.04
	1983	0.05	0.02
B	1982	1.00	0.11
	1983	0.48	0.07
C	1982	0.48	0.06
	1983	0.36	0.05

Table IV.4: Total opportunity for selection (IT) derived from four selection episodes: survival of breeding adults (I1), mating success (I2), clutch size (I3), and fertilization efficiency (I4).

Sex	Opportunity for selection	Site		
		A	B	C
<u>Males</u>	I_1	0.065	0.74	0.42
	I_2	1.29	2.30	0.74
	I_3	0.14	0.135	0.13
	I_4	0.003	0.003	0.003
	$I_T = I_1 + I_2 + I_3 + I_4$	1.498	3.178	1.293
	I'_2	1.39	5.42	1.165
	$I'_T = I_1 + I'_2 + I_3 + I_4$	1.598	6.298	1.718
<u>Females</u>	I_1	0.03	0.09	0.055
	I_2	0	0	0
	I_3	0.14	0.135	0.13
	I_4	0.003	0.003	0.003
	$I_T = I_1 + I_2 + I_3 + I_4$	0.173	0.228	0.188

LITERATURE CITED

Arak, A. 1983. Male-male competition and mate choice in anuran amphibians. Pages 181-210/in/P. Bateson, ed. Mate choice. Cambridge Univ. Press, Cambridge.

Arnold, S.J. and M.J. Wade. 1984a. On the measurement of natural and sexual selection: theory. Evolution 38:709-719.

______ 1984b. On the measurement of natural and sexual selection: applications. Evolution 38: 720-734.

Clutton Brock, T.H., F.E. Guiness, and S.D. Albon. 1982. Red deer: behaviour and ecology of two sexes. Univ. Chicago Press, Chicago.

Crow, J.F. 1958. Some possibilities for measuring selection intensities in mann. Human Biol. 30:1-13.

Davies, N.B., and T.R. Halliday. 1977. Optimal mate selection in the toad Bufo bufo. Nature 269:56-58.

______ 1979. Competitive mate searching in male common toads, Bufo bufo. Anim. Behav. 27:1253-1267.

Emlen, S.T., and L.W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223.

Fincke, O.M. 1982. Lifetime mating success in a natural population of the damselfly, Enallagma hageni (Walsh) (Odonata: Coenagrionidae). Behav. Ecol. Sociobiol. 10:293-302.

Hausfater, G., C.D. Saunders, and M. Chapman. 1981. Some applications of computer models to the study of primate mating and social systems. Pages 345-360 *in* R.D. Alexander and D.W. Tinkle, eds. Natural selection and social behavior: recent research and new theory. Chiron Press, New York.

Howard, R.D. 1978. The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. Evolution 32:850-871.

______ 1981. Male age-size distribution and male mating success in bullfrogs. Pages 61-77 *in* R.D. Alexander and D.W. Tinkle, eds. Natural selection and social behavior: recent research and new theory. Chiron Press, New York.

______ 1983. Sexual selection and variation in reproductive success in a long-lived organism. Amer. Nat. 122:301-325.

Howard, R.D., and A.G. Kluge. 1985. Proximate mechanisms of sexual selection in Woodfrogs. Evolution 39:260-277.

Kluge, A.G. 1981. The life history, social organization, and parental behavior of *Hyla rosenbergi* Boulenger, a nest-building gladiator frog. Miscel. Public. Mus. Zool. Univ. Mich. 160:1-170.

Koenig, W.D., and S.S. Albano. 1986. On the measurement of sexual selection. Amer. Nat. 127:403-409.

______. 1987. Lifetime reproductive success, selection, and the opportunity for selection in the white-tailed skimmer Plathemis lydia (Odonata: Libellulidae). Evolution 41: 22-36..

Licht, L.E. 1976. Sexual selection in toads (Bufo americanus). Can. J. Zool. 54:1277-1284.

McCauley, D.E. 1983. An estimate of the relative opportunities for natural and sexual selection in a population of milkweed beetles. Evolution 37:701-707.

McGregor, P.K., J.R. Krebs, and C.M. Perrins. 1981. Song repertoires and lifetime reproductive success in the great tit (Parus major). Amer. Nat. 118:149-159.

Olson, D.H. 1988a. Breeding ecology and variable mating patterns in the western toad (Bufo boreas). Submitted.

______ 1988b. The role of mate choice and mate competition in western toad (Bufo boreas) nonrandom mating. Submitted.

______ 1988c. Multiyear breeding schedules and adult survival in the western toad (Bufo boreas). Submitted.

Olson, D.H., A.R. Blaustein and R.K. O'Hara. 1986. Mating pattern variability among western toad (Bufo boreas) populations. Oecologia 70:351-356.

Payne, R.B. 1979. Sexual selection and intersexual differences in variance of breeding success. Amer. Nat. 114:447-452.

______ 1984. Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. Ornithological Monograph 33, Amer. Ornith. Union.

Payne, R.B. and K. Payne. 1977. Social organization and mating success in local song populations of village indigobirds. Z. Tierpsychol. 45:113-173.

Ryan, M.J. 1980. Female mate choice in a Neotropical frog. Science 209:523-525.

______ 1985. The Tungara Frog: A study in sexual selection and communication. Univ. Chicago Press, Chicago.

Samollow, P.B. 1980. Selective mortality and reproduction in a natural population of <u>Bufo</u> <u>boreas</u>. Evolution 34:18-39.

Sullivan, B.K. 1982. Sexual selection in Woodhouse's toad (<u>Bufo</u> <u>woodhousei</u>). I. Chorus organization. Anim. Behav. 30:680-686.

______ 1983. Sexual selection in Woodhouse's toad (<u>Bufo</u> <u>woodhousei</u>). II. Female choice. Anim. Behav. 31:1011-1017.

______ 1986. Intra-populational variation in the intensity of sexual selection in breeding aggregations of Woodhouse's toad (*Bufo woodhousei*). J. Herpet. 20:88-90.

______ 1987. Sexual selection in Woodhouse's toad (*Bufo woodhousei*). III. Seasonal variation in male mating success. Anim. Behav. 35:912-919.

Trail, P.W. 1985. The intensity of selection: intersexual and interspecific comparisons require consistent measures. Amer. Nat. 126:434-439.

Trivers, R.L. 1976. Sexual selection and resource-accruing ability in *Anolis garmani*. Evolution 30:253-269.

Wade, M.J. 1979. Sexual selection and variance in reproductive success. Amer. Nat. 114:742-764.

Wade, M., and S.J. Arnold. 1980. The intensity of sexual selection in relation to male sexual behaviour, female choice, and sperm precedence. Anim. Behav. 28:446-461.

Wells, K.D. 1977. The social behavior of anuran amphibians. Anim. Behav. 25:666-693.

Woodward, B.D. 1982. Sexual selection and nonrandom mating patterns in desert anurans (*Bufo woodhousei*, *Scaphiopus couchi*, *S. multiplicatus* and *S. bombifrons*). Copeia 1982:351-355.

CHAPTER V

PREDATION ON BREEDING WESTERN TOADS (Bufo boreas)

ABSTRACT

Predation by ravens (Corvus corax) on western toads (Bufo boreas) was observed at three of fifteen toad explosive breeding aggregations. At one aggregation, over 20% of the toad annual breeding population was killed and found eviscerated near the communal breeding site. Predation was observed when toads were breeding in shallow water, 5-25 cm deep, but not when toads remained in deeper water. During censusing of toads, paired males released their mates before oviposition more often at aggregations with predation. There were some body size differences between toads in mating pairs that remained together and pairs in which males released their mates. At one aggregation, releasing males were larger than non-releasing males, and at a second aggregation, males that released their mates were clasping smaller females than females of pairs remaining together. In breeding western toads, predation risk may be reduced by remaining in deeper water,

the unclasping behavior of paired males, and the spatial and temporal synchronization of breeding activities.

INTRODUCTION

Sociality is usually explained by fitness benefits gained by individuals living in social groups (Alexander, 1974). A lower risk of predation is one prime benefit of group-living (Alexander, 1974; Brown and Orians, 1970; Williams, 1964). Antipredator defenses (Endler, 1986) displayed by social animals include early predator detection, predator deterrence by group defense, predator confusion, avoiding predator detection, and reducing the chance of being a prey for a predator by either dilution of the predator's effects or selfish herd effects (e.g. Pulliam and Caraco, 1984; Bertram, 1978; Hamilton, 1971).

Communal breeding may reduce the risk of predation (e.g. Hoogland and Sherman, 1976; Kruuk, 1964; Ryan et al., 1981). In anuran amphibians, communal breeding is largely the result of patchy breeding sites, but it may also function to reduce predation risk. There have been many reports of predation on anurans at breeding sites (e.g. Dickerson, 1969; Groves, 1980; Howard, 1978; Kagarise Sherman, 1980; Kluge, 1981; Mulder et al., 1978; Perrill and Magier, 1988; Ryan, 1980; Ryan et al., 1981; Schaaf and Garton, 1970; Tuttle et al., 1982). However, per capita predation rates for anuran breeding aggregations are largely unavailable because accurate records of mortality from predation for an entire breeding season are not known. This paper reports predation by ravens (Corvus corax) at the communal breeding sites of adult western toads (Bufo boreas) and seasonal predation rates for western toad breeding aggregations.

MATERIALS AND METHODS

I censused western toad breeding aggregations throughout their breeding seasons during 5 years at 3 lakes in the Oregon Cascade Mountains: Lost Lake (site A, Linn Co., elevation 1220 m), Little Three Creeks Lake (site B, Deschutes Co., elevation 1950 m), Todd Lake (site C, Deschutes Co., elevation 1860 m). Breeding toads were captured and measured, uniquely marked by toe-clipping, their pairing status and general breeding behavior was recorded, and they were returned to their place of capture. At all 15 aggregations (5 yrs. x 3 sites), I measured snout-urostyle length (SUL ± 1mm) by pressing the toad against a ruler. I also collected toad mass (± 1g, spring scale) and forearm lengths (radio-ulna lengths, ± 1mm) at some aggregations (Olson 1988a). I did not separate mating pairs for marking and measuring at the three 1982 aggregations, but I separated pairs after capture at all aggregations in 1983-1986. At most aggregations, I re-paired mates before putting them back into the breeding site; males usually readily clasped their previous mate. I noted if a male immediately released his mate after being returned to the lake (= pair separation). I did not record pair separations at site A in 1985 and 1986 because pairs were not returned to the breeding site. At site C in 1985, pair separations were not recorded for toads captured during the last 2 of 5 census days.

I used the number of toads captured at a breeding aggregation as a direct estimate of breeding population size in a year. It is likely that nearly all of the actively breeding toads were censused because I monitored breeding thoroughly at most aggregations, breeding occurred explosively (the breeding season usually lasted one week) in very localized areas of the lakes and both sexes were very conspicuous at the sites and easily captured. However, I monitored breeding less thoroughly at 4 aggregations: site A in 1982, 1985, 1986, and site C in 1985. At these aggregations, I either censused breeding on a subset of the days toads were present at the lakes (site A, 1982; site C, 1985) or sampled less rigorously every day (site A, 1985 and 1986). Because toads often arrived and departed from the breeding sites sporadically throughout a breeding season, my estimates of breeding population size in a season may be low at site A in 1982 and site C in 1985, whereas the population estimates of the daily-sampled sites (site A, 1985 and 1986) are probably representative of the actual numbers of actively breeding toads.

I recorded predation when partially-eaten toad carcasses were found at the breeding sites. I determined predator identity directly from visual sitings of toads being captured and consumed, and indirectly from the position of carcasses along the lake shores and the inspection of the shore for tracks left by predators in the mud and snow surrounding the carcasses. I estimated predation rate for an entire breeding season at a toad breeding aggregation by the ratio of the number of toads known to be killed (partially-eaten toad carcasses were easily counted) divided by the number of live toads captured. This rate would be an underestimate if not all carcasses of toads killed by predators were found, if predators ate some toads in entirety, or if a toad considered alive at the breeding site was actually killed by ravens. Predation rate overestimates are possible if the breeding population size was higher than determined, or if the primary cause of the observed toad mortality was not predation.

At aggregations with higher rates of pair separations, I compared toad sizes between pairs that separated and pairs that remained together (Student's t-test; Snedecor and Cochran, 1980). These comparisons included differences in male size (SUL, mass and forearm length if collected), female size (SUL), and the sexual size dimorphism within the pairs (female minus male SUL).

RESULTS

Predation.--Ravens were observed eating western toads and toad carcasses were found along the shores adjacent to the breeding sites at 3 of the 15 breeding aggregations (Table 1). First, at site A in 1984, 10 toad carcasses were found on the last 3 days of breeding (breeding season length = 23 days) scattered around the toad oviposition site on stumps and logs emerging from the water. On these 3 days, toads were ovipositing in shallow water (5-25 cm deep), whereas they had remained in deeper water (> 1m) during the first 20 days of breeding activity. I saw ravens eating toads around the shallow oviposition site on 2 of these 3 days as I approached the site in the morning for the first toad census of the day. At this aggregation, I captured 157 toads on the last three breeding days and 602 toads throughout the whole season. Thus, predation rates were 6.4% for the 3 days and 1.6% for the season (Table 1).

I also observed predation at site C in 1985 and 1986. I found toad carcasses on all days of my attendance at the site each year (3 days in 1985 and 6 days in 1986) and saw a raven eating toads on 2 days in both 1985 and 1986 as I approached the lake in the morning for the first toad census of the day. A newly-killed toad was also reported on the last day of censused breeding at this site in 1985 (M. McDowell, personal communication). On one day during breeding (20 June 1985), I left the breeding site in midday, remained hidden in a forested area adjacent to the site, and watched for the return of a predator. After 2 hours, a raven visited the breeding area, captured a toad from the water's edge and started eating it. Site C toads usually remained along the lake shore in shallow water during breeding and always oviposited in fairly shallow water (Table 1).

Observed toad mortality due to predation was much greater at site C. In 1986, 59 partially-eaten carcasses and 250 living toads were found (Table 1). On the first two days of breeding at this aggregation, I censused 28 living toads and 42 carcasses, a predation rate of 60% for these days. The predation rate decreased in the following days, when only 17 additional carcasses were found and the bulk of the breeding population arrived at the site.
The seasonal predation rate at this aggregation may be slightly overestimated because toads found dead on the first days of breeding were not included in the estimate of breeding population size (because they were never captured alive during the season). Adding the 42 dead toads found on the first days of breeding into the estimate of population size yields a predation rate of 20.2% (59 of 292 toads).

In 1985, 5.3% of the toads at site C were found dead and partially-consumed. This seasonal estimate of predation may be high because breeding was monitored less carefully at this aggregation and although the number of partially-eaten carcasses along the lake shore could be accurately assessed, the breeding population size is probably underestimated. However, the 1985 population was accurately censused the first 3 days of breeding. On these days, 6 of 90 toads were found dead (6.7% mortality).

There are probably few other errors in the estimates of predation rates on breeding western toads. Ravens were never seen carrying toads away from the breeding sites and eviscerated toads were found only along the lake shores. Dead toads previously captured alive may have been considered twice (dead and alive) in the estimate of population size, causing the predation rate to be underestimated for a breeding aggregation. However, the chance for this type of error is minimized at site C in 1986 where dead toads were found primarily on the first few days of breeding activity before most of the toads had arrived at the site, and this error would have little effect on the seasonal predation rate at site A in 1984 because of the large number of toads captured during breeding and the relatively few toads killed.

The condition of toad carcasses at the 3 breeding aggregations were similar. Toads were eviscerated and remaining body parts included portions of the dorsal skin, head, some limbs, and eggs from gravid females. The skin from many limbs had been peeled off and the limb removed. Reliable sexing of dead toads and identification of toe-clips were not possible.

Ravens were the most likely cause of death for western toads at these 3 aggregations for several reasons. First, ravens disturbed from eating toads as I entered a breeding site often left toads they had just begun to eviscerate. The condition of the skins and organs of these toads suggested they were fresh kills, rather than scavenged carcasses left by another animal. The observation of a raven taking and eviscerating a toad from the water's edge at site C in 1985 supports the contention that ravens were predators rather than scavengers on toads. In addition, dead toads at site A were primarily found on logs and stumps which were used as perches by ravens (logs and stumps were not present at site C). I never saw carnivorous mammals or their tracks along the lake shores in the mud and snow. It is unlikely that potential mammalian predators of toads could have walked along the lake shore without leaving marks in the snow which covered the areas surrounding toad activity. Lastly, there is no evidence that freezing or disease could have been the primary cause of death for the toads. Cold weather conditions were often much more severe at aggregations without observed toad mortality, and toad carcasses were visually disease-free (e.g. neither parasites nor symptoms of the somewhat-common red leg virus were apparent).

Raven sitings were probably rare because they were extremely wary of human activities in the area. Ravens were never seen at the 3 sites when I was censusing toads, and left the sites as I approached them to within approximately 50 m (site A) to 200 m (site C). My presence at the lakes may have greatly affected toad mortality.

I have found dead western toads on two other occasions. At site C in 1982, two dried eviscerated toads were found. At another Oregon Cascade Mountain lake (Crane Prairie Reservoir, Deschutes Co.) in 1983, I counted over 40 freshly-killed, eviscerated adult western toads on stumps and logs in an inlet. The use of these potential perches suggests an avian predator as the cause of death. This inlet may have been an oviposition site, although only 9 live toads were found and there were no eggs or larvae.

Mating behavior.--At aggregations with high predation rates, males were often difficult to re-attach to their mates after I had separated them for marking and measuring. There was an association between seasonal predation rate and pair separation rate ($r=0.80$, $df=11$, $p<0.01$), although most aggregations had no predation (Table 1). At site A in 1984, some males may have released their mate because they had been clasping for an extended period of time. Communal oviposition of all pairs occurred 21 days after the onset of breeding activity at this aggregation and some males had been clasping gravid females for several days. At site C, pair separations were probably not a result of extended time of clasping because pairs usually oviposited within a day.

At the 3 aggregations with raven predation, there were some differences between the pairs that remained together and pairs in which males released their mates. At site C in 1985, releasing males were larger than males remaining with their mates with regard to SUL and mass, but not with respect to forearm length (comparisons of male sizes: Site A in 1984- SUL: $t=0.25$, $df=219$, $p>0.05$; Site C in 1985- SUL: $t=3.67$, $df=31$, $p<0.01$, mass: 3.81, $df=31$, $p<0.01$, forearm length: $t=1.65$, $df=31$, $p>0.05$; Site C in 1986- SUL: $t=0.60$, $df=131$, $p>0.05$; mass: $t=0.41$, $df=131$, $p>0.05$, forearm length: $t=0.08$, $df=131$, $p>0.05$). Males that released their mates were clasping significantly smaller females at site A in 1984 (comparisons of female SUL between separating and non-separating pairs: site A in 1984: $t=2.03$, $df=219$, $p<0.05$; site C in 1985: $t=0.22$, $df=31$, $p>0.05$; site C in 1986: $t=1.11$, $df=131$, $p>0.05$). The degree of sexual size (SUL) dimorphism between males and females in pairs did not differ between pairs that separated and those remaining together at any of the three aggregations (site A in 1984: $t=1.92$, $df=218$, $p>0.05$; site C in 1985: $t=1.51$, $df=31$, $p>0.05$; site C in 1986: $t=0.67$, $df=131$, $p>0.05$).

DISCUSSION

Raven predation was seen at 3 of 15 western toad breeding aggregations. Apparent raven predation killed up to 20% of a breeding population in a season. This rate exceeds most estimates of predation risk at other anuran communal breeding sites. Kagarise Sherman (1980) reported that avian predators killed about 2% of the breeding populations of Yosemite toads, Bufo canorus, and black toads, B. exsul. On a nightly basis in the Tungara frog (Physalaemus pustulosus), from 1.5-19.1% of a breeding chorus was captured by predators (Ryan et al., 1981). Because Tungara frogs have prolonged breeding seasons, the predation rate over an entire season is difficult to ascertain.

Mass predation on bufonids, such as the 59 western toad carcasses seen at site C in 1986 and the 40+ carcasses at Crane Prairie Reservoir in 1983, may be common. Schaaf and Garton (1970) found 50 and Groves (1980) found 46 partially-eaten American toads (Bufo americanus), and Kagarise Sherman (1980) recorded 83 black toad carcasses in one year. In addition, a great number of Tungara frogs were observed taken by predators at their natural breeding aggregations: 39 frogs were taken by opossums (Tuttle et al., 1981), 95 by bats and 15 by South American bullfrogs (Ryan et al., 1981). The seasonal predation rates on other anuran breeding populations may be high, as it is for the western toad, although population size estimates are necessary to assess the predation risk to individuals.

Adult anurans may have several potential mechanisms to reduce predation risk. In many anurans, especially bufonids, toxic skin secretions are effective repellents to some predators (e.g. Brodie and Formanowicz, 1987; Formanowicz and Brodie, 1982; Daly and Myers, 1967; Flier et al., 1980; Musgrave, 1930; Wright, 1966). However, many predators are not bothered by this defense mechanism: snakes (e.g. Fitch 1960) and bullfrogs (e.g. Clarke, 1977) have been found with whole toads in their stomachs, and raccoons (Schaaf and Garton, 1970; Wright, 1966), skunks (Hansen and Vial, 1956; see also Groves, 1980) and several birds in the family Corvidae have been reported to eviscerate toads (this study; Kagarise Sherman, 1980; Mulder et al., 1978).

Breeding anurans also can have antipredator behaviors. For example, males may reduce their predation risk by modifying their advertisement calls and chorus structure (Nunes, 1988; Ryan, 1980; Tuttle and Ryan 1981, 1982; Tuttle et al. 1982), and by alternative male mating strategies such as non-calling satellite males (e.g. Perrill and Magier, 1988). However, western toads do not give advertisement calls.

A western toad behavior to reduce predation risk may be to mate in deeper water. All three instances of predation on breeding western toads occurred when toads were in relatively shallow water (5-25 cm). Western toad breeding activity and oviposition in deeper water (1-2 m) was found only at site A. This was the only lake of the three study sites with vegetation in deeper water around which pairs could wind their egg strings. It is interesting that during the one study year that site A toads bred in shallow water, predation was observed. Mating in deeper water may have allowed toads to avoid avian predation at the lake shore.

Unclasping behavior by paired males also may reduce predation risk. However, this behavior probably also reduces the male's mating success during the explosive breeding season. For example, of the 27 males that released their mate after handling at site C in 1986, only 4 were observed later clasping another female. Because many males return to breed year after year (in the 5 years of this study at site C, up to 75% of breeding males were recaptures from previous years), loss of mating success in one year may not result in lifetime failure to reproduce. Male unclasping behavior in times of predation may be a trade-off with regard to reproductive success and survival.

At two aggregations where raven predation was observed, there were interesting toad body size differences between separating pairs and pairs remaining clasped after handling. The release of a female by a clasping male may not always be a random event. For example, at one aggregation, females released by males were significantly smaller than females to which males remained clasped. In anurans, female clutch size usually increases with female size (e.g. Salthe and Duellman, 1973). The overall reproductive success of a paired male, therefore, would also increase with female size. Hence, from a male's point of view, the cost of releasing a small female may be less than losing a larger one. The differential release of females based on their size during times of high predation may be interpreted as male mate choice. Evidence for male mate choice is rare (e.g. papers in Bateson, 1983).

In addition, the size differences between toads separating from their initial mates and those remaining together may affect the occurrence of size-dependent mating patterns at the breeding aggregations. Mating was random with regard to toad size at the three aggregations with predation, whereas size-dependent mating was found at many of the other aggregations monitored (Olson, et al. 1986; Olson 1988a). Predation could easily disrupt the behavioral dynamics of pairing leading to nonrandom mating.

Lastly, communal breeding, communal oviposition, and explosive breeding seasons may also function to reduce predation risk of adult anurans (e.g. Kagarise Sherman, 1980). Western toad communal breeding may reduce predation risk by dilution of the predator's effects (Hamilton, 1971; Williams, 1964), especially because the predation rate did not increase disproportionately with the size of the breeding aggregation (Table 1). Communal and synchronized oviposition greatly increases toad density, enhancing these geometric benefits of grouping. In the western toad and other anurans with periodically high predation rates during breeding, the spatial and temporal synchronization of breeding may be an effective antipredator defense.

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Table V.1: Seasonal predation rates, pair separation rates, oviposition site depths, and sample sizes of the 15 western toad breeding aggregations examined.

Table V.1

	Site A					Site B					Site C				
	1982	1983	1984	1985	1986	1982	1983	1984	1985	1986	1982	1983	1984	1985	1986
Breeding Population Size	284	554	602	352	264	260	438	384	348	281	322	271	497	131	250
Raven Predation Observed	no	no	yes	no	no	no	no	no	no	no	no	no	no	yes	yes
No. Eviscerated Toads	0	0	10	0	0	0	0	0	0	0	2	0	0	7	59
Predation Rate	0	0	1.7	0	0	0	0	0	0	0	0.6	0	0	5.3	23.6
Pair Separation Rate	5.3	0.5	10.4	-	-	3.9	2.1	0	3.1	0	1.2	3.8	1.8	18.2	20.3
No. Pairs	113	185	221	-	-	76	96	88	98	80	85	130	280	33	133
Oviposition Site Depth	1m	1-2m	5-25cm	1-2m	1-2m	5-25cm	5-25cm	5-25cm	5-25cm	5-25cm	5-25cm	5-25cm	5-25cm	5-25cm	5-25cm

LITERATURE CITED

Alexander, R.D. 1974. The evolution of social behavior. Ann. Rev. Ecol. Syst. 5:325-383.

Bateson, P. 1983. Mate coice. Cambridge University Press, Cambridge.

Bertram, B.C.R. 1978. Living in groups: predators and prey, p. 64-96. In: Behavioral ecology: an evolutionary approach. J.R. Krebs and N.B. Davies (eds.). Sinauer Assoc., Inc., Sunderland, Massachusetts.

Brodie, E.D., Jr., and D. R. Formanowicz, Jr. 1987. Antipredator mechanisms of larval anurans: protection of palatable individuals. Herpetologica 43:369-373.

Brown, J.L., and G.H. Orians. 1970. Spacing patterns in mobile animals. Ann. Rev. Ecol. Syst. 1:239-262.

Clarke, R.D. 1977. Postmetamorphic survivorship of Fowler's toad, Bufo woodhousei fowleri. Copeia 1977:594-597.

Daly, J.W. and C.W. Myers. 1967. Toxicity of Panamanian poison frogs (Dendrobates): some biological and chemical aspects. Science 156:970-973.

Dickerson, M.C. 1969. The frog book, North American toads and frogs. Dover Publications, Inc., New York.

Endler, J.A. 1986. Defense against predators, p. 109-134. In: Predator-prey relationships. M.E. Feder and G.V. Lauder (eds.). The University of Chicago Press, Chicago, Illinois.

Fitch, H.S. 1965. An ecological study of the garter snake, Thamnophis sirtalis. University of Kansas Publications of the Museum of Natural History 15:493-564.

Flier, J., M.W. Edwards, J.W. Daly, and C.W. Myers. 1980. Widespread occurrence in frogs and toads of skin compounds interacting with the ouabain site of Na+, K+-ATPase. Science 208:503-505.

Formanowicz, D.R., Jr., and E.D. Brodie, Jr. 1982. Relative palatabilities of members of a larval amphibian community. Copeia 1982:91-97.

Groves, J.D. 1980. Mass predation on a population of the American toad, Bufo americanus. Amer. Midl. Nat. 103:202-203.

Hamilton, W.D. 1971. Geometry for the selfish herd. J. Theor. Biol. 31:295-311.

Hansen, J.A., and J.L. Vial. 1956. Defensive behavior and effects of toxins in Bufo alvarius. Herpetologica 12:141-149.

Hoogland, J.L. and P.W. Sherman. 1976. Advantages and disadvantages of bank swallow (Riparia riparia) coloniality. Ecol. Monog. 46:33-58.

Howard, R.D. 1978. The evolution of mating strategies in bullfrogs, Rana catesbeiana. Evolution 32:850-871.

Kagarise Sherman, C. 1980. A comparison of the natural history and mating system of two anurans: Yosemite toads (Bufo canorus) and black toads (Bufo exsul). Unpubl. Ph.D. thesis, University of Michigan, Ann Arbor.

Kluge, A.G. 1981. The life history, social organization, and parental behavior of Hyla rosenbergi Boulenger, a nest-building gladiator frog. Miscellaneous Publications of the Museum of Zoology, University of Michigan, No. 160:1-170.

Kruuk, H. 1964. Predators and anti-predator behaviour of the black-headed gull (Larus ridibundus L.). Behaviour (Suppl.) 11:1-129.

Mulder, B.S., B.B. Schultz, and P.W. Sherman. 1978. Predation on vertebrates by Clark's nutcrackers. Condor 80:449-451.

Musgrave, M.E. 1930. Bufo alvarius, a poisonous toad. Copeia 1930:96-98.

Nunes, V. da Silva. 1988. Vocalizations of treefrogs (Smilisca sila) in response to bat predation. Herpetologica 44:8-10.

Olson, D.H. 1988a. Breeding ecology and variable mating patterns in the western toad (Bufo boreas). Submitted.

Olson, D.H., A.R. Blaustein, and R.K. O'Hara. 1986. Mating pattern variability among western toad (Bufo boreas) populations. Oecologia 70:351-356.

Perrill, S.A., and M. Magier. 1988. Male mating behavior in Acris crepitans. Copeia 1988:245-248.

Pulliam, H.R. and T. Caraco. 1984. Living in groups: Is there an optimal group size?, p. 122-147. In: Behavioural Ecology: An evolutionary approach. Second edition. J.R. Krebs and N.B. Davies (eds.). Sinauer Assoc. Inc., Sunderland, Massachusetts.

Ryan, M.J. 1980. The reproductive behavior of the bullfrog (Rana catesbeiana). Copeia 1980:108-114.

Ryan, M.J., M.D. Tuttle, and L.K. Taft. 1981. The costs and benefits of frog chorusing behavior. Behav. Ecol. Sociobiol. 8:273-278.

Salthe, S.N., and W.E. Duellman. 1973. Quantitative constraints associated with reproductive mode in anurans, p. 229-249. In: Evolutionary biology of the anurans. J.L. Vial (ed.). University of Missouri Press, Columbia, Missouri.

Schaaf, R.T., and J.S. Garton. 1970. Raccoon predation on the American toad, Bufo americanus. Herpetologica 26:334-335.

Snedecor, G.W., and W.G. Cochran. 1980. Statistical methods. Seventh edition. The Iowa State University Press, Ames, Iowa.

Tuttle, M.D., and M.J. Ryan. 1981. Bat predation and the evolution of frog vocalizations in the Neotropics. Science 214:677-678.

_______. 1982. The role of synchronized calling, ambient light and ambient noise, in anti-bat predator behavior of a treefrog. Behav. Ecol. Sociobiol. 11:125-131.

Tuttle, M.D., L.K. Taft, and M.J. Ryan. 1981. Acoustical location of calling frogs by Philander opossums. Biotropica 13:233-234.

_______. 1982. Evasive behaviour of a frog in response to bat predation. Anim. Behav. 30:393-397..

Williams, G.C. 1964. Measurement of consociation among fishes and comments on the evolution of schooling. Publications of the Museum, Michigan State University, Biological Series 2:351-383.

Wright, J.W. 1966. Predation on the Colorado River toad, Bufo alvarius. Herpetologica 22:127-128.

CHAPTER VI

BREEDING SITE DISPLACEMENT OF *Hyla regilla* BY *Rana cascadae*

ABSTRACT

Interspecific encounters were observed between male Cascade frogs, (*Rana cascadae*) and Pacific treefrogs (*Hyla regilla*) at a breeding pond in two years. Interspecific encounters usually were initiated by *R. cascadae*, resulted in the displacement of *H. regilla*, and were seen most often in the central area of *R. cascadae* breeding activity, an area of the pond which had the warmest water temperature.
The dominance of Cascade frogs during encounters was probably a result of their much larger body size. Interspecific interactions may have resulted in the complementary spatial distributions of the two species during breeding.

INTRODUCTION

Interspecific aggression, territoriality, and competition is widely documented (e.g. reviews- Schoenner, 1983; Connell, 1983; birds- Orians and Willson, 1964; Moore, 1978; Walters, 1979; fish- Ebersole, 1977; lizards- Stamps, 1977). However, the extent of interspecific aggression and territoriality among anuran amphibians is largely unknown. Geographic distribution patterns of some ranids have been attributed to both competition (e.g. between *Rana pretiosa* and *R. pipiens*, Dumas, 1964) and predation (by *R. catesbeiana* on other anurans, Dumas, 1966; Nussbaum et al., 1983). Complementary spatial distributions of closely related species in breeding ponds are often viewed in the context of premating isolation and are sometimes associated with male anuran calling position (e.g. Etges, 1987; Oldham and Gerhardt, 1975), ecological components of the breeding habitat (e.g. vegetation structure, Etges, 1987), and the location of suitable oviposition sites (e.g. Howard, 1978; Ryan, 1980). However, the proximate mechanisms mediating anuran spatial distributions, such as species-specific breeding site preferences or competition for breeding sites, are not well understood.

Intraspecific competition has been often observed among male anurans contending for breeding sites (e.g. Emlen, 1976; Fellers, 1979; Howard, 1978; Ryan, 1980;

Wells, 1978). In these studies, dominant males in territory disputes maintain breeding locations whereas subordinate males are displaced. Interspecific anuran breeding site differences may be a result of similar behavioral interactions. This paper reports interspecifc encounters between the Cascades frog (Rana cascadae) and the Pacific treefrog (Hyla regilla) resulting in displacements of the treefrogs, and their complementary spatial distributions in a breeding pond.

METHODS

R. cascadae and H. regilla breeding activity was monitored through the end of the R. cascadae breeding season in 1985 and 1986 (30 April - 10 May 1985, 29 March - 7 April 1986) at a pond (Linn Co., elevation 1190 m, approximately 100 x 90 m) in the Oregon Cascade Mountains. The onset of breeding of both anurans occurred when the ice and snow was melted from about 5 m of the pond (east edge). H. regilla breeding choruses continued at the site for several weeks. The main area of breeding activity was mapped into quadrats (5 m^2), with flags at quadrat-corners. Up to 16 quadrats were placed along the length of the east shore (0-5 m from shore) and as the pond melted, up to two additional quadrat rows were added to the mapped area.

All R. cascadae and some H. regilla were captured at the site, marked by toe-clipping, and measured for body size. Body lengths (snout-urostyle lengths) were measured to the nearest mm and mass were measured to the nearest g (pesola scale). Mass of females were sometimes not collected because females often extruded eggs during handling. Capture and handling of frogs disturbed their breeding behavior for up to 30 min, after which normal breeding activity resumed.

During observatons of breeding behavior, the behavioral sequences and locations within-quadrats of interspecific encounters were recorded. The number of individuals (primarily males) of each species on the water surface within each quadrat was counted during daily periodic censuses. During censuses, *H. regilla* were sometimes heard to call from flooded areas near the pond-shore in dense vegetation. These *H. regilla* were not included in a census but from the strength of the chorus present in the open-water of the pond, most of the actively calling *H. regilla* appeared accessible to counting. The number of *H. regilla* counted during a census, therefore, is lower than the actual number present at the pond. *R. cascadae* were sometimes seen in areas of dense shore vegetation at the very beginning of the breeding season, and in the early morning and late night when frogs were largely inactive. Few *R. cascadae* males were probably in the areas of dense shore vegetation during censusing because censuses were conducted in times of peak frog activity which occurred in open water.

Additionally, quadrat water temperatures were collected, and on one occasion during the peak of R. cascadae breeding activity (5 May 1985, approximately 15 m of the east pond was free of ice and snow) estimates of H. regilla egg mass deposition in quadrats were collected by counting all visible egg masses in three transect samples along the east pond-edge (0-1 m, 4-5 m, and 5-6 m from the shore-vegetation).

The null-hypothesis that the frequency distributions of R. cascadae and H. regilla were equal among quadrats was assessed for each census by comparing the number of individuals of each species counted in the 5 m^2 quadrats (contingency table analysis, Chi-square test). The expected frequencies of treefrog quadrat-attendance were determined by multiplying the proportion of the R. cascadae breeding population present in each quadrat by the H. regilla breeding population size from that census. If the number of H. regilla expected to be present in any quadrat was less than 4.5, the number of frogs from adjacent quadrats were lumped to provide a sufficient sample size for analysis. Lumping was necessary to some extent in every comparison of frog distributions because not all quadrats were used by frogs. On most days, a single representative census of frog distributions during a peak breeding activity period was analysed. However, two censuses were analyzed on one day when a great deal of frog movement throughout the breeding area was observed.

RESULTS and DISCUSSION

R. cascadae males initiated encounters with *H. regilla* in 44 of 46 interactions recorded during over 100 hrs of observations at the breeding site in 1985 and 1986. Treefrogs were displaced in 72% of these *R. cascadae*-intitiated encounters (19 of 30 encounters in 1985 and 14 of 14 encounters in 1986). In these interactions, male *R. cascadae* usually approached and clasped treefrogs, often deflated male treefrog vocal sacs with their clasps, and treefrogs responded by diving, swimming or jumping up to 7 m away. In 11 *R. cascadae*-initiated encounters, either treefrogs were not displaced or the result of the interaction was inadvertently not recorded. *R. cascadae* were never displaced by *H. regilla*, and in the two *H. regilla*-initiated encounters, individuals of both species remained in the area of interaction.

R. cascadae and *H. regilla* distributions were always different (Table 1; example censuses in Table 2; also personal observations in 1983-1984). In 1985, the areas of treefrog egg deposition mirrored the adult distributions (Table 2). A partially-submerged log extending 20 m into the pond, lying perpendicular to the shore in an approximately east-west position, bisected the central area of R. cascadae breeding activity. Most R. cascadae communal oviposition and male breeding behavior occurred within 10 m north or south of this log. R. cascadae breeding activity and oviposition sites were centered in this area during 1980-1988 (personal observations and R. O'Hara and J. Peterson, personal communications).

The use of this area of the pond as the R. cascadae breeding site may be related to the water temperature gradient at the pond; the highest water temperatures were recorded near the log (Table 2). During R. cascadae breeding and the first weeks of the H. regilla breeding season, it often snowed and nightly low air temperatures dropped below freezing. In the morning, a sheet of ice sometimes covered the melted portion of the pond. However, the log seemed to act as a heat reservoir and ice melted from the log-area before other areas of the pond. Warmer temperatures may reduce egg loss from freezing (e.g. Licht, 1971), increase hatching success (Waldman, 1982) and accelerate development (e.g. Herreid and Kinney, 1967). Accelerated development may increase frog survival in several ways: by reducing mortality of larvae in drying temporary ponds (e.g. Herreid and Kinney, 1967), by providing a temporal escape from predators appearing at the pond later in the summer (the abundance of most insect predators increased as the summer progressed at my study pond, personal observations, personal communication from J. Peterson), or by providing a size-escape from predators that cannot prey on large larvae (e.g. in my study pond - dragonfly naiads, Aeshna umbrosa, and the rough-skinned newt, Taricha granulosa) (Calef 1973, Heyer et al. 1975).

The locations of H. regilla breeding activity varied daily but were always clumped (e.g. Table 2; personal observations in 1983-1986). During the short R. cascadae breeding seasons (lasting approximately 1 week in 1983-1986), H. regilla males usually called in choruses concentrated 15 m or more away from the center of the R. cascadae breeding site although some H. regilla were almost always seen in the breeding area of R. cascadae. During a census, up to 25 male H. regilla were present in a quadrat bordering the log when no R. cascadae were there. As the pond continued to melt, H. regilla breeding choruses moved to newly opened areas. Thus, large H. regilla choruses did not usually move to the central area used by R. cascadae after R. cascadae completed breeding. A more definitive test of competitive exclusion of H. regilla would be to show that treefrogs used the R. cascadae breeding area after the removal of R. cascadae. I did not remove

R. cascadae from their breeding site because the primary goal of my research was to examine R. cascadae intraspecific breeding dynamics.

Whitney and Krebs (1975a) found that the distribution of H. regilla breeding choruses was often clumped at a pond with apparently homogeneous habitat. During the R. cascadae breeding season, habitat used by the two frog species did not seem to vary in the amount of emergent vegetation, vegetation density, and the presence of potential egg predators (leeches and caddis fly larvae were seen on egg masses of both anurans in all quadrats, personal observations). The consistently complementary distributions between the two anurans suggests interspecific interactions affect treefrog dispersion patterns and breeding sites. This hypothesis is supported by reports that H. regilla spacing and chorus densities are influenced by intraspecific aggression (Whitney and Krebs, 1974a; Perrill, 1984).

R. cascadae dominance in interspecific encounters may be related to their larger body size. R. cascadae males were on average 1 cm longer and over 3 times heavier than H. regilla , and gravid female R. cascadae were 3 cm longer and weighed over 5 times as much as gravid H. regilla females (Table 3).

Interspecific clasping may be costly in terms of time and energy, and may increase an individual's risk of injury and predation (e.g. Moore, 1978; Orians and Willson, 1964). Anuran complementary spatial distributions may reduce the energetic and reproductive costs of interspecific interactions (Etges, 1987). Because the *H. regilla* mating system is not characterized by a search and struggle competition among males for mates (Whitney and Krebs, 1975a, 1975b; Perrill, 1984), repeated encounters with clasping *R. cascadae* males may upset the *H. regilla* chorus organization, reduce male calling time, and affect individual mating success. Although interspecific interactions seemed to have little influence on *R. cascadae* males (personal observations), male-male fights probably have an energetic cost (Wells, 1978). Although interspecific pairings (male-female) were never observed and probably rarely result in complete loss of annual reproductive success, such pairings may be energetically costly to both males and females, costly in terms of wasted time for *R. cascadae* because of their explosive breeding season, and may result in egg loss. During my capture and handling of females of both species, extremely gravid individuals often extruded eggs. Egg loss may also occur during interspecific struggles if females are mistakenly clasped by males of the wrong species.

In conclusion, the dominance of *R. cascadae* males in interspecific interactions evidently resulted in the use of different breeding sites by *H. regilla*. In general, interspecific interactions occurred in the central part of the traditional location of *R. cascadae* breeding (which was associated with warm water temperatures), were initiated by *R. cascadae*, and resulted in the displacement of *H. regilla*. The spatial distributions of these anurans were different in every census taken in 2 years of study. Energetic and reproductive costs of interspecific interactions probably reinforce the use of different breeding sites in these anurans.

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Table VI.1: Results of chi-square analyses of frog distributions in daily censuses.

Table VI.1

Date	Time	No. <u>H.regilla</u> in Census	No. <u>R.cascadae</u> in Census	No.Quadrats in Analysis	X^2
4 May 1985	1100	119	8	2	75.8*
	1515	96	22	4	182.4*
6 May 1985	1510	58	12	3	90.5*
7 May 1985	1345	52	21	6	148.1*
8 May 1985	1700	126	28	7	143.3*
9 May 1985	1145	120	28	5	182.3*
6 Apr 1986	1620	59	42	4	202.5*
7 Apr 1986	1120	70	28	3	169.1*
10 Apr 1986	1600	47	15	3	124.8*

* $p<0.005$

Table VI.2: Frog numbers (census I: 4 May 1985, II: 6 April 1986), *H. regilla* egg numbers (5 May 1985), and pond water temperatures in quadrats (A = first row of quadrats 0-5 m from east pond shore, B = second row of quadrats 5-10 m from shore, "-" indicates data were not collected usually because a quadrat was snow-covered.

Table VI.2

	QUADRAT										
	m North of log					m South of Log					
	15-20	10-15	5-10	0-5	LOG	0-5	5-10	10-15	15-20	20-25	25-30
<u>Frog Distributions</u>											
No. <u>H</u>. <u>regilla</u>											
I- (A)	1	3	4	0		3	8	9	12	29	27
(B)	0	0	0	0		0	0	0	0	0	0
II- (A)	-	-	4	3		7	23	21	-	-	-
(B)	-	-	1	0		0	0	-	-	-	-
No. <u>R</u>. <u>cascadae</u>											
I- (A)	0	1	0	6		4	4	1	0	0	0
(B)	0	0	0	5		0	0	0	1	0	0
II- (A)	-	-	13	17		7	0	0	-	-	-
(B)	-	-	4	1		0	0	-	-	-	-
<u>Egg Distributions</u>											
No. <u>H</u>. <u>regilla</u> egg masses in transect:											
0-1 m from shore	0	0	2	2		0	8	5	4	5	8
4-5 m from shore	0	0	5	0		1	3	0	12	42	32
5-6 m from shore	0	0	0	0		0	0	1	4	12	24
<u>Pond Temperatures</u>											
6 April 1986 (A)	-	-	-	5.6	6.1	5.6	4.4	-	-	-	-
(B)	-	-	3.9	2.2	5.3	-	10.0	8.6	8.6	-	-
10 April 1986 (A)	7.2	7.2	8.9	8.9	9.7	9.4	-	-	-	-	-

Table VI.3: Sizes of R. *cascadae* and H. *regilla*.

Table VI.3

		1985			1986		
		$\bar{x}$	SD	N	$\bar{x}$	SD	N
R. cascadae							
Males:	SUL	5.53	0.24	57	5.50	0.30	69
	Mass	18.09	2.17	55	17.38	3.02	68
Females:	SUL	7.07	0.36	13	6.92	0.26	10
	Mass	45.90	6.49	10	40.78	4.70	9
H. regilla							
Males:	SUL	4.01	0.35	25	3.87	0.29	23
	Mass	4.94	1.17	16	5.71	0.70	7
Females:	SUL	4.09	0.14	8	4.14	0.24	16
	Mass	-	-	-	8.00	1.32	3

LITERATURE CITED

Calef, G.W. 1973. Natural mortality of tadpoles in a population of *Rana aurora*. Ecology 54:741-758.

Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. Amer. Nat. 122:661-696.

Dumas, P.C. 1964. Species-pair allometry in the genera *Rana* and *Phrynosoma*. Ecology 45:178-181.

______. 1966. Studies of the *Rana* complex in the Pacific Northwest. Copeia 1966:60-74.

Ebersole, J.P. 1977. The adaptive significance of interspecific territoriality in the reef fish *Eupomacentrus leucostictus*. Ecology 58:914-920.

Emlen, S.T. 1976. Lek organization and mating strategies in the bullfrog. Behav. Ecol. Sociobiol. 1:283-313.

Etges, W.J. 1987. Call site choice in male anurans. Copeia 1987:910-923.

Fellers, G.M. 1979. Aggression, territoriality, and mating behaviour in North American treefrogs. Anim. Behav. 27:107-119.

Herreid, C.F., II, and S. Kinney. 1967. Temperature and development of the wood frog, *Rana sylvatica*, in Alaska. Ecology 48:579-590.

Heyer, W.R., R.W. McDiarmid, and D.L. Wiegmann. 1975. Tadpoles, predation and pond habitats in the tropics. Biotropica 7:100-111.

Howard, R.D. 1978. The evolution of mating strategies in bullfrogs, Rana catesbeiana. Evolution 32:850-871.

Licht, L.E. 1971. Breeding habits and embryonic thermal requirements of the frogs, Rana aurora aurora and Rana pretiosa pretiosa, in the Pacific Northwest. Ecology 52:116-124.

Moore, F.R. 1978. Interspecific aggression: Toward whom should a mockingbird be aggressive? Behav. Ecol. Sociobiol. 3:173-176.

Nussbaum, R.A., E.D. Brodie, Jr., and R.M. Storm. 1983. Amphibians and reptiles of the Pacific Northwest. University Press of Idaho, Moscow, Idaho.

Oldham, R.S., and H.C. Gerhardt. 1975. Behavioral isolating mechanisms of the treefrogs Hyla cinerea and Hyla gratiosa. Copeia 1975:223-231.

Orians, G.H. and M.F. Willson. 1964. Interspecific territories of birds. Ecology 45:736-745.

Perrill, S.A. 1984. Male mating behavior in Hyla regilla. Copeia 1984:727-732.

Ryan, M.J. 1980. The reproductive behavior of the bullfrog (Rana catesbeiana). Copeia 1980:108-114.

Schoener, T.W. 1983. Field experiments on interspecific competition. Amer. Nat. 122:240-285.

Stamps, J.A. 1977. The relationship between resource competition, risk, and aggression in a tropical territorial lizard. Ecology 58:349-358.

Waldman, B. 1982. Adaptive significance of communal oviposition in wood frogs (Rana sylvatica). Behav. Ecol. Sociobiol. 10:169-174.

Walters, J. 1979. Interspecific aggressive behaviour by long-toed lapwings (Vanellus crassirostris). Anim. Behav. 27:969-981.

Wells, K.D. 1978. Territoriality in the green frog (Rana clamitans): vocalisations and agonistic behaviour. Animal Behaviour 26:1051-1063.

Whitney, C.L., and J.R. Krebs. 1975a. Spacing and calling in Pacific tree frogs, Hyla regilla. Canad. J. Zool. 53:1519-1527.

________ 1975b. Mate selection in Pacific treefrogs. Nature 255:325-326.

BIBLIOGRAPHY

Alexander, R.D. 1974. The evolution of social behavior. Ann. Rev. Ecol. Syst. 5:325-383.

Alexander, R.D., J.L. Hoogland, R.D. Howard, K.M. Noonan, and P.W. Sherman. 1979. Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates and humans. Pages 402-435 _in_ N.A. Chagnon and W. Irons, editors. Evolutionary Biology and Human Social Behavior. Duxbury Press, North Scituate, Massachusetts, USA.

Arak, A. 1983. Male-male competition and mate choice in anuran amphibians. Pages 181-210 _in_ P. Bateson, editor. Mate Choice. Cambridge University Press, Cambridge, Great Britain.

Arnold, S.J., and M.J. Wade. 1984a. On the measurement of natural and sexual selection: theory. Evolution 38:709-719.

_______. 1984b. On the measurement of natural and sexual selection: applications. Evolution 38:720-734.

Bateson, P. 1983. Mate Choice. Cambridge University Press, Cambridge, Great Britain.

Bertram, B.C.R. 1978. Living in groups: predators and prey, p. 64-96. _In:_ Behavioral ecology: an evolutionary approach. J.R. Krebs and N.B. Davies (eds.). Sinauer Assoc., Inc., Sunderland, Massachusetts.

Berven, K.A. 1981. Mate choice in the wood frog, _Rana sylvatica_. Evolution 35:707-722.

Blaustein, A.R. 1988. Ecological correlates and potential functions of kin recognition and kin association in anuran larvae. Behavior Genetics 18:449-464.

Blum, M.S., and N.A. Blum. 1979. Sexual Selection and Reproductive Competition in Insects. Academic Press, New York, USA.

Brodie, E.D., Jr., and D. R. Formanowicz, Jr. 1987. Antipredator mechanisms of larval anurans: protection of palatable individuals. Herpetologica 43:369-373.

Brown, J.L., and G.H. Orians. 1970. Spacing patterns in mobile animals. Ann. Rev. Ecol. Syst. 1:239-262.

Calef, G.W. 1973. Natural mortality of tadpoles in a population of *Rana aurora*. Ecology 54:741-758.

Clarke, R.D. 1977. Postmetamorphic survivorship of Fowler's toad, *Bufo woodhousei fowleri*. Copeia 1977:594-597.

Clutton Brock, T.H., F.E. Guiness, and S.D. Albon. 1982. Red deer: behaviour and ecology of two sexes. Univ. Chicago Press, Chicago.

Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. Amer. Nat. 122:661-696.

Crow, J.F. 1958. Some possibilities for measuring selection intensities in mann. Human Biol. 30:1-13.

Daly, J.W. and C.W. Myers. 1967. Toxicity of Panamanian poison frogs (Dendrobates): some biological and chemical aspects. Science 156:970-973.

Darwin, C. 1871. The Descent of Man and Selection in Relation to Sex. John Murray, London, Great Britain.

Daugherty, C.H., and A.L. Sheldon. 1982. Age-determination, growth, and life history of a Montana population of the tailed frog (*Ascaphus truei*). Herpetologica 38: 461-468.

Davies, N.B., and T.R. Halliday. 1977. Optimal mate selection in the toad *Bufo bufo*. Nature 269:56-58.

_______. 1979. Competitive mate searching in male common toads, *Bufo bufo*. Animal Behaviour 27:1253-1267.

Dickerson, M.C. 1969. The frog book, North American toads and frogs. Dover Publications, Inc., New York.

Dumas, P.C. 1964. Species-pair allometry in the genera *Rana* and *Phrynosoma*. Ecology 45:178-181.

______. 1966. Studies of the *Rana* complex in the Pacific Northwest. Copeia 1966:60-74.

Ebersole, J.P. 1977. The adaptive significance of interspecific territoriality in the reef fish *Eupomacentrus leucostictus*. Ecology 58:914-920.

Emlen, S.T. 1976. Lek organization and mating strategies in the bullfrog. Behav. Ecol. Sociobiol. 1:283-313.

Emlen, S.T., and L.W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223.

Endler, J.A. 1986. Defense against predators, p. 109-134. In: Predator-prey relationships. M.E. Feder and G.V. Lauder (eds.). The University of Chicago Press, Chicago, Illinois.

Etges, W.J. 1987. Call site choice in male anurans. Copeia 1987:910-923.

Fellers, G.M. 1979. Aggression, territoriality, and mating behaviour in North American treefrogs. Anim. Behav. 27:107-119.

Fincke, O.M. 1982. Lifetime mating success in a natural population of the damselfly, Enallagma hageni (Walsh) (Odonata: Coenagrionidae). Behav. Ecol. Sociobiol. 10:293-302.

Fitch, H.S. 1965. An ecological study of the garter snake, Thamnophis sirtalis. University of Kansas Publications of the Museum of Natural History 15:493-564.

Flier, J., M.W. Edwards, J.W. Daly, and C.W. Myers. 1980. Widespread occurrence in frogs and toads of skin compounds interacting with the ouabain site of Na+, K+-ATPase. Science 208:503-505.

Formanowicz, D.R., Jr., and E.D. Brodie, Jr. 1982. Relative palatabilities of members of a larval amphibian community. Copeia 1982:91-97.

Frazer, J.F.D. 1966. A breeding colony of toads (*Bufo bufo* L.) in Kent. British J. Herpetol. 3:236-252.

Gatz, A.J. 1981a. Size selective mating in *Hyla versicolor* and *Hyla crucifer*. Journal of Herpetology 15:114-116.

_______. 1981b. Non-random mating by size in American toads, *Bufo americanus*. Animal Behaviour 29:1004-1012.

Gill, D.E. 1978. The metapopulation ecology of the Red-spotted newt, *Notophthalmus viridescdens* (Rafinesque). Ecol. Monogr. 48:145-166.

Gill, D.E., K.A. Berven, and B.A. Mock. 1983. The environmental component of evolutionary biology. Pages 1-36 *in* Population biology: retrospect and prospect. C.E. King and P.S. Dawson (eds.). Columbia Univ. Press, New York.

Gittins, S.P., A.G. Parker, and F.M. Slater. 1980. Population characteristics of the common toad (*Bufo bufo*) visiting a breeding site in mid-Wales. J. Anim. Ecol. 49:161-173.

Groves, J.D. 1980. Mass predation on a population of the American toad, _Bufo americanus_. Amer. Midl. Nat. 103:202-203.

Halliday, T.R. 1978. Sexual selection and mate choice. Pages 180-213 _in_ J.R. Krebs and N.B. Davies, editors. Behavioral Ecology: An Evolutionary Approach, Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

Hamilton, W.D. 1971. Geometry for the selfish herd. J. Theor. Biol. 31:295-311.

Hansen, J.A., and J.L. Vial. 1956. Defensive behavior and effects of toxins in _Bufo alvarius_. Herpetologica 12:141-149.

Hausfater, G., C.D. Saunders, and M. Chapman. 1981. Some applications of computer models to the study of primate mating and social systems. Pages 345-360 _in_ R.D. Alexander and D.W. Tinkle, eds. Natural selection and social behavior: recent research and new theory. Chiron Press, New York.

Herreid, C.F., II, and S. Kinney. 1967. Temperature and development of the wood frog, _Rana sylvatica_, in Alaska. Ecology 48:579-590.

Heyer, W.R., R.W. McDiarmid, and D.L. Wiegmann. 1975. Tadpoles, predation and pond habitats in the tropics. Biotropica 7:100-111.

Hillis, D.M., A.M. Hillis, and R.F. Martin. 1984. Reproductive ecology and hybridization of the endangered Houston toad (Bufo houstonensis). J. Herpetology 18:56-72.

Hoogland, J.L. and P.W. Sherman. 1976. Advantages and disadvantages of bank swallow (Riparia riparia) coloniality. Ecol. Monog. 46:33-58.

Howard, R.D. 1978. The evolution of mating strategies in bullfrogs, Rana catesbeiana. Evolution 32:850-871.

_______. 1981. Male age-size distribution and male mating success in bullfrogs. Pages 61-77 in R.D. Alexander and D.W. Tinkle, editors. Natural Selection and Social Behavior: Recent Research and New Theory, Chiron Press, New York, USA.

_______. 1983. Sexual selection and variation in reproductive success in a long-lived organism. American Naturalist 122:301-325.

Howard, R.D., and A.G. Kluge. 1985. Proximate mechanisms of sexual selection in wood frogs. Evolution 39:260-277.

Kagarise Sherman, C. 1980. A comparison of the natural history and mating system of two anurans: Yosemite toads (Bufo canorus) and black toads (Bufo exsul). Unpubl. Ph.D. thesis, University of Michigan, Ann Arbor.

Kluge, A.G. 1981. The life history, social organization, and parental behavior of Hyla rosenbergi Boulenger, a nest-building gladiator frog. Miscellaneous Publications of the Museum of Zoology, University of Michigan, No. 160:1-170.

Koenig, W.D., and S.S. Albano. 1986. On the measurement of sexual selection. American Naturalist 127:403-409.

______. 1987. Lifetime reproductive success, selection, and the opportunity for selection in the white-tailed skimmer Plathemis lydia (Odonata: Libellulidae). Evolution 41: 22-36.

Kruuk, H. 1964. Predators and anti-predator behaviour of the black-headed gull (Larus ridibundus L.). Behaviour (Suppl.) 11:1-129.

Lamb, T. 1984. Amplexus displacement in the southern toad Bufo terrestris. Copeia 1984:1023-1025.

Lawrence, W.S. 1986. Male choice and competition in Tetraopes tetraophthalmus: effects of local sex ratio variation. Behavioral Ecology and Sociolbiology 18:289-296.

Lee, J.C., and M.L. Crump. 1981. Morphological correlates of male mating success in Triprion petasatus and Hyla marmorata (Anura: Hylidae). Oecologia 50:153-157.

Licht, L.E. 1971. Breeding habits and embryonic thermal requirements of the frogs, *Rana aurora aurora* and *Rana pretiosa pretiosa*, in the Pacific Northwest. Ecology 52:116-124.

______. 1976. Sexual selection in toads (*Bufo americanus*). Canadian Journal of Zoology 54:1277-1284.

McCauley, D.E. 1983. An eestimate of the relative opportunities for natural and sexual selecion in a population of milkweed beetles. Evolution 37:701-707.

McGregor, P.K., J.R. Krebs, and C.M. Perrins. 1981. Song repertoires and lifetime reproductive success in the great tit (*Parus major*). Amer. Nat. 118:149-159.

Moore, F.R. 1978. Interspecific aggression: Toward whom should a mockingbird be aggressive? Behav. Ecol. Sociobiol. 3:173-176.

Mulder, B.S., B.B. Schultz, and P.W. Sherman. 1978. Predation on vertebrates by Clark's nutcrackers. Condor 80:449-451.

Musgrave, M.E. 1930. *Bufo alvarius*, a poisonous toad. Copeia 1930:96-98.

Nunes, V. da Silva. 1988. Vocalizations of treefrogs (*Smilisca sila*) in response to bat predation. Herpetologica 44:8-10.

Nussbaum, R.A., E.D. Brodie, Jr., and R.M. Storm. 1983. Amphibians and reptiles of the Pacific Northwest. University Press of Idaho, Moscow, Idaho.

Oldham, R.S., and H.C. Gerhardt. 1975. Behavioral isolating mechanisms of the treefrogs _Hyla_ _cinerea_ and _Hyla_ _gratiosa_. Copeia 1975:223-231.

Olson, D.H. 1988a. Breeding ecology and variable mating patterns in the western toad (_Bufo_ _boreas_). Submitted. (Ph.D. Dissertation, Chapter I).

______ 1988b. The role of mate choice and mate competition in western toad (_Bufo_ _boreas_) nonrandom mating. Submitted. (Ph.D. Dissertation, Chapter II).

______ 1988c. Multiyear breeding schedules and adult survival in the western toad (_Bufo_ _boreas_). Submitted. (Ph.D. Dissertation, Chapter III).

______ 1988d. Reproductive success and the opportunity for selection in the western toad (_Bufo_ _boreas_). Submitted. (Ph.D. Dissertation, Chapter IV).

______ 1989. Predation on breeding western toads (_Bufo_ _boreas_). Copeia 1989 (in press).

Olson, D.H., A.R. Blaustein, and R.K. O'Hara. 1986. Mating pattern variability among western toad (_Bufo_ _boreas_) populations. Oecologia 70:351-356.

Orians, G.H. 1969. On the evolution of mating systems in birds and mammals. American Naturalist 103:589-603.

Orians, G.H. and M.F. Willson. 1964. Interspecific territories of birds. Ecology 45:736-745.

Partridge, L., and T. Halliday. 1984. Mating patterns and mate choice. Pages 222-250 in J.R. Krebs and N.B. Davies, editors. Behavioral Ecology: An Evolutionary Approach, Second Edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Payne, R.B. 1979. Sexual selection and intersexual differences in variance of breeding success. Amer. Nat. 114:447-452.

______ 1984. Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. Ornithological Monograph 33, Amer. Ornith. Union.

Payne, R.B. and K. Payne. 1977. Social organization and mating success in local song populations of village indigobirds. Z. Tierpsychol. 45:113-173.

Perrill, S.A. 1984. Male mating behavior in *Hyla regilla*. Copeia 1984:727-732.

Perrill, S.A., and M. Magier. 1988. Male mating behavior in *Acris crepitans*. Copeia 1988:245-248.

Pulliam, H.R. and T. Caraco. 1984. Living in groups: Is there an optimal group size?, p. 122-1 . In: Behavioural Ecology: An evolutionary approach. Second edition. J.R. Krebs and N.B. Davies (eds.). Sinauer Assoc. Inc., Sunderland, Massachusetts.

Raney, E.C., and W.M. Ingram. 1941. Growth of tagged frogs (Rana catesbeiana Shaw and Rana clamitans Daudin) under natural conditions. Amer. Midl. Nat. 26:201-206.

Raney, E.C., and E.A. Lachner. 1947. Studies on the growth of tagged toads (Bufo terrestris americanus Holbrook). Copeia 1947:113-116.

Robertson, J.G.M. 1986. Female choice, male strategies and the role of vocalizations in the Australian frog Uperoleia rugosa. Animal Behaviour 34:773-784.

Ryan, M.J. 1980a. Female mate choice in a neotropical frog. Science 209:523-525.

______. 1980b. The reproductive behavior of the bullfrog (Rana catesbeiana). Copeia 1980:108-114.

______. 1985. The Tungara Frog: a study in sexual selection and communication. University of Chicago Press, Chicago, Illinois, USA.

Ryan, M.J., M.D. Tuttle, and A.S. Rand. 1982. Bat predation and sexual advertisement in a neotropical anuran. American Naturalist 119:136-139.

Ryan, M.J., M.D. Tuttle, and L.K. Taft. 1981. The costs and benefits of frog chorusing behavior. Behav. Ecol. Sociobiol. 8:273-278.

Ryan, R.A. 1953. Growth rates of some ranids under natural conditions. Copeia 1953:73-80.

Salthe, S.N., and W.E. Duellman. 1973. Quantitative constraints associated with reproductive mode in anurans. Pages 229-249 *in* J.L. Bial, editor. Evolutionary Biology of the Anurans. University of Missouri Press, Columbia, Missouri, USA.

Samollow, P.B. 1980. Selective mortality and reproduction in a natural population of *Bufo boreas*. Evolution 34:18-39.

Schaaf, R.T., and J.S. Garton. 1970. Raccoon predation on the American toad, *Bufo americanus*. Herpetologica 26:334-335.

Schoener, T.W. 1983. Field experiments on interspecific competition. Amer. Nat. 122:240-285.

Shine, R. 1979. Sexual selection and sexual dimorphism in the Amphibia. Copeia 1979:297-306.

Smits, A.W. 1984. Activity patterns and thermal biology of the toad *Bufo bufo halophilus*. Copeia 1984: 689-696.

Snedecor, G.W., and W.G. Cochran. 1980. Statistical methods. Seventh edition. The Iowa State University Press, Ames, Iowa.

Stamps, J.A. 1977. The relationship between resource competition, risk, and aggression in a tropical territorial lizard. Ecology 58:349-358.

Sullivan, B.K. 1982. Sexual selection in Woodhouse's toad (*Bufo woodhousei*) I. Chorus organization. Animal Behaviour 30:680-686.

_______. 1983. Sexual selection in Woodhouse's toad (*Bufo woodhousei*) II. Female choice. Animal Behaviour 31:1011-1017.

_______. 1984. Size dimorphism in Anurans: a comment. American Naturalist 123:721-724.

_______. 1986. Intra-populational variation in the intensity of sexual selection in breeding aggregations of Woodhouse's toad (*Bufo woodhousei*). Journal of Herpetology 20:88-90.

_______. 1987. Sexual selection in Woodhouse's toad (*Bufo woodhousei*). III. Seasonal variation in male mating success. Animal Behaviour 35:912-919.

Tracy, C.R., and J.W. Dole. 1969. Orientation of displaced California toads, *Bufo boreas*, to their breeding sites. Copeia 1969:693-700.

Trail, P.W. 1985. The intensity of selecion: intersexual and interspecific comparisons require consistent measures. Amer. Nat. 126:434-439.

Trivers, R.L. 1972. Parental ivnvestment and sexual selection. In B. Campbell, editor. Sexual Selection and the Descent of Man. Aldine Publishing Co., Chicago , Illinois, USA.

______. 1976. Sexual selection and resource-accruing ability in *Anolis garmani*. Evolution 30::253-269.

Turner, F.B. 1962. The demography of frogs and toads. Quart. Rev. Biol. 37:303-314.

Tuttle, M.D., and M.J. Ryan. 1981. Bat predation and the evolution of frog vocalizations in the Neotropics. Science 214:677-678.

______. 1982. The role of synchronized calling, ambient light and ambient noise, in anti-bat predator behavior of a treefrog. Behav. Ecol. Sociobiol. 11:125-131.

Tuttle, M.D., L.K. Taft, and M.J. Ryan. 1981. Acoustical location of calling frogs by Philander opossums. Biotropica 13:233-234.

______. 1982. Evasive behaviour of a frog in response to bat predation. Anim. Behav. 30:393-397.

Vehrencamp, S.L., and J.W. Bradbury. 1984. Mating systems and ecology. Pages 251-278 in J.R. Krebs and N.B. Davies, editors. Sinauer Associates, Sunderland, Massachusetts, USA.

Wade, M.J. 1979. Sexual selection and variance in reproductive success. American Naturalist 114:742-747.

Wade, M.J., and S.J. Arnold. 1980. The intensity of sexual selection in relation to male sexual behavior, female choice, and sperm precedence. Animal Behaviour 28:446-461.

Waldman, B. 1982. Adaptive significance of communal oviposition in wood frogs (Rana sylvatica). Behav. Ecol. Sociobiol. 10:169-174.

Walters, J. 1979. Interspecific aggressive behaviour by long-toed lapwings (Vanellus crassirostris). Anim. Behav. 27:969-981.

Wells, K.D. 1977. The social behaviour of Anuran Amphibians. Animal Behaviour 25:666-693.

_______. 1978. Territoriality in the green frog (Rana clamitans): vocalisations and agonistic behaviour. Animal Behaviour 26:1051-1063.

_______. 1979. Reproductive behavior and male mating success in a neotropical toad, Bufo typhonius. Biotropica 11:301-307.

Whitney, C.L., and J.R. Krebs. 1975a. Spacing and calling in Pacific tree frogs, Hyla regilla. Canad. J. Zool. 53:1519-1527.

________ 1975b. Mate selection in Pacific treefrogs. Nature 255:325-326.

Wilbur, H.M., D.I. Rubenstein, and L. Fairchild. 1978. Sexual selection in toads: the roles of female choice and male body size. Evolution 32:264-270.

Williams, G.C. 1964. Measurement of consociation among fishes and comments on the evolution of schooling. Publications of the Museum, Michigan State University, Biological Series 2:351-383.

Woodward, B.D. 1982a. Male persistence and mating success in Woodhouse's toad (*Bufo woodhousei*). Ecology 63:583-585.

_______. 1982b. Sexual selection and nonrandom mating patterns in desert anurans (*Bufo woodhousei*, *Scaphiopus couchi*, *S*. *multiplicatus* and *S*. *bombifrons*). Copeia 1982:351-355.

Woolbright, L.L. 1983. Sexual selection and size dimorphism in Anuran Amphibia. American Naturalist 121:110-119.

Wright, J.W. 1966. Predation on the Colorado River toad, *Bufo alvarius*. Herpetologica 22:127-128.