Alternative Mating Behaviors of Young Male Bullfrogs[1]

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Synopsis. Yearling male bullfrogs often attempt to intercept and mate with females attracted to older, larger males (male parasitism) instead of defending a territory and attracting their own mates. Mating behaviors like male parasitism are thought to occur only when individuals suffer some strong disadvantage in using the behaviors that are more typical of their species. In this paper, I consider the relative benefits and costs of territoriality *vs* male parasitism for yearling males. Yearlings employing male parasitism are only occasionally successful at mating, and in years of reduced male-male competition, they produce significantly fewer young than territorial males of their age. Yearling males that vary in the degree to which they employ territorial behaviors instead of male parasitism do not differ measurably in growth rate or chances of mortality; however, indirect information suggests that territoriality should entail a greater chance of mortality. A computer simulation based solely on observed demographic parameters predicts that yearling males should be territorial whenever they can compete as effectively as two-year-old males. This condition appears to provide little restriction on the breeding tactics of yearling males; however, data on male-male aggressive encounters show that the size differences between one-year-old and two-year-old males are usually sufficient to preclude yearling males from competing successfully. Thus, the observed behavioral plasticity of yearling males may be best interpreted as a means of adjusting their behavioral tactics to levels of male-male competition that can vary within and between breeding seasons.

Introduction

Variability in many biological phenomena is often not considered until long after their central tendency is well established. Research on mating behavior provides no exception. Species are usually classified according to their most conspicuous mating behavior with little or no reference to intraspecific variation in mating tactics of either males or females (exceptions include Bateson and Brindley, 1892; Scott, 1926; Darling, 1937; Hogan-Warburg, 1966). Biologists have just now begun to devote attention to alternative mating behaviors by considering ecological and social conditions that favor their proliferation (*e.g.*, Van Rhijn, 1973; Howard, 1981; Waltz, 1982), genetic, ontogenetic, and environmental bases that underlie their expression (*e.g.*, Hogan-Warburg, 1966; Semler, 1973; Constantz, 1975; Alcock *et al.*, 1977; Dominey, 1980), and evolutionary pressures that maintain them in a population (*e.g.*, Gadgil, 1972; Maynard Smith and Parker,

1976; Rubenstein, 1980; Gross, 1982; Maynard Smith, 1982).

Young male bullfrogs, *Rana catesbeiana*, employ an alternative mating behavior in which they secretively attempt to intercept and mate with females attracted to larger, older territorial males (Emlen, 1976; Howard, 1978, 1981). This behavioral pattern, which I refer to as male parasitism (Howard, 1978), is similar to the satellite phenomenon in ruffs (Hogan-Warburg, 1966; Van Rhijn, 1973) except that it results from age differences among males rather than from genetic differences. Male parasitism is almost exclusively observed in one-year-old males, and even these males can also employ territorial behaviors, the most common mating behavior used by male bullfrogs. Male parasitism and similar phenomena in other species are often considered options of last resort for males that are at some disadvantage in male-male competition. Thus, these males are thought to be making the best of a bad situation (*e.g.*, Dawkins, 1980; Rubenstein, 1980; Howard, 1981; Krebs and Davies, 1981, p. 154).

In this paper, I address the question: How bad is the situation? I first consider how both territoriality and male parasitism

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influence survivorship, size-specific growth rates, and yearly reproductive success (RS) of young males, and then predict what would happen to "mutant" male bullfrogs that never employed male parasitism but were always territorial as one-year-olds. To even begin to predict how such males would fare involves comparing their expected lifetime reproductive success (LRS). LRS of both types of males is predicted with a computer simulation procedure that uses field-corrected data on age-specific survivorship and fecundity. The computer simulation thus provides a way to estimate how much the fecundity of one-year-old mutant males would have to be increased to offset the greater risks of mortality that could result from early territorial behavior.

Materials and Methods

Field estimates

Data used in this paper were gathered during 1975–1978 on a population of bullfrogs in Crane Pond in the Edwin S. George Reserve of the University of Michigan; most methodology used has been described elsewhere (Howard, 1978; 1983). Individual growth rates for males and females of all ages were obtained by measuring changes in body size (snout–ischium length) with a metric ruler mounted on a board (Howard, 1978). I took initial measurements at the date of first capture which was usually during late May or early June. Last measurements were obtained near the end of the breeding season in late July–early August. During 1978, I also collected most individuals within a 72-hour period during the midpoint of the breeding season. During 1975–1977, individuals were collected during the breeding season only if they had lost or damaged their identifying waistbands.

Analyses of how growth rates and relative reproductive success varied with percent territorial activity of one-year-old males utilized any 1978 data. In this year, a within-age group comparison was possible because the population contained a large number of yearling males of roughly similar body size. Growth in this analysis reflects changes in body size during a 25-day period in which active chorusing

occurred; I chose this time period to avoid including in the analysis those days during the breeding season when no breeding activity occurred in the population (Howard, 1981). I only used males that were present in more than 60% of the 25 nightly choruses, and to minimize the complications of size-specific growth rates, I restricted the analysis to males that were between 105–120 mm snout–ischium length. All these restrictions were applied to make the analysis maximally sensitive to the relationship between reproductive behaviors and growth rate. Relative reproductive success estimates encompass the entire 1978 breeding season, not just a portion of it, and are defined as the number of hatchlings produced by an individual divided by the average number of hatchlings produced by all males in the population (Howard, 1978, 1983). Percent territorial activity equals the number of nights an individual was territorial divided by the number of nights he was either territorial or parasitic. I calculated percent territorial activity for the 25 nights of breeding in the growth rate analysis and for the entire breeding season in the analysis of relative RS.

Field data used in the computer simulation included estimates of age (Howard, 1981, 1983; see also Collins, 1975), age-specific survivorship, and age-specific probabilities of mating and fecundity of all successfully breeding individuals (Howard, 1983). I used the survivorship and fecundity data obtained during 1975 and 1976 (Table 1). These years were used because all age classes were present in the breeding chorus and reasonable numbers of individuals breeding in 1975 returned in 1976 thus facilitating estimates of age-specific survival. During 1976, most one-year-old males employed male parasitism except at the very end of the mating season when many became territorial. Fecundity of one-year-old males (Table 1) only reflects the success of male parasitism because no territorial yearling male successfully mated in 1976.

Computer simulation

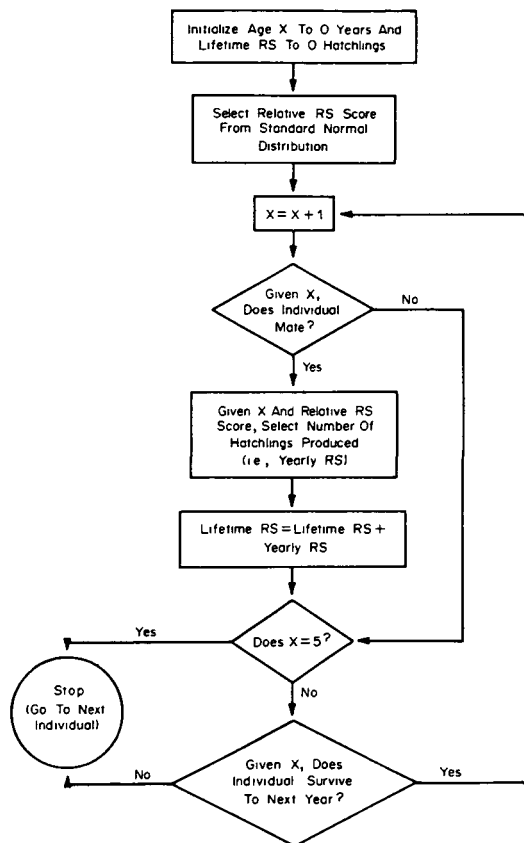A computer simulation was used to predict LRS. Survival of each individual was

Initialize Age X To 0 Years And
Lifetime RS To 0 Hatchlings

Select Relative RS Score
From Standard Normal
Distribution

X = X + 1

Given X,
Does Individual   No
Mate ?

Yes

Given X And Relative RS
Score, Select Number Of
Hatchlings Produced
(i e , Yearly RS)

Lifetime RS = Lifetime RS +
Yearly RS

Yes
Does X = 5 ?

Stop
(Go To Next   No
Individual)

No   Given X, Does   Yes
Individual Survive
To Next Year ?

FIG. 1. Flow diagram illustrating the computer simulation procedure used to predict LRS for wild type and mutant males. Each male was assigned a relative RS score at age zero and retained this score throughout life. Age-specific distributions based on field data were used to determine if an individual mated at a particular age, the number of hatchlings produced if successfully mated, and whether or not he survived to the next breeding season. Maximum lifespan was 5 years. See text for fuller explanation.

TABLE 1. Demographic data on male bullfrogs collected during 1975–1976 at Crane Pond.*

Age x (yr)	Probability of survival (age x − 1 to age x)	Probability of successfully mating	Number of hatchlings ($\bar{x}$ ± SD)
1		0.11	2,732 ± 1,289
2	0.42	0.55	3,581 ± 2,671
3	0.42	0.69	6,402 ± 3,986
4	0.52	0.83	17,511 ± 8,687
5	0.23	1.00	19,346 ± 10,035

* Survivorship data based on mark-recaptures of known individuals between 1975–1976. Fecundity data were obtained during 1976 only (Howard, 1983).

determined at each age by selecting a random number between zero and one from a uniform distribution; if the number chosen was less than or equal to the individual's age-specific probability of survival based on field data, the individual survived to the next year. Otherwise the individual died. This procedure was repeated at each age for every individual until death occurred (Fig. 1).

The age-specific fecundity of each individual in the simulation depended on whether or not the individual mated and how many hatchlings were produced if the individual did mate. An individual was "successful" in mating when a number randomly chosen from a uniform distribution was less than or equal to the observed age-specific probability of mating (Table 1).

To simulate the number of hatchlings produced, I first randomly assigned a relative RS score from a standard normal distribution to each individual at age zero. Then, if the individual successfully mated, I transformed the relative RS score to the observed normal distribution of hatchling production that corresponded to the individual's age. Such transformations were performed using the equation, number of hatchlings = (RS score × σ) + μ; where σ and μ refer to the standard deviation and mean of the observed age-specific normal distribution. Each individual retained the original randomly chosen relative RS score for life (Fig. 1). However, any individual that bred each year did not produce the same number of offspring every year because the observed fecundity distributions varied with age (Table 1). The procedure of transforming from a specific part of a standard normal distribution to other normal distributions was used to produce a positive correlation in reproductive performance among years for the same individual. Thus, genetic or developmental differences are simulated in that some individuals consistently produce more (or less) offspring than others of the same age (Howard, 1983).

The methods were then used to simulate the LRS of a cohort of 200 one-year-old "wild type" and 200 one-year-old "mutant" males. A simulation "run," based on the

same survivorship and fecundity distributions, was performed 100 times; this corresponded to viewing 100 different cohorts in populations with similar demographic characteristics. The relative LRS (mutant males/wild type males) was calculated for each run and an average ratio was obtained for all 100 runs.

Wild type males possessed the demographic characteristics listed in Table 1; "mutant" males had these same characteristics except during their first year of life. In this year, their probability of survivorship from age 1 to age 2 was reduced to reflect the increased mortality that older territorial males experienced in nature. In Crane Pond, this increased mortality resulted from snapping turtle predation (Howard, 1981). The fecundity of mutant males was also adjusted during their first breeding season; all adjustments involved giving these males various fecundity characteristics of older males.

Although analytic solutions provide an alternative and often simpler means to compare the relative LRS of different "types" of males I chose to use simulations because they treat each individual separately and generate a distribution of expected outcomes given the same set of initial parameters. Thus, they provide some clue as to the effect of chance on final outcomes and a means of statistical comparison with observed results. The simulations require many assumptions as would alternative analytic procedures: First, I assume that equal numbers of both types of males occur in the population. Second, age-specific survivorship is independent of the particular level of RS it achieved; however, for *all* individuals, both the chances of mortality and of higher RS increased during the latter years of life. Third, for each individual, the chance of successfully mating in any year is assumed to be independent of mating success in other years. Fourth, the yearly relative reproductive performance of successfully breeding individuals remains the same for life. Fifth, because I consider all progeny to be of equal value with respect to the age of their parent, I assume that the population size remains relatively constant. Sixth, because

I use number of hatchlings as a measure of RS rather than number of reproductively successful offspring, I assume that there is a direct relationship between these two measures of RS (Howard, 1979). Seventh, I assume that age-specific fecundity based on one year's data accurately describes the range of possibilities an individual can experience during each year of life. In nature, a male's age-specific fecundity depends not only on his size at any particular age but also the size and number of competing males (Howard, 1981), and the size distribution of females. Such interrelationships affect the way this simulation should be interpreted because the male age-specific fecundity estimates used were those observed in the context of a particular age/size distribution, that of the 1976 Crane Pond population. Thus, the simulation depicts two cohorts of animals that are part of a larger population; although the individuals in the cohorts age, the age-size structure of the population remains the same.

RESULTS

Field data

Although male parasitism was observed each year during 1975–1978, the 1978 breeding season presented a rare opportunity to evaluate the costs and benefits of this behavior. Unlike the previous years, there were a large number of one-year-old males in 1978 (n = 25) and most of these males employed both male parasitism and territorial behaviors to obtain mates. Five older males were also present in the population in this year but these males employed only territorial behaviors (Howard, 1981).

One-year-old males that spent more time being territorial had greater RS (Fig. 2). The 25 young males present in this year obtained 24 of the 38 known matings (63%), yet only 4 of these 24 matings (17%) were obtained while employing male parasitic behaviors; the rest were achieved as the result of territoriality. Success by young males was much higher in 1978 than in other years. In 1976, only 1 of the 10 one-year-old males (26% of all males present) achieved a mating out of the 27 known
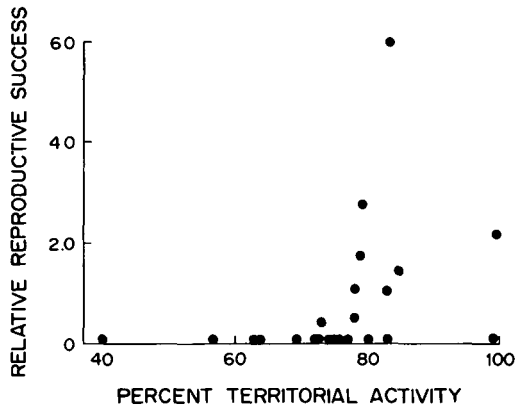
FIG. 2. Relative reproductive success (number of hatchlings each male produced divided by the average number of hatchlings produced by all males in the population) as a function of percent territorial activity for 23 one-year-old males in 1978; $r_s = 0.62; P = 0.002$.
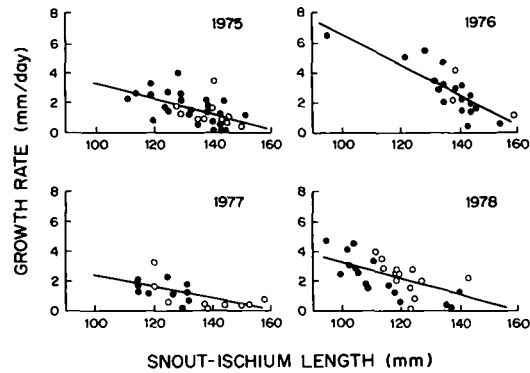

SNOUT-ISCHIUM LENGTH (mm)

FIG. 3. Growth rate of males (closed circles) and females (open circles) during the 1975–1978 breeding seasons. In all years, most individuals grew; however, the rate of growth was inversely related to body size. No significant differences in growth rate were noted between the sexes with the possible exception of 1978 (see text). Regression equations and associated statistics for each year (sexes combined for analyses):

1975: Y = −0.005x + 0.842;
$\quad R^2 = 0.27; P = 0.002; n = 35.$

1976: Y = −0.011x + 1.743;
$\quad R^2 = 0.69; P = 0.001; n = 21.$

1977: Y = −0.004x + 0.636;
$\quad R^2 = 0.35; P = 0.022; n = 19.$

1978: Y = −0.006x + 0.891;
$\quad R^2 = 0.29; P = 0.001; n = 29.$

matings; in 1977, only 1 of the 10 yearling males (38% of all males present) obtained a mating out of the 29 known matings. Moreover, both of these matings were achieved by young males as a result of male parasitism. Thus, young males not only varied the type of mating behavior they employed but the relative success of these tactics also varied.

Male parasitism, like most "low male" behaviors has been predicted to involve reduced mortality and/or lower energetic costs relative to "high male" aggressive behaviors (Gadgil, 1972). During the 4 years of observation, an average of 18% of the older (≥3 yr) territorial males were preyed upon by snapping turtles (range: 8–30%). However, no one-year-old males died during any breeding season regardless of the mating behaviors they used. In theory, male parasitic behaviors should be associated with greater survivorship. In practice, however, even young territorial males had high survivorship, even in 1978 when 96% of the 25 one-year-old males were at least occasionally territorial. Absence of mortality related to breeding activity in this year also may have resulted from an overall reduction in predation rate: only 8% of the older territorial males died, the lowest incidence of predation observed during any breeding season. Alternatively, because younger territorial males were involved in

fewer aggressive encounters which incidentally attract predators (Howard, 1981), they may always have greater chances of survival.

Before addressing the relationship between male mating behaviors and growth rate, general growth trends must be established for this population. Most males and females continued to grow during the 1975–1978 breeding seasons (Fig. 3); the sexes appeared to have similar growth rates in all years. For both sexes, smaller individuals grew faster than larger individuals.

To minimize the effect of possible extraneous factors (e.g., age-specific differences in levels of reproductive effort, size-specific differences in maintenance costs), I used only one-year-old males to evaluate the effects of mating behavior on growth rate. I predicted that territoriality would reduce growth rate more than male parasitism; however, the percent territorial activity of
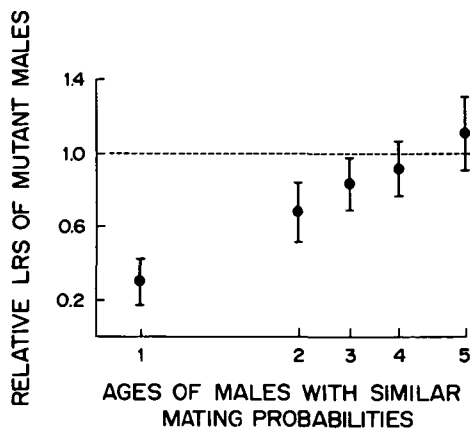
FIG. 4. Relative LRS of mutant males (ratio of total number of hatchlings produced by a cohort of 200 mutant males divided by that produced by a cohort of 200 wild type males) increases when one-year-old mutants are given the mating probabilities achieved by older males (exact values of the mating probabilities that correspond to these male ages are given in Table 1). The dashed line indicates when mutant males and wild type males have equal LRS. Each point represents the average ratio of LRS obtained from 100 computer simulation runs. Bars indicate SD about each mean. Survivorship from age 1 to age 2 was reduced by 18% in mutant males and changes in their mating probability were in effect only during age 1 (see text).

FIG. 5. Relative LRS of mutant males (as defined in Fig. 4) remains essentially unchanged when one-year-old mutants are only given the fecundity characteristics ($\bar{x} \pm$ SD number of hatchlings produced) of older males. One-year-old mutant males retained the mating probability of one-year-old wild type males. Exact values of the fecundity characteristics that correspond to these male ages are given in Table 1. Each point represents the average ratio of LRS obtained from 100 computer simulation runs. Bars indicate SD about each mean. As in Figure 4, mutant survivorship from age 1 to age 2 was reduced by 18% and changes in fecundity characteristics for these males were in effect only during age 1.

yearling males did not affect growth rates ($r = 0.21$; $P > 0.05$; $n = 12$). Thus, any energetic differences that may exist between territoriality and male parasitism must have been negligible in terms of the total energy budget of these young males.

Computer simulations

In the simulation, wild type males were given the demographic characteristics observed during the 1975 and 1976 field season (Table 1); "mutant" males were given these same characteristics except their chances of survival from age 1 to age 2 was reduced by 18%, the average percent mortality that older males faced as a result of their territoriality. Although this level of mortality may be an exaggeration, such costs of territoriality should produce more conservative predictions; lowering territorial costs should always make territoriality a more effective behavioral tactic.

If mutant males suffered the increased

mortality that older territorial males face during the breeding season but did not realize any increase in fecundity, their relative LRS would equal only 0.30 when compared to wild type males. I then varied the fecundity characteristics of one-year-old mutant males in three ways to determine how much fecundity would have to be increased to offset the reduction in survivorship: increasing their probability of mating without changing the fecundity distributions used for successful males; keeping their probability of mating constant but giving successful breeders the fecundity distributions of older males; and finally, giving young mutant males both the probability of mating and fecundity distributions of older males.

If only the probability of mating is varied, mutant males are predicted to achieve LRS levels similar to wild type males only if they could realize the same chance of mating as five-year-old males (Fig. 4). That is, mutant males would essentially have to obtain a mating probability of 1.0. If mat-
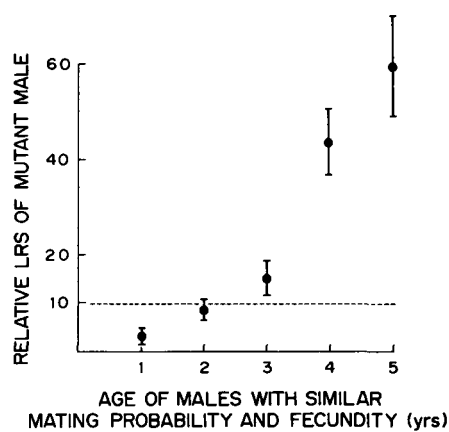
FIG. 6. Relative LRS of mutant males (as defined in Fig. 4) increases sharply if these males are given both the mating probabilities and fecundity characteristics of older males (exact values used are given in Table 1). Each point represents the average ratio of LRS obtained from 100 computer simulation runs. Bars indicate SD about each mean. As in earlier simulations, demographic parameters of mutant males were only altered during age 1.

FIG. 7. The number of male-male encounters is plotted against the body size differences (differences in snout–ischium length) of contestants. This analysis includes 148 encounters that occurred between males of various body sizes (and age) during 1975–1978. Encounters in which contestants were equal in body size were excluded. Above the horizontal: those encounters which the larger male won; below the horizontal: encounters which the smaller male won.

ing probability remains unchanged but successfully breeding one-year-old mutant males have fecundity distributions similar to older males, no level of fecundity is predicted to result in mutant males being as successful as wild type males (Fig. 5). However, if yearling mutant males are given both the mating probability and fecundity distributions of older males, the model predicts that mutant males only have to perform as well as two-year-old males to be as successful reproductively as wild type males (Fig. 6). This prediction differs qualitatively from the two earlier ones because of a synergism between chances of mating and the fecundity distributions of successfully breeding individuals.

The prediction of conditions in which mutant males realize the LRS of wild type males considers only demographic parameters not behavioral ones. Male-male interactions suggest that conditions for equality of LRS between the two male types are quite restrictive because the relative body size of males strongly determines the outcome of male-male encounters (Fig. 7). During the four years of this study, the
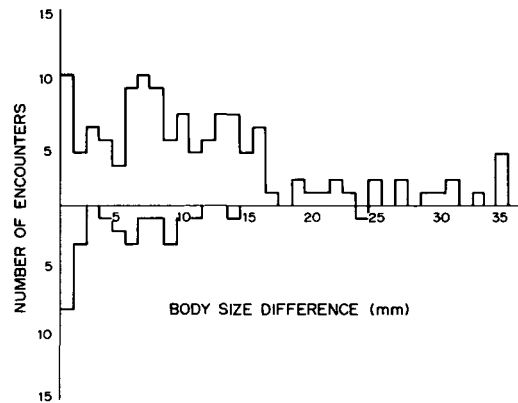
95% confidence interval for the difference in average body size between one-year-old and two-year-old males was 10–15 mm. Using this range of body size differences, behavioral data (Fig. 7) indicate that larger males nearly always win encounters ($\chi^2 = 25.97$; $P = 0.001$; 37 male encounters). Hence if male-male competition is intense, yearling males stand little chance of success against two-year-old males. Even in the most favorable circumstances when a large one-year-old male is within 5 mm of a small two-year-old male a similar conclusion results: the older, larger male should win most encounters ($\chi^2 = 4.67$; $P = 0.031$; 42 male encounters). These analyses include encounters between males of all sizes and ages, and are not limited to interactions between one- and two-year-old males; yet, the few observations of such encounters (n = 5) during the four years of study revealed no case in which a yearling male defeated a two-year-old male.

No information exists concerning how females might discriminate between one- and two-year-old males. However, absolute rejection of yearling males by females was not observed; in 1978, yearling males obtained many matings despite the mating

advantage of larger, older males. Success-
ful breeding by one-year-old males was also
consistent with the pattern of positive size
assortment of mated pairs (Howard, 1978,
1983): Mate preference for larger, older
males was most strongly expressed by
larger, older females; young females
appeared to mate at random with respect
to male size (hence age).

DISCUSSION

Field results indicate the relative impact
of an alternative mating behavior on yearly
RS, chances of mortality, and seasonal
growth rate. During all four years, yearling
males employing male parasitism were
rarely successful in mating. Such low suc-
cess appears to result from females actively
avoiding parasitic males (Howard, 1981).
Yearling males that are territorial are also
usually unsuccessful in mating; the only
exception occurred in 1978 when the level
of male competition was greatly reduced.

Regardless of which mating behavior
they employed, yearling males were never
preyed upon during the mating season; this
contrasts with the relatively high predation
levels on older territorial males. However,
it is probably reasonable to assume that
young territorial males should incur some
degree more risk of predation than young
parasitic males. I suggest this possibility
because of the nature of prey location by
snapping turtles, the only predator
observed to prey on Crane Pond bullfrogs
during the breeding season. These turtles
are attracted by the commotion that male
bullfrogs produce when they call, fight, or
mate. Male parasites are generally motion-
less and secretive in their behavior, thus
they should rarely attract snapping turtles.
However, young territorial males call fre-
quently and engage in at least some aggres-
sive encounters; as a result, they should
face greater risks of predation.

Most bullfrogs, regardless of mating
behavior (or even sex), grew in each breed-
ing season. Yearly differences in growth
rate were noted. An analysis of covariance
indicated that the growth rate of both males
and females could be described as $1977 \leq
1975 = 1978 < 1976$. Reasons for these
differences are unknown; however, popu-
lation density appeared to have no effect.
Growth of individuals during the breeding
season in this population contrasts with the
lack of growth either observed during
reproductive periods in other anuran pop-
ulations (e.g., Martof, 1956; Fellers, 1976;
Wells, 1978; Morton, 1981) or predicted
in species with prolonged breeding seasons
(Woolbright, 1983). However, such growth
is not surprising given that individuals are
only reproductively active at night, and
forage during the day.

Growth rates of young males appear to
be unaffected by the type of mating behav-
ior they employ. Although it seems rea-
sonable to suppose that territoriality is more
energetically demanding than male para-
sitism, it is unknown if differences in such
behaviors can significantly alter growth
rates. An implicit but usually untested
assumption necessary for such a relation-
ship is that organisms are energy limited.
There appears to be little support for this
assumption for bullfrogs in Crane Pond.

Simulations of LRS, based solely on
demographic parameters, predict that
yearling males should have a reasonable
chance of success if they use only territorial
behaviors and refrain from male parasit-
ism. Such young males only have to per-
form as effectively as two-year-old males
rather than as, for example, four- or five-
year-old males. This prediction exists
despite the significant reduction in survi-
vorship expected from territoriality and the
large impact of such early mortality of LRS
(Wiley, 1974; Howard, 1983). However,
field observations on male aggression
greatly dampen the generality of the sim-
ulation's predictions because one-year-old
males are at a strong competitive disad-
vantage even relative to two-year-old males.
Thus, the set of social conditions where
territoriality might be advantageous in
yearling males should be limited to times
of reduced male-male competition. The
observed ability of yearling males to be ter-
ritorial and their plasticity in switching back
and forth between territoriality and male
parasitism suggests that such periods of
relaxed male-male competition must have
been common during the evolutionary his-
tory of this species. Present results indicate

that this condition occurs near the end of some breeding seasons when larger males reduce or terminate reproductive activity, or when high male mortality greatly lowers the number of larger competitors (Howard, 1981a).

Studies of alternative reproductive tactics on other species have revealed a wide array of intraspecific variation in mating behavior, and in many species considerable plasticity in behaviors used by the same individual. Simulations and field data on bullfrogs may lend some insight into the evolution of alternative mating tactics, particularly for those species in which individuals possess sufficient phenotypic plasticity to vary their mating behavior. For bullfrogs, a crucial criterion for behavioral plasticity is that the high benefit/high cost behavioral option (territoriality) must provide a viable alternative only under a restricted range of social and ecological conditions; this contrasts with the low benefit/low cost option (male parasitism) which appears to be equally successful under a wide range of social and ecological conditions. If territoriality resulted in equal or greater LRS under most conditions, tendencies to employ male parasitism should disappear and with them the plasticity in using alternative mating behaviors. Species in which some males employ an alternative mating tactic but lack plasticity in changing behavior patterns may meet one of two criteria that species like bullfrogs do not. The LRS of males using the different types of behavior must be similar at least at some frequencies of the two types of males (e.g., Gadgil, 1972; Gadgil and Taylor, 1975; Charlesworth and Charlesworth, 1975; Maynard Smith, 1982); alternatively, parents that produce multiple male behavioral morphs must, on average, have the same number of grand-offspring as parents that produce any one type of male behavioral morph.

ACKNOWLEDGMENTS

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