

## Oviposition Site Choice and Life History Evolution<sup>1</sup>

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**SYNOPSIS.** Studies of life history evolution, as well as much of life history theory, have typically focused on "hard" components of life histories; phenotypic characteristics that can be readily observed, quantified, and ultimately, connected rather directly to fitness. Typical of these are propagule size, propagule number, and age and size at maturity. What is largely missing from the study of life history evolution is consideration of the role of behavior, principally female oviposition site choice, in the evolution of life histories. For oviparous organisms, natural selection cannot produce locally optimized "hard" components of life history phenotypes without a consistent environmental context (whether invariant or variable); in a variable environment, that consistent environmental context can be most effectively provided by interactive oviposition site choice. I present a model of selection on oviposition site choice in the context of the evolution of "hard" components of life history phenotypes, along with some experimental data illustrating oviposition site choice in response to predators. The model and data are then related to the overall question of the role of oviposition site choice in life history evolution. The conclusion is that oviposition site choice must be under equally strong selection with egg size, egg number and the other hard components of life histories in order to generate and optimize locally adapted or ecologically specialized life history phenotypes, and must therefore, play a significant role in the evolution of life histories.

### INTRODUCTION

The study of life history in animals has a long and vigorous tradition, with the modern age of life history studies being ushered in by the classic papers of Cole (1954) and Lack (1947). Since that time, a principal focus of life history studies of both plants and animals has been the evolution of propagule size, propagule number, and the tradeoff between these two critical components of life histories (*e.g.*, Lack, 1947; Smith and Fretwell, 1974; Wilbur, 1977; see summaries in Roff, 1992; Stearns, 1992; Bernardo, 1996a). In these and most other studies of life history, emphasis has been placed on

what may be called "hard" life history components: phenotypic traits that can be directly affected by selection, *e.g.*, body size, number and size of offspring, age at maturity, etc. Because these phenotypic traits are rather obviously linked to fitness and are easily quantified, they have become the focus of life history theory. A more mechanistic formulation of life history theory defines life histories as a set of biological algorithms that translate the energy acquired by an organism into an allocation pattern that results in the observed life history phenotype upon which selection may act (Dunham *et al.*, 1989). Regardless of how life histories are defined or the theories formulated, the suite of characters that comprise a life history phenotype are presumed to have evolved under strong natural selection to optimize parental fitness *in specific habitats*.

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What is largely missing from current life history theory is the consideration of the role of behavior, principally female oviposition site choice, in the evolution of life histories. Behavioral ecologists have convincingly documented the role of behavior in determining fitness via sexual selection (Arnold and Duval, 1994). However, behavior has not been integrally incorporated into the study of life history evolution (Wilbur *et al.*, 1974). For oviparous organisms, the "how big" and "how many" components of life history so commonly studied are entirely dependent upon the "when" and "where" components so commonly ignored. Natural selection cannot produce locally optimized "hard" components of life history phenotypes without a consistent environmental context (whether invariant or variable).

A consistent environmental context can be achieved in one of four ways: first, the habitat may be uniform with respect to the environmental components that determine post-oviposition reproductive success; a possible example is mass spawning in marine invertebrates having planktonic larvae. Second, physiological/ecological tolerances of adults and larvae may be sufficiently similar that females may survive to oviposit only in the environment in which they can successfully produce replacements. Third, females may exhibit philopatry in oviposition, thus allowing selection to operate in a consistent environment (McPeck, 1989), as in many anadromous fishes and some amphibians. And, fourth, females may actively assess the relative suitability of potential oviposition sites and discriminate among them based on a set of criteria that have presumably evolved in concert with the other components of her life history phenotype (*e.g.*, Rausher, 1979 1983; Singer, 1984; Papaj and Rausher, 1987; Singer *et al.*, 1988, 1994; Resetarits and Wilbur, 1989). Because the first two mechanisms are unlikely in many systems, they can be viewed as somewhat special cases. Hence, in most systems only the last two mechanisms, philopatry and female oviposition site discrimination, remain as viable mechanisms for providing a stable environmental context in which the hard components of life histories

can evolve towards adaptive peaks. Here I focus primarily on oviposition site choice and return briefly to discuss the limitations of philopatry later.

The adaptive fine tuning that is presumed to shape the life history phenotype must simultaneously mold the behaviors associated with egg deposition; selection cannot optimize a life history for a specific habitat unless the behavior of females is constrained by selection to operate within that habitat. An implicit assumption of life history theory is that females place their optimized clutch of eggs in the appropriate habitats at the appropriate time. However, even females in simple environments face a bewildering array of potential sites for egg deposition, and these sites vary along an equally bewildering array of axes. If these breeding sites simply function as islands (in the biogeographic sense: MacArthur and Wilson, 1967) which are colonized by females as they are encountered and which have equal value in terms of potential reproductive output, then oviposition site choice should be of little consequence for life history evolution. If, however, breeding sites function as patches within a mosaic, each containing varying levels of resources and risk (Levin and Paine, 1974; Whittaker and Levin, 1977) then oviposition site choice should play a critical role in the evolution of life histories. I would suggest that the latter scenario is true for many oviparous species, because the variation among potential breeding sites typically involves factors, from variation in temperature (Seale, 1982; John-Alder *et al.*, 1988), to variation in host-plant chemistry (Rausher, 1981a; Feeney *et al.*, 1983) to variation in relative arrival times of colonists (Wilbur and Alford, 1985; Alford, 1989; Lawler and Morin, 1993), that profoundly affect their suitability for egg deposition and offspring development. Thus, given the potential impact of maternal oviposition site choice on offspring performance and survival (*e.g.*, Rausher, 1983; Papaj and Rausher, 1983; Singer *et al.*, 1988; Singer *et al.*, 1994), it is likely that oviposition site choice is under at least as strong selection as propagule size/propagule number (see Bernardo, 1996b). Indeed, because sensory and, es-

pecially, behavioral traits are less likely to be correlated genetically with the hard components of life history phenotypes than these hard components are to be linked genetically themselves, the components of oviposition site choice are less likely to be constrained. For behavioral traits at least, selection should act independently of (though in concert with) selection on hard components. Thus, an optimum combination of hard phenotypic characters and sensory/behavioral components is more easily attainable than the optimum combination of egg size and egg number, which are potentially subject to significant tradeoffs and genetic correlations (Smith and Fretwell, 1974).

#### A MODEL OF SELECTION ON OVIPOSITION SITE CHOICE

Anuran amphibians can deposit their eggs in a wide range of aquatic habitats. For many, including almost all temperate zone species, water is the minimum requirement for successful oviposition. Yet, the diversity of aquatic habitats in which anurans specialize, from temporary storm puddles to large, permanent lakes, or extensive eutrophic river swamps to oligotrophic mountain streams, suggest that all water is not equally suitable. A species that typically breeds in temporary ponds is unlikely to oviposit in a rushing stream, or, having done so, be expected to realize the same fitness. Clearly, there is some level of discrimination among sites, at least at that level. How fine is the level of discrimination? Insects can discriminate among sites across a surprisingly diverse range of environmental axes (see Rausher, 1983; Singer, 1984; Bernardo, 1996*b* for reviews), and oviposition decisions based on these axes can directly affect offspring performance and parental fitness (*e.g.*, Rausher, 1980, 1983). Some animals are clearly able to discriminate at a very fine level, presumably because the outcome strongly affects fitness. Selection has driven the evolution of the sensory capabilities necessary to discriminate along these axes (unless they existed before), and likewise driven the evolution of behaviors that act on that sensory information (*e.g.*, Rausher, 1978, 1981*a, b*; Fee-

ney *et al.*, 1983). What factors might be expected to influence offspring performance and parental fitness in anurans? For anura that breed in temporary ponds, hydroperiod is a critical determinant of reproductive success (Wilbur, 1984, 1987). The relationship between hydroperiod and reproductive success (fitness) is convex; ponds must hold water long enough for offspring to reach metamorphosis, but the longer the pond holds water, the greater the number and diversity of predators, at least until ponds become permanent and fish become established. At that point, reproductive success approaches zero for most temporary pond anurans.

Assume that a species has evolved to effectively utilize temporary ponds of short duration; that is, it lays relatively few large eggs that hatch into relatively large larvae that, in turn, grow rapidly and metamorphose at a small size. Presumably, the life history phenotype described is near the center of a normal distribution, which as a result of selection for success in temporary ponds has a relatively small variance. Within the range of pond types to which the species is adapted, the highest fitness for all phenotypes is near the mean of this distribution and drops off in either direction away from the mean. The initial distribution of oviposition sites available is illustrated in Fig. 1 (top). The four lefthand lower graphs Figures 1A–D (corresponding to the positions on the pond duration axis A–D) indicate the consequences of oviposition by the entire population in ponds of different duration. For duration A (very short duration), only females in the righthand tail of the distribution (corresponding to a phenotype of few, large eggs) produce clutches with characteristics that allow rapid growth and metamorphosis, and therefore produce metamorphs before ponds of duration A dry. Fitness is nonzero only for females in the solid portion of curve A, but is still lower for these females than in ponds nearer to the “optimum” duration (closer to B). For females in the dotted portion of curve A, fitness is zero in ponds of duration A. For individuals ovipositing in ponds of duration B, fitness is positive for all phenotypes. In ponds of duration C, that is, longer duration

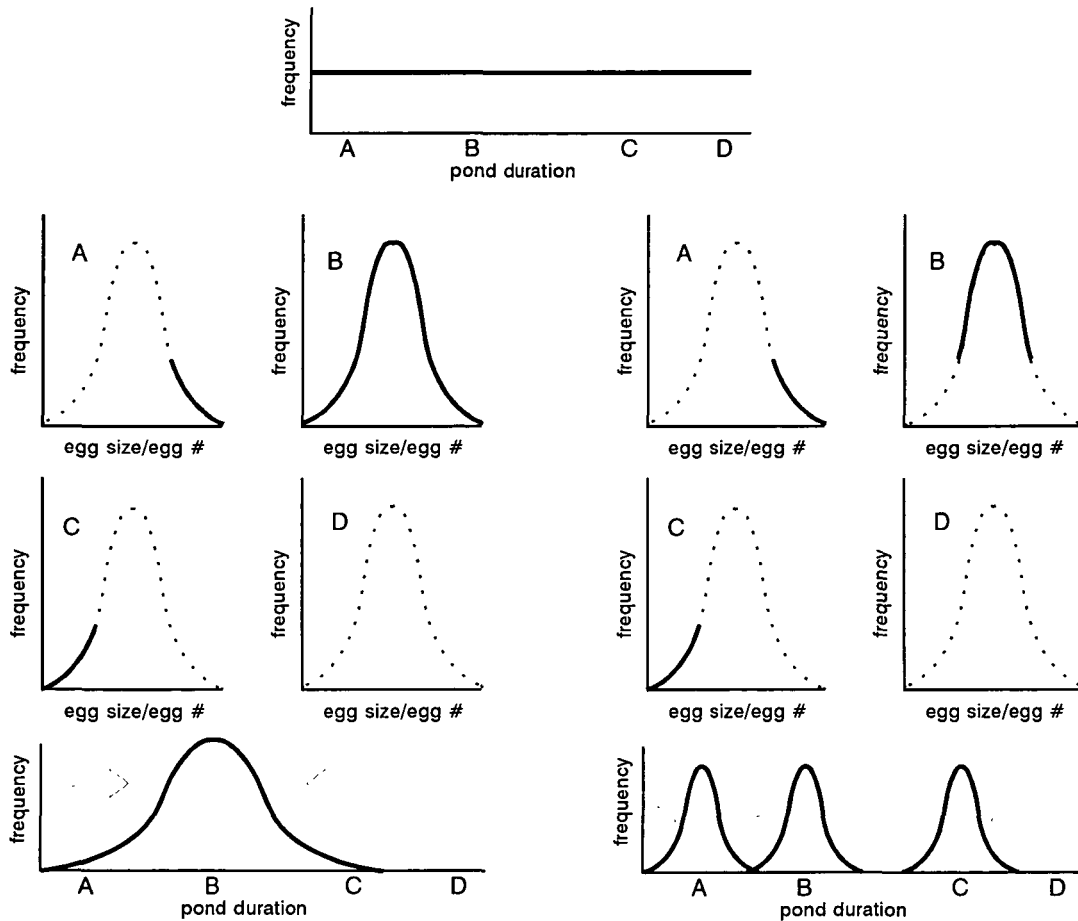


FIG. 1. A graphical model illustrating the importance of selection on oviposition site choice for local adaptation/ecological specialization of clutch phenotypes in a hypothetical frog. Arrows indicate direction of selection. The top panel illustrates the initial uniform distribution of oviposition along a gradient of pond duration (increasing from left to right): this is indicative of no oviposition site choice. The lefthand graphs illustrate the effect of selection when all extant clutch phenotypes (normal curves in A–D) have greater fitness in habitat B; the x axis (clutch phenotype) is represented as the ratio between egg size and egg number, so that the left tail of the distribution corresponds to many small eggs and the right tail few, large eggs). In ponds of duration A, only females in the righthand tail produce clutches with characteristics that allow metamorphosis before “A” ponds dry; fitness is nonzero only in the solid portion of curve A, but still lower than in ponds nearer B. Fitness is positive for all females ovipositing in ponds of duration B. In “C” ponds (longer duration ponds without fish), only the left hand tail of the distribution (curve C) has nonzero fitness, because the large number of predators present necessitates predator satiation. In permanent ponds with fish (D) fitness for all phenotypes is zero. Selection will act in the direction of the arrows in the left lowermost panel to narrow the range of oviposition sites. The right panel illustrates the effect of selection on oviposition site choice when A, B and C curve individuals each have greater fitness in the corresponding (A–C) habitat. Oviposition site choice will be under strong selection (graphs A–D in the righthand panel) to match clutch phenotypes to the appropriate habitat, resulting in a polymodal distribution of oviposition site preferences. See text for further details.

ponds without fish, only the left hand tail of the distribution (curve C), corresponding to a phenotype of large numbers of small eggs, has nonzero fitness. This is because of the large number of predators present,

necessitating predator satiation via large numbers of offspring to assure any offspring survival to metamorphosis. In permanent ponds with fish (D), fitness for all phenotypes is zero. The result of this sce-

nario is that selection will act in the direction of the arrows in the left lowermost panel of Figure 1 to narrow the range of oviposition sites used by this species.

If the assumptions are relaxed just a bit, such that the individuals with phenotypes illustrated in graphs A or C have greater fitness in ponds of duration A and C, respectively, than in ponds of duration B, then oviposition site choice will still be under strong selection (as illustrated in graphs A–D in the righthand panel), in this case to match clutch phenotypes to the appropriate habitat, as illustrated in the lower righthand panel. The result is a polymodal distribution of oviposition site preferences, in which clutch phenotypes are matched to the appropriate habitat, a scenario which could lead to population subdivision and potentially speciation. Fry (1996) discusses a relevant alternation mechanism for generating host/habitat specialization without such tradeoffs in fitness.

My example suggests that selection on oviposition site choice might be comparable, if not stronger, than on fine details of clutch phenotypes or other hard components of life history phenotypes. Selection cannot optimize reproductive allocation in a given habitat unless females oviposit there. A generalized strategy of ovipositing in a wide variety of habitats potentially sacrifices fitness maxima in one habitat for nonmaximized fitness across a range of habitats (Rausher, 1983); it is an inefficient compromise that would provide selection for the ability to discriminate among oviposition sites (e.g., Roosenburg, 1996). Oviposition behavior and the hard components of life history phenotypes must exist in a mutual feedback loop that should fine tune both behavioral and morphological/physiological components of the life history phenotype to maximize fitness. Females must match their life history phenotype to the appropriate habitat; unless they do, the evolutionary machinery brought to bear in adapting the hard components of life history phenotypes to specific habitats may be moot.

However, the way to begin an assay of the ability to discriminate among habitats is not to examine continuous variables such as

hydroperiod, which, of itself, is primarily a statistical property of a pond which may only be assayable post hoc, but to use bivariate, presence/absence characters. Thus, empirical tests for oviposition site choice should initially focus on such simple binomial choices. Predation and competition are important processes affecting temporary pond amphibians (e.g., Heyer *et al.*, 1975; Morin, 1983; Smith, 1983; Woodward, 1983; Wilbur, 1987; Fauth and Resetarits, 1991; Werner and McPeck, 1994). The composition of the temporary pond community profoundly affects the larval performance of most species. The larvae of the gray treefrog, *Hyla chrysoscelis*, are sensitive to the presence of predators, competitors and the density of conspecifics (e.g., Morin, 1983; Wilbur and Alford, 1985; Wilbur, 1987). In dealing with potential predators and competitors we would expect selection to be strong, as in the hydroperiod example, but the determination of suitability based on presence/absence of particular species should be more straightforward than judging pond duration.

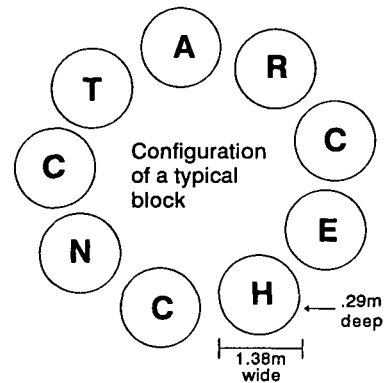
#### EXPERIMENTAL DATA

Henry Wilbur and I conducted an experiment (Resetarits and Wilbur, 1989) to determine whether females of Cope's gray treefrog, *Hyla chrysoscelis*, could discriminate among experimental ponds (wading pools) that varied in faunal composition and alter their oviposition behavior accordingly. The biology of *Hyla chrysoscelis* closely resembles the frog in my model. It is primarily a species of temporary or fish-free permanent ponds, having a relatively short larval period and being highly sensitive to both predation and competition (Morin, 1983; Wilbur and Alford, 1985; Wilbur, 1987; Fauth and Resetarits, 1991). Our assay was a single stage assay, that is, we tested oviposition responses only; a significant difference in egg deposition simultaneously signified an oviposition response and the implicit ability to discriminate on the basis of faunal composition. A negative result only provided information on the absence of oviposition choice, which could result from either a lack of preferences or a

lack of ability to discriminate along the axis being tested.

The primary focus of this experiment was the effects of oviposition site choice on the assembly of communities, so the number of eggs laid in a habitat was the critical variable of interest. Thus, we used the number of eggs laid in experimental ponds (wading pools) of varying faunal composition as our assay of oviposition site choice (Resetarits and Wilbur, 1989). From the perspective of actual oviposition behavior of females, a difference in the number of eggs laid in a pool could result from several mechanisms, including more females laying eggs in preferred pools than in avoided pools, each individual female partitioning her clutch among pools of differing faunal composition, or larger (older) females choosing preferred pools while the smaller (younger) females (presumably) erred by laying in avoided pools. While these different potential mechanisms are themselves interesting and important, they are not critical to the question that was asked, "Do females discriminate among oviposition sites with respect to the presence of potential predators and competitors." The logistics of managing this experiment precluded detailed investigation of exact behavioral mechanisms underlying distribution of eggs among treatments, but it constituted a rigorous test of whether female gray treefrogs discriminated among oviposition sites. All things being equal, more metamorphs should emerge from preferred pools than from avoided pools. If eggs were not distributed randomly with respect to treatments, selection presumably had acted and was continuing to act on oviposition site choice.

Five arrays containing nine wading pools each (Fig. 2a) were set in an old field surrounded by forest at the Duke University Zoology Field Station (Fig. 2b). The experiment was run for four weeks, dismantled, set up again using the same locations for each array, and run for another three weeks. An individual array comprised a block in the design, meaning that a block consisted of both a temporal and a spatial component. Each block of nine pools contained one replicate of each of six treatments plus three



Block locations - Duke Zoology Field Station.

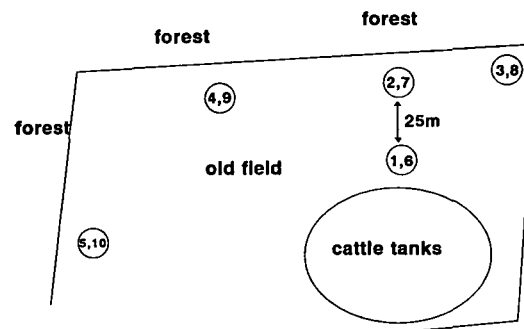


FIG. 2. a). Configuration of a typical block in the oviposition site choice experiment. Letters indicate treatments: A = *Ambystoma*, R = *Rana*, C = control, E = *Enneacanthus*, H = *Hyla*, N = *Notophthalmus*, T = *Traema*. b). Schematic of the experimental site showing the spatial distribution of blocks within the experiment. 1-5 refer to the first run of the experiment and 6-10 the second run. All cattle tanks were covered at night and did not serve as alternative oviposition sites to the wading pools.

replicates of a control (Fig. 2a). Each treatment consisted of the addition of a single species into otherwise identical pools. Species added were either predators of *H. chrysosecelis* (adult newts *Notophthalmus viridescens*, larval salamanders *Ambystoma maculatum*, larval dragonflies *Traema carolina*, and adult dwarf sunfish *Enneacanthus chaetodon*), or competitors (larval bullfrogs *Rana catesbeiana*, or larval conspecifics). Controls contained only the pond litter which was added to all pools. For each predator species the combination of predator size and number were kept low to minimize effects of actual egg consumption

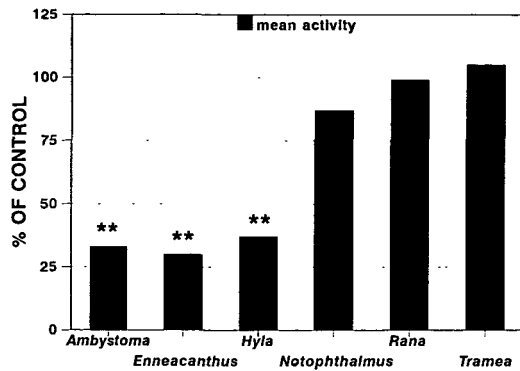


FIG. 3. Results of the oviposition site choice experiment for the principal variable of interest, mean activity (see text). Double asterisks indicate treatments significantly different from the controls at the  $P < .01$  level using Dunnett's procedure. The other treatments were not significantly different ( $P \gg .05$ ) from the controls.

(see Resetarits and Wilbur, 1989). Pools were assayed each morning and eggs removed and counted. More than 145,000 eggs were deposited in the pools during the experiment. Data were analysed using analysis of variance; Dunnett's procedure, which compares all treatments to a control, was used for hypothesis testing (Dunnett, 1955; Steele and Torrie, 1980).

This experiment provided striking evidence that female *H. chrysoscelis* discriminate among potential oviposition sites (Fig. 3), choosing sites that maximize their potential reproductive success. Mean activity (mean number of eggs laid in a pool [including zero values] on nights when any pool in its block received eggs) was the principal response variable; it measures the attractiveness of a treatment relative to all other treatments with a given block (Resetarits and Wilbur, 1989). The results indicated that the frogs perceived two categories of treatments, those that were equivalent to controls (preferred pools) and those that received significantly fewer eggs than controls (avoided pools). Clearly, this population of *Hyla chrysoscelis*, via some mechanism of discrimination (probably chemosensory: Petranksa *et al.*, 1987) and based on some criterion (a) of oviposition site choice (presumably expected larval performance), distributed its eggs in a non-random manner with respect to predators

and competitors. The three species that were avoided were two predators, *Enneacanthus* and *Ambystoma*, and larval conspecifics, *H. chrysoscelis*. Pools containing *Notophthalmus*, *Tramea*, and *Rana*, along with the controls, were preferred sites. The potential reasons for this dichotomy are discussed in detail elsewhere (Resetarits and Wilbur, 1989), but relate primarily to three factors: the strength of the potential negative impacts (selection), the reliability of current presence/absence information for predicting presence/absence during the period of larval development, and likelihood of being able to avoid a species.

In the same experiment, females also showed preferences among the spatial locations indicated in Figure 2b, and those preferences changed between the first and second runs of the experiment (Resetarits and Wilbur, 1991), probably based largely on temperature (unpublished data). What is most interesting is that, although male choice of calling site and female choice of oviposition site largely corresponded with respect to treatments (faunal composition) the correspondence breaks down with respect to locations. Females choose locations largely independent of the size of the chorus associated with that location, suggesting that, for *Hyla chrysoscelis*, maximizing the quality of an oviposition site may be more important to females than maximizing the quality of the mate obtained (Resetarits and Wilbur, 1991). This further underscores the potential importance of oviposition site choice and its capacity to shape life history evolution.

#### IMPLICATIONS AND APPLICATIONS

We can now come full circle and ask, "What are the consequences of such behaviors for life history evolution?" In both the hypothetical and real frog, the consequences of ovipositing in ponds containing fish is reproductive failure. But suppose that there is a clutch configuration that allows offspring to recruit from ponds with fish, and further, that this configuration is quite different than the optimum for fishless, temporary ponds. The evolutionary "decision" that the hypothetical frog faces is between a generalist strategy that allows a certain,

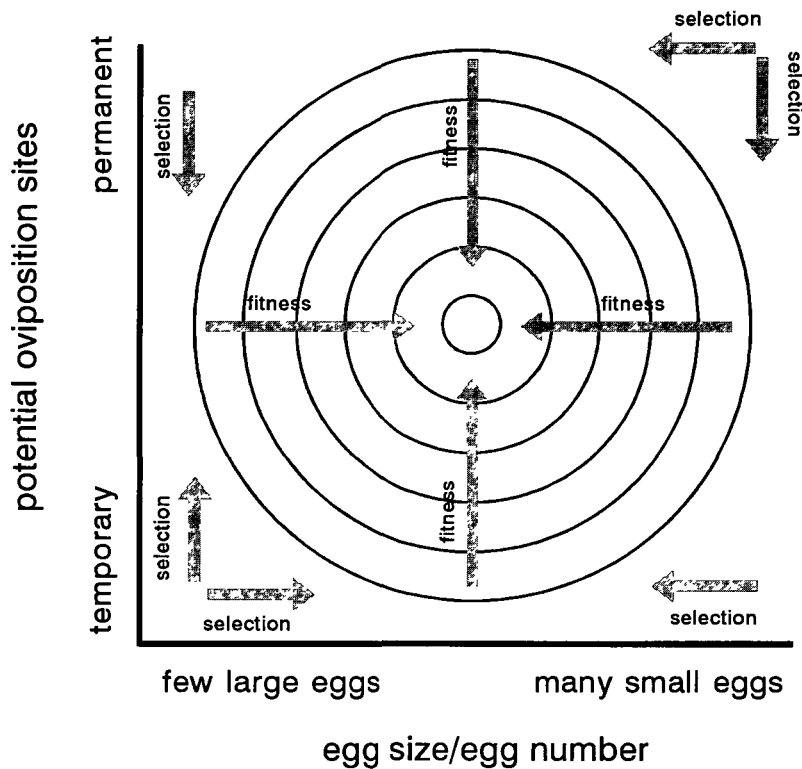


FIG. 4. Selection surface relating selection on oviposition site choice along a gradient of pond permanence to selection on reproductive allocation pattern (represented by egg size-clutch size parameters). Concentric circles represent topographic fitness lines, with fitness increasing in the direction of the fitness arrows. The greater the magnitude of the fitness advantage gained by fine tuning clutch phenotypes to a specific habitat (that is, the steeper the east and west slopes of the fitness peak), the stronger the concomitant selection on oviposition site choice (that is, the steeper the north and south slopes will be). The height a population can climb on the adaptive peak is dependent on selection being able to act simultaneously on both the physical (*e.g.*, clutch phenotype) and behavioral (*e.g.*, oviposition site choice) components of life history phenotypes.

albeit highly reduced, success (fitness) in both habitats versus a specialist strategy that confers high fitness in one or the other habitat. The specialist strategy, observed in many species of amphibians (*e.g.*, Smith, 1983; Wilbur, 1984; Skelly, 1994; Werner and McPeck, 1994), cannot evolve and be maintained without concomitant selection on female behavior to restrict oviposition to those sites which are suited to the hard life history phenotype that confers high fitness as a specialist. Figure 4 illustrates simultaneous selection on these different components of the reproductive strategy, the kind of selection necessary to fine tune life histories to specific environmental conditions. Oviposition site choice must be under equally strong selection with egg size, egg

number and the other hard components of life histories in order to generate and optimize locally adapted or ecologically specialized life history phenotypes. If a highly variable environment favors the evolution of phenotypic plasticity in life history phenotypes, then oviposition site choice is still required to match realized phenotypes to the appropriate habitats, unless the habitat directly drives the development of the phenotypes and restricts oviposition to the appropriate sites.

A scenario which in theory would allow local adaptation in hard characteristics without oviposition site choice is one in which successful reproduction can only occur in a restricted set of habitats, but oviposition is random with respect to habitats



and the distribution of "hard" life history phenotypes is unrelated to oviposition behavior. Here only the outcome of oviposition in suitable habitats would matter, and life history could be optimized without any oviposition site choice being involved. However, selection would be extremely strong for the ability to discriminate among sites and for limiting oviposition to only those sites which were suitable (fitness is non-zero). In this case the random oviposition strategy would be highly invasible and unstable unless the sensory machinery required for site discrimination was simply evolutionarily unavailable.

What about philopatry as a mechanism allowing local adaptation/ecological specialization? While philopatry certainly has potential for facilitating adaptation of life histories to a consistent ecological context (McPeck, 1989), it also imposes serious limitations on dispersal capabilities and the ability to colonize or recolonize habitats. Thus, while clearly a potentially important mechanism for many organisms, it cannot replace interactive choice for species in which dispersal is important or for those that occur in temporally variable habitats.

How important is oviposition site choice? A brief survey suggests that when we look for evidence of oviposition site choice, which hasn't been often for most taxa, we often find it. The evidence from phytophagous insects and insect parasitoids is the most extensive and compelling, indicating tremendous potential to discriminate along a diverse suite of environmental axes (Rausher, 1983; Singer, 1984; Bernardo, 1996b). However, oviposition site choice has been virtually ignored for aquatic insects. There is evidence that mosquitos and phantom midges (*e.g.*, Chesson, 1984; Petranka and Fakhoury, 1991; Richie and Addison, 1992; Richie and Laidlaw-Bell, 1994), as well as aquatic beetles (hydrophilidae: Resetarits, unpublished data) respond to biotic or abiotic factors in the environment, but the broader ramifications have been largely ignored by aquatic ecologists (Resetarits and Wilbur, 1989; Petranka and Fakhoury, 1991). For vertebrates, Roosenburg (1996) provides evidence that turtles match the size of the eggs they are carrying to the tem-

perature of nest sites and I have provided evidence from a single species of frog (Resetarits and Wilbur, 1989) that oviposition decisions are made on the basis of the faunal composition of ponds. Other amphibians may also choose sites based on expected larval performance based on both biotic and abiotic factors (frogs: Howard, 1978; Seale, 1982; Waldman, 1982; Banks and Beebee, 1987; Magnusson and Hero, 1991; Hopey and Petranka, 1994; Petranka, et al., 1994. salamanders: Kats and Sih 1992). As counter-examples, McPeck found that *Enallagma* damselflies did not show an oviposition response to the presence or absence of fish, in spite of the role of fish in their distribution (McPeck, 1989) and Herbert and Fauth (personal communication) found no evidence of an oviposition response by the salamander *Desmognathus fuscus* to presence of predators.

While documentation of oviposition site choice is not extensive for most groups of egg-laying animals, the available evidence is compelling. The potential importance of oviposition site choice should encourage the incorporation of behavioral components of life history phenotypes into both theoretical treatments and empirical studies of life history evolution. Of equal importance (though beyond the scope of this paper) are the consequences of oviposition site choice for the population biology of individual species and the assembly of natural communities (Resetarits and Wilbur, 1989, 1991; Petranka and Fakhoury, 1991; Resetarits, 1995).

#### SUMMARY

Where a female places her annual (or lifetime) reproductive investment can be as important as how that investment is packaged or the quality of mate she obtains, two components of reproductive success that have received a great deal of attention in studies of life history and reproductive biology. The suitability of an oviposition site affects hatching success, larval performance, recruitment and consequently, parental fitness; therefore selection should be strong for the ability to discriminate and choose oviposition sites on the basis of expected larval performance. This is especial-

ly true when other aspects of the "hard" life history phenotype, such as egg size and egg number, represent an adaptation to a specific set of conditions found in only a subset of available sites for oviposition and offspring development, *i.e.*, when life histories represent local adaptation or ecological specialization. Local adaptation or specialization depends on oviposition site choice to attain the "optimum" life history so often invoked in theories of life history evolution.

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