

A Classification of Alternative Reproductive Behaviors and Methods for Field-testing ESS Models¹

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SYNOPSIS. A number of superficially similar evolutionary phenomena are often lumped together as "alternative reproductive behaviors (ARBs)." Several authors have previously organized the broad array of reproductive alternatives by their relation to ESS theory. Because such an organizing scheme begs the question of how much ESS models can contribute to our understanding of ARBs, I suggest a different scheme—devoid of ESS connotations—which classifies alternatives according to whether they represent genetic differences between individuals (genotypic *versus* phenotypic alternatives), whether the alternatives can be expected to manifest equal or unequal fitnesses (isogynous *versus* allogynous alternatives), and whether individuals may switch back and forth between alternatives (reversible *versus* irreversible alternatives). I point out that plausible selective regimes other than frequency-dependence can maintain genotypic alternatives, and that explanations for the maintenance of phenotypic alternatives usually can be examined only theoretically. I also urge more rigor in the field-testing of ESS models, review criteria which putative ESSs should meet, and suggest a statistical approach for evaluating evidence with regard to equality of fitnesses of reproductive alternatives.

INTRODUCTION

Although alternative reproductive behaviors (ARBs) have been documented for decades (*e.g.*, Morris, 1951), they became the focus of particular interest after the development of the theory of evolutionarily stable strategies (ESSs) (Maynard Smith and Price, 1973; Maynard Smith, 1974). A common conclusion of early ESS modelling was that a stochastic mixture of two "pure" behavioral strategies could result in an uninvadable evolutionary equilibrium (Maynard Smith, 1974; Maynard Smith and Parker, 1976). Thus these models presented plausible scenarios for the coexistence of two or more forms of reproductive behavior within a single population. Following Gadgil (1972) and Gadgil and Taylor's (1975) conceptual lead, a succession of theoretical papers used ESS analysis specifically to probe conditions favorable for the evolution and maintenance of ARBs (Brockmann *et al.*, 1979; Hamilton, 1979; Gross and Charnov, 1980; Rubenstein, 1980) and empirical evidence

was marshalled in support of these analyses (Brockmann *et al.*, 1979; Hamilton, 1979; Krebs and Davies, 1981; Gross, 1982).

ESS theory has now become a rapidly established new orthodoxy in behavioral ecology. But its general acceptance derives more from the intuitive appeal of its logic than from a large body of supporting evidence. The study of ARBs affords an opportunity to examine rigorously the relevance of ESS theory to the maintenance of behavioral variation. However there are two potentially unfortunate consequences in prematurely linking empirical ARBs with ESS theory. First, the multiplicity of functionally distinct types of ARBs is easily overlooked. ESS theory is not equally applicable to all forms of behavioral variation (Dawkins, 1980; Dominey, 1984), and attention may be unduly concentrated on only a few types. Second, the reflexive invocation of ESS explanations for the widespread existence of ARBs may cause, indeed has caused, the evidence to be treated rather casually, which is fair neither to the theory nor the phenomena. Consequently, after a brief digression to define ARBs, I want to suggest a taxonomy of them which is devoid of ESS connotations. My hope is that such a classification will allow discussion of variation in reproductive behavior without implying the

¹ From the Symposium on *Alternative Reproductive Tactics* presented at the Annual Meeting of the American Society of Zoologists, 27–30 December 1982, at Louisville, Kentucky.

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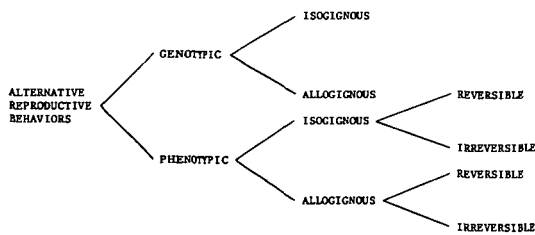


FIG. 1. A taxonomy of alternative reproductive behaviors. Definitions and examples given in the text.

behavior does, or does not, conform to the expectations of ESS analysis. Finally, I wish to consider special problems in the methodology of field-testing ESS models.

WHAT ARE ARBs?

A startling variety of behavioral phenomena have been called ARBs. However, what makes them distinctive is not clear, because at some level no two individuals will be identical in all aspects of reproductive behavior. There will be inevitable differences, for instance, in tenacity of courtship, time and place of parturition, degree of parental care, or any of a host of other variables. When does unavoidable variation in reproductive behavior transmute into those discrete categories which might be termed "alternatives"? Even assuming that certain reproductive behaviors are discrete alternatives, if their respective consequences are indistinguishable, should they be considered ARBs? For instance, the stripe-backed wren, *Campylorhynchus nuchalis*, sometimes reproduces in stick nests appropriated from thornbirds, *Phacellodomus rufifrons*, and sometimes builds its own grass nest in mistletoe clumps. There is no evidence that nest-type affects individual reproductive success or mortality, or that certain birds specialize in either nest type (K. N. Rabenold, personal communication). The evolutionary implications of this variation in nesting habits are unclear and probably inconsequential. Therefore, to limit somewhat the scope of this paper and focus on the key problem of how they are maintained in evolution, I will provisionally define ARBs as *any discontinuous variation in an aspect of reproductive behavior among one sex in a single popu-*

lation with associated differences in the behaviors' costs and/or benefits. Admittedly, this definition excludes certain intriguing and well-documented cases such as the distribution of male dung fly (*Scatophaga stercoraria*) residence times around fresh cow pats, because the flies exhibit a continuum of residence times (Parker, 1970, 1974). However, for purposes of comparative analysis, it seems more straightforward to consider discrete behavioral alternatives separately.

A TAXONOMY OF ARBs

Several authors have already recognized the need for organization of the multiplicity of described ARBs (Alcock, 1979; Davies, 1982; Dunbar, 1982; Maynard Smith, 1982). In suggesting yet another classification scheme, I want not only to present the phenomena divested of their relation to ESS theory, but also to emphasize two factors critical to understanding the selective regimes under which ARBs will be maintained: (1) whether the alternatives represent underlying genetic differences between individuals, and (2) whether the alternatives are expected to confer equal fitnesses on individuals manifesting them. To the extent that this classification is successful, I would hope it might assist fieldworkers in clarifying their research goals.

A primary distinction within the array of ARBs is between what I call *genotypic* and *phenotypic* alternatives (Fig. 1), which are defined according to whether behavioral differences between individuals derive from genetic differences. It is important to note that this distinction does not address the extent to which any specific behavior is programmed by the genes, only whether behavioral differences between individuals stem from genetic differences. Thus, I consider the female chigger wasp reproductive alternatives "dig a burrow" and "enter an existing burrow" phenotypic, despite evidence suggesting that the relative probabilities of "dig" and "enter" decisions are genetically hardwired (Brockmann and Dawkins, 1979), because all females are similarly wired. Also note that "genotypic" ARBs can result from quantitative as well

TABLE 1. Possible mechanisms for the maintenance of genotypic ARBs *

Isogynous ARBs:	Negative frequency-dependent selection Disruptive selection
Allogynous ARBs:	Temporally oscillating selection Spatially oscillating selection Heterozygote superiority

* See text for explanation of terms.

as Mendelian genetic variation, and that the genes' influence on behavior may be direct or indirect. For example, suppose decisions to defend territory as opposed to parasitize other males' territories is a strict function of male body size. Body size, when heritable, is generally a trait with additive genetic variance, but selection on body size in this instance would have indirect and dichotomous behavioral consequences.

Genotypic ARBs

Considering its importance for understanding the maintenance of behavioral variation, there has been surprisingly little research on the genetics of ARBs. The only published study is Cade's (1981) successful attempt to select for high and low calling frequencies among male field crickets (*Gryllus interger*). The paucity of genetic experimentation is unfortunate for two reasons. First and foremost, putative explanations for the maintenance of genetic polymorphisms are often amenable to experimental confirmation. If frequency-dependent selection, for example, is invoked as the factor stabilizing relative morph frequencies in nature, those frequencies could be experimentally altered to determine whether morph fitnesses changed in the expected direction. Such an experimental approach is more straightforward than inquiring why a single existing genotype which codes for behavioral dimorphism is superior to hypothetical alternative genotypes—a problem faced by workers investigating "phenotypic" ARBs. Second, only by understanding the genetics of behavioral alternatives can we sensibly speculate on their evolutionary stability. Thus, if field studies revealed that territory-defending male beetles achieve, on average, five times the reproductive suc-

cess of satellite males, our interpretation as to the persistence of satellite behavior would depend on its underlying genetics.

Often, controlled selection experiments like those performed by Cade (1981) are impossible to carry out, because the animals in question cannot be reared in captivity. But even in these instances, less direct methods of heritability estimation such as measurement of repeatability (Ehrman and Parsons, 1976) can be used.

Even though particular ARBs do represent more or less stable genetic polymorphisms, the lifetime fitnesses associated with the morphs do not have to be equivalent (Haldane and Jayakar, 1963) (Table 1). It is important to emphasize this point, because it is often overlooked as a result of the current interest in ESS analysis. ESS models depict frequency-dependent selection, equilibrating where fitnesses of the behaviors are equal (*e.g.*, Maynard Smith, 1974). The general popularity of the ESS concept has consequently intensified the search for equal fitnesses in nature.

To stress that fitnesses need not be equal, I have divided genotypic ARBs into two categories, which I call isogynous and allogynous (*gignō* = to produce, *L.*) to describe alternatives with the same and different fitnesses, respectively. There are two mechanisms by which isogynous ARBs may be maintained: negative frequency-dependent selection and disruptive selection (Table 1). Let me distinguish between the mechanisms using some hypothetical characteristics of Cade's field crickets. As mentioned previously, variation in the frequency of calling among male field crickets represents genetic variation (Cade, 1981). Females are attracted to male calls, but noncalling males often linger near callers

and attempt to mate with approaching females (Cade, 1979). Suppose there were only callers and noncallers—no intermediate types. If the selective advantages of calling and noncalling were primarily a function of their relative frequency in the population, then a stable ratio of callers and noncallers could only be achieved by negative frequency-dependent selection. Plausibly, if calling males were much more common than noncallers, each caller would attract few females, so that a roving noncaller might “steal” more copulations than the average caller would garner. Thus the relative frequency of noncallers would increase. On the other hand, if calling were rare and noncalling common, each caller would attract numerous females and would likely achieve more copulations than an average noncaller, leading to an increase in calling. If the selective advantages of calling and noncalling were not primarily influenced by their relative frequency, their ratio could be stabilized by disruptive selection. For instance, if a certain proportion of females chose to mate only with noncallers and the rest only with callers, the ratio would be stabilized as long as there were no selection on female mating preference.

Genotypic ARBs may persist even though they are allogynous (Table 1). If one type of behavior is at a selective advantage at low population density and the other at high population density, for example, and population fluctuations occur at intervals of every few generations or less, then both behaviors will be maintained through temporally oscillating selection. Similarly, certain reproductive behaviors may seesaw in selective value as a function of the habitat in which they occur. In coarse-grained environments (Levins, 1968), dispersal between patch-types can maintain polymorphisms via spatially oscillating selection. Finally, population geneticists have shown that overdominance, or heterozygote superiority, can preserve genetic polymorphisms (Falconer, 1960).

To date, most discussions of ARBs emphasize ESS explanations (Hamilton, 1979; Rubenstein, 1980; Dawkins, 1980; Krebs and Davies, 1981). In discussing

mechanisms for the allogynous maintenance of behavioral variation, I only mean to stress that other sorts of explanations than ESS theory are plausible and should not be prematurely dismissed by fieldworkers. It is instructive that a “classic” case of behavioral dimorphism, the ruff (*Philomachus pugnax*), gives evidence that factors other than negative frequency-dependence may be at work.

Male ruffs manifest one of three broad plumage color types (van Rhijn, 1973) which does not change after sexual maturity (Hogan-Warburg, 1966; Shepard, 1975). Primarily dark males contend for display territories on the leks where ruffs breed. Primarily white males assume satellite positions in the territories of dominant males who will tolerate them. Satellites may obtain some matings when the territory resident is mating with another female or is preoccupied with a potential intruder. Males with plumage of intermediate color may assume either role (van Rhijn, 1973).

The genetics of plumage coloration is unknown, but evidence, including the facts that morph ratios conform to the same apparent Hardy-Weinberg distribution in Holland and Sweden (Table 2) and simple Mendelian control of plumage dichromatism is known in other birds (O’Donald, 1980; Cooke and Cooch, 1968), suggests plumage types are largely controlled by two alleles at a single genetic locus. Given this simple genetic basis, it seems perfectly conceivable that the behavioral flexibility associated with intermediate plumage color (*i.e.*, the putative heterozygote) may allow that morph to best adapt to local conditions. There is evidence that the relative mating success of satellites and dominants alters with the number of males on the lek (Hogan-Warburg, 1966) and time of year (van Rhijn, 1973), so behavioral flexibility could be an advantage.

Both density-dependent and negative frequency-dependent selection have also been hypothesized to account for maintenance of this polymorphism (Hogan-Warburg, 1966; van Rhijn, 1973), so clearly the situation is far from understood. However it behooves fieldworkers to bear in

mind the variety of mechanisms which can maintain genotype ARBs.

Phenotypic ARBs

The bulk of ARBs reported to date do not derive from genetic differences between individuals. Observed alternatives are simply manifold expressions of basically one behavioral genotype. I call these "phenotypic" ARBs, regardless of the degree to which genes program individual behavior because it will be programmed to the same degree for all individuals. The critical issue in understanding the evolution and maintenance of phenotypic ARBs is why the existing genotype has not been replaced by one or more different genotypes, *i.e.*, a genotype more (or less) responsive to environmental circumstances, or one responsive at different thresholds. However since competing genotypes do not actually exist, it will always be difficult to confirm or confute explanatory hypotheses. In this sphere modelling has been most useful in evolutionary biology. Modelling allows, within the assumptions of the specific model in question, exploration of conditions under which the existing genotype ought to be superior to a range of theoretical genotypes. Data may then be gathered to determine whether the conditions predicted by the model indeed exist in nature.

In organizing phenotypic alternatives, I have used two criteria which I feel will be most useful to fieldworkers. First, are the alternatives isogynous? Second, are they reversible? That is, can individuals switch back and forth between alternatives within their lifetime? Combining the two criteria, there are four classes of phenotypic ARBs.

Isogynous, reversible

In this class, alternatives are isogynous in the sense that an individual achieves the same expected fitness during the time he is exhibiting one behavior as when exhibiting the other. Note that the classification ignores whether switching from one alternative or the other is stochastic or depends upon environmental conditions. Generally though, it may be expected that switching between isogynous alternatives will be

TABLE 2. Possible genetics of ruff plumage coloration.*

	Dark	Light	Inter- mediate	P (from χ^2)
Hogan-Warburg (1966) (analyzed by van Rhijn, 1973)				
Observed	79	36	102	>0.95
Predicted	78.1	34.7	104.2	
Shepard (1975)				
Observed	7	5	11	>0.90
Predicted	8.3	3.7	11	

* The underlying model is a Hardy-Weinberg distribution of two codominant alleles at a single locus. Assumed allele frequency (best fit to Hogan-Warburg data): dark = 0.6, light = 0.4.

environment-independent, because if short-term environmental fluctuations spur switching, it is probably to a superior option.

A well-documented case of this class of ARB is the nesting behavior of female digger wasps, *Sphex ichneumoneus* (Brockman and Dawkins, 1979; Brockmann *et al.*, 1979). Females deposit eggs in underground burrows provisioned with paralyzed katydids. Sometimes females dig their own burrows and sometimes they enter and use burrows abandoned by others. There is no statistically significant tendency for certain individuals to specialize in digging or entering, and the decision to do one or the other is independent of female history, her size, or the time of the season. In one of two populations studied, 59% of females' decisions were "dig" and 41% "enter," yielding approximately equal reproductive success.

That there are not more described cases of condition-independent ARBs is not surprising. For logistical reasons, gathering the relevant data is difficult. More importantly, natural selection would seemingly most often favor adaptations allowing individuals to modify their behavior in response to short-term changes in local conditions. In fact, the second population of digger wasps studied by Brockmann *et al.* (1979) showed that 84% of wasp decisions were "dig," even though that alternative was significantly less profitable in reproductive reward. West-Eberhard (1979) suggests that condition-independent systems are likely

to occur only when individuals have no way to assess the appropriateness of switching from one alternative to another.

Isogynous, irreversible

In this category, once individuals assume behavioral roles they cannot change to alternative roles. Yet the roles, on average, provide equal reproductive rewards. The only way to distinguish between these ARBs and genotypic ARBs is by genetic experimentation (Maynard Smith, 1982). If the specific reproductive alternative individuals eventually assume is not determined by amount or kind of parental care, then genetic experimentation is the only way to identify where selection is acting to equalize fitnesses. If the ARBs are genotypic or derive from type of parental care, then selection is acting on parents. If not, then selection is acting on individuals' abilities to assess the reproductive environment while they are still immature, then assume the alternative which best suits that environment.

A possible example of this type of ARB is the bluegill (*Lepomis macrochirus*) in which evidence suggests the roles of "sneak" and "parental" males are irreversible and achieve equal fitnesses (Gross, 1982), yet preliminary genetic experiments indicate the roles are not based on genetic differences (Dominey, 1984).

Allogynous, reversible

This category of ARBs should be common when reproductive roles do not result from morphological specialization and when environmental contingency can alter an adult's reproductive competitive ability. Selection should act to refine individuals' abilities to determine the best option available to them. For instance, yearling male bullfrogs (*Rana catesbeiana*) usually employ satellite mating behavior because their small size makes it unlikely they will be able to acquire a good territory. Yet in a year when larger males were rare, yearlings became territorial, and their reproductive success increased accordingly (Howard, 1981).

Likewise, male *Panorpa* scorpionflies

alter their mating behavior according to short-term changes in prey availability (Thornhill, 1981). Females prefer to mate with males bearing dead arthropods, yet if prey are scarce, males can secrete a salivary mass which females may consume during mating. In the worst case—that male nutritional state makes impossible the secretion of a salivary mass—males attempt forced copulations. Reproductive rewards are highest for males with arthropods, lower for males with salivary masses, and lowest for males attempting forced copulations.

Allogynous, irreversible

When reproductive competition is intense (that is, variance in reproductive success is high), and past or present environmental conditions can cement an individual into a single reproductive role for life, this category of ARBs is expected to be common. It should be especially common in insects, because they do not molt after maturation, hence are fixed in their body size and form. A conceivable example is the male dimorphism of the dynastine beetle, *Podischnus agenor* (Eberhard, 1982). One morph is large, has well-developed horns used in fighting, and is active at the peak female availability. The other is small, has poorly-developed horns, emerges early, and is rare by the time of peak female abundance. No genetic evidence is available, but Eberhard considers it unlikely that the dimorphism is a genetic one, because the genes for body size, horn size, and emergence time would have to be very tightly linked. (There are no small males with large horns and late emergence, or large males with small horns and early emergence.) Furthermore, there is an insect precedent in nutritional control of male dimorphism (Kuhl, 1928, cited in Eberhard, 1982), and larval food availability is known to affect adult size and morphology in many insects (e.g., Wilson, 1971).

The evolution and maintenance of these allogynous ARBs would stem from selection on the parents, even though there is no parental care (females of this species oviposit in the soil and larvae feed on humus). Imagine an ancestral population

in which larval nutrition determined adult body size and male body size was highly correlated with success in intense reproductive competition. Because of chance variation females all have about the same expected distribution of offspring body sizes. If there is a male size threshold below which expected male reproductive success is vanishingly small, then any mutation which would increase the small males' chances to reproduce would be expected to spread, because females bearing that mutation would have greater expected fitness than those without it. Such a mutation might divert energy from fighting apparatus of small males and use it to speed development, so they might emerge when intrasexual competition is reduced.

On the other hand, adults of species with parental care can presumably affect the distribution of available nutrition among their offspring. It is conceivable that some optimum relationship between offspring number and total nutrition available will result in a bimodal distribution of parental investment. This intriguing notion was advanced by Alcock *et al.* (1977) for the anthophorid bee, *Centris pallida*, a species in which males exhibit irreversible ARBs that are size-dependent. Large males patrol areas where females are likely to emerge and often fight for access to newly emerged virgins. Small males tend to hover near areas where unmated females are likely to fly. Every indication is that patrollers' reproductive success is considerably greater than hoverers'. Females control body size of their offspring by the amount of pollen and nectar they place in the brood cell. Unfortunately, it is not known how individual females allocate their resources among brood cells. But a study examining resource distribution in this species would greatly enlarge our understanding of the maintenance of irreversible ARBs.

Maintenance of allogynous ARBs, whether or not they represent genetic differences between individuals, can always be reconciled with individual selection if we consider that selection is operating on parents. However, whether evolution has achieved the optimal allocation of behav-

ioral alternatives according to some specific model is another question. This question has most commonly been addressed by ESS analysis.

TESTING ESS MODELS

ESS theory, because some models predict equilibria which include a mixture of behaviors, and because negative frequency-dependence often seems a necessary consequence of behavioral polymorphism associated with intense reproductive competition, is the most common analytical tool for trying to understand ARB evolution (Brockmann *et al.*, 1979; Hamilton, 1979; Dawkins, 1980; Gross and Charnov, 1980; Rubenstein, 1980; Parker, 1982). Owing largely to the intuitive plausibility of the structure of many models and the conclusions reached, critical empirical examination of ESS models has been remarkably rare. In the following section, I would like to make some suggestions as to how the models might be tested with more rigor.

A first consideration is what does "testing ESS models" mean? In a recent paper, Davies (1982) states "... we are not using the field data to 'test ESS theory.' ... If we collect good data that show two strategies have different success, this does not mean that ESS theory is wrong." Davies is not implying ESS theory is unfalsifiable, but that the ESS concept is only an analytical tool for solving evolutionary models. However, it would seem to me that field data should be used to determine whether the ESS concept is relevant to our understanding of how evolution works, as supported by empirical phenomena. In this sense, field data are testing *the applicability of ESS theory*.

Two aspects of ESS modelling to date invite caution as to the general applicability of the approach. First, the models are not genetic models, *per se*, rather analytically simpler approximations of genetic models. Specifically, reproduction is assumed to be asexual. Simple one locus (Maynard Smith, 1981) or multilocus (Slatkin, 1979; Eshel, 1982) genetic models assuming no inbreeding usually reach the same ESS as asexual models (Maynard

Smith, 1982). However the models all assume their genetic structures obey Fisher's fundamental theorem of natural selection. It is now generally acknowledged that Fisher's theorem is mathematically false for most multilocus genetic systems (Karlín, 1975; Eshel, 1982). Therefore, until we know more about the genetics of behavior, it is difficult to assess the significance of the asexuality assumption.

A second assumption is that population size is infinite. In finite populations, some degree of inbreeding is inevitable. ESS modelling of the effects of inbreeding on a sexual population has proved difficult (Maynard Smith, 1982). Also Riley (1979) has shown that ESSs derived in these infinite population size models are often not stable in finite population models. The few available data on the sizes of natural populations suggest that, at least for vertebrates, populations may often be smaller than 100 individuals (Wilson, 1975).

Given the potential complications arising from the above assumptions, it seems advisable to approach empirical investigations of the predictions of ESS modelling with maximal rigor.

Certain ARBs have been tentatively advanced as "mixed" ESSs (Brockmann *et al.*, 1979; Krebs and Davies, 1981). A mixed strategy is one which chooses randomly from a set of possible actions (Maynard Smith, 1982). Decisions are not responses to short-term fluctuations in environmental conditions, but are probabilistic mixtures of behaviors. Dawkins (1980) has suggested that a better term might be "stochastic" strategy. There are two extreme sorts of mixed strategies along a continuum of possible types. In one type, the strategy mixture is expressed in all individuals in the population. A decision rule for members of a population of this sort would be "with probability P , perform action A, with probability $(1 - P)$ perform action B." The other strategy mixture is a population phenomenon. All individuals do either A or B exclusively, but P proportion of the population do A and $(1 - P)$ proportion do B.

A rigorous demonstration that any population is exhibiting either type of mixed

ESS, requires evidence that three criteria are met. First, the propensity to do A or B must be shown to be genetically mediated, not environmentally mediated. Second, the average fitness associated with each alternative must be equal. If the mixed ESS in question is exhibited within individuals, then the individuals must accrue on average the same rate of fitness gain when exhibiting one behavior as when exhibiting the other. If the ESS is a population phenomenon, those individuals who always do A must show equal fitness to those who always do B. Finally, it should be demonstrated that a change in the relative frequencies of the behavioral alternatives would lower the fitness associated with the behavior made more common and increase that of the behavior made less common.

Without question, gathering the data to examine each of these criteria critically would be arduous, as well as technically difficult. Most field studies address themselves only to the second criterion—that alternatives exhibit equal fitnesses. The issue of negative frequency-dependence is generally considered only vaguely, most often by merely emphasizing that if one behavior were nonexistent or extremely rare, the other would show lowered fitness. Yet demonstrating with minimal equivocation the existence of mixed ESSs requires all criteria be met. The only study published to date which approaches a consideration of all the criteria is that of Brockman *et al.* (1979) on the digger wasp. But it is in that direction that empirical research should proceed.

Statistical considerations

The ESS perspective includes a statistical problem in the interpretation of field data which seemingly has not yet been fully appreciated. That problem is how to evaluate evidence that fitnesses are equal. The common approach is to use standard statistical tests and infer equality of fitnesses unless a statistically "significant" difference is found. But biologists typically use statistical tests to detect nonrandom patterns or differences. In testing ESS models by similar methods, one cannot distinguish between an hypothesis of no difference and

simple random patterns, or simply a lack of information.

Let me try to clarify this with an example. Suppose fitness is directly related to the rate at which individuals encounter resources. Resources are distributed uniformly within patches of various sizes—the total resource abundance in any patch being a simple linear function of patch size. A population exhibiting an ESS would allocate individuals among patches so that the density of individuals was constant across patch sizes. A linear regression of population density in patches against patch size should show zero slope. However, the slope-is-zero hypothesis might be accepted for any one of several reasons (Fig. 2). In Figure 2a, inspection of the data suggests that within-patch density is indeed stabilized as a function of patch size, yet 2b and c, neither of which reject a slope-is-zero hypothesis, give no support to the hypothesis. The scatter in 2b is so great that it suggests individuals are distributed randomly with respect to patch size, and 2c is suggestive but contains too little information to make a judgment. Thus a simple statistical test which accepts or rejects the slope-is-zero hypothesis is of little help by itself (Austad *et al.*, 1979).

Ideally, we would like to assess the probability of making a type II error, that is erroneously accepting a false null hypothesis. However, it is impossible to do so unless a quantifiable alternative hypothesis exists. A simple solution to this dilemma is simply to specify the data's confidence limits. Note that the 95% confidence limits in Figure 2a would exclude many alternative hypotheses about the value of the regression line's slope, whereas those in 2b and c allow almost any hypothesis.

A similar approach can apply to frequency data. For instance, Perrill *et al.* (1978) experimentally released thirty female green tree frogs (*Hyla cinerea*) near calling males and their associated satellites. The callers mated in 17 cases, the satellites in 13. These data are consistent with an hypothesis that callers and satellites have equal mating success. They are also consistent with hypotheses that callers mate 2.5 times as often as satellites or that callers

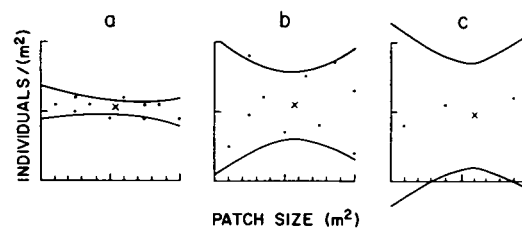


FIG. 2. A complication in the statistical analysis of an ESS hypothesis. In none of these three cases will the slope-is-zero hypothesis about the regression line be rejected, however failure to reject may (a), or may not (b and c), give much support to an ESS prediction of equal population density across patch sizes. The degree to which the data support the ESS prediction may be clarified by the addition of confidence limits. The solid curved lines represent the 95% confidence band for the slope of the regression line. Any regression line passing through the "x" yet staying within the confidence band cannot have its slope rejected by the data.

mate only 0.6 times as often as satellites (χ^2 , $P < 0.05$). The specification of confidence limits, then, allow researchers to better evaluate how adequately ESS hypotheses are addressed by the data.

CONCLUSION

It has now become widely appreciated that the range of intraspecific diversity in reproductive behavior represents a number of adaptively distinct solutions to environmental contingency. In this paper, I have suggested an organizing scheme for ARBs, which I hope will be of special assistance to fieldworkers in designing their observations, experiments, and data analysis. A fundamental, yet understudied, aspect of ARBs is their degree of genetic determination. Therefore a primary goal in future research should be to ascertain the behavioral genetics of the systems in question.

A potentially broadly-applicable explanation for the evolution and maintenance of reproductive alternatives lies in the ESS concept. Largely because of their intuitive appeal, ESS explanations of existing reproductive alternatives have seldom been rigorously tested. Because the most useful scientific stance toward untested concepts continues to be skepticism, it would be to the benefit of both the ESS concept and

the understanding of behavioral evolution if future research focused on the precise predictions of ESS modelling.

ACKNOWLEDGMENTS

For helpful comments on an earlier draft of this paper, I am grateful to Rick Howard, John Robinson, Ed Waltz, Peter Waser, and Larry Wolf.

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