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ABSTRACT: The evolution of reproductive isolation is examined using optimal mate
choice models. Even given a stage of so-called "incipient speciation", where
heterozygotes produce relatively unfit offspring, isolating mechansims may not evolve
because of a variety of economic considerations such as other determinants of fitness,
encounter rates, and costs of choosing. Conflicts of interest can also exist in which
one sex or genotype evolves in the direction of speciation, while the other
sex/genotype evolves to circumvent speciation. It is possible that many populations
possess the necessary genetic differentiation to speciate, but are prevented by the
economics of mate choice.

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Speciation is a process that involves both the evolution of genotypes with
heterozygote disadvantage, and the evolution of reproductive isolation between the
genotypes, splitting them into separate species. Most contemporary treatments of
speciation focus primarily on the evolution of genetic differences, and in particular,
whether these differences can evolve without geographical isolation (e.g. Bush 1975,
Pimm 1979, Rosenweig 1978, White 1978; see Futuyma 1979, Futuyma and Mayer 1980 and
Dobzhansky et al. 1977 for reviews).

Although the evolution of reproductive isolation has been studied both in the
laboratory (Koopman 1950, Kessler 1966, Thoday and Gibson 1970, Paterniani 1969, Soans
et al. 1974, Hurd and Eisenberg 1975) and the field (e.g. investigations of the
"Wallace effect"; Grant 1966, reviewed by Murray 1972, Blair 1974, Littlejohn 1981),
it has not received as much attention from theorists. Often an author will imply that
if genetic differences can arise and be maintained despite heterozygote disadvantage,
then the subsequent evolution of reproductive isolation is a relatively
straightforward matter. For example Dobzhansky (1970, p. 377) states, "Suppose that
incipient species, A and B, are in contact in a certain territory. Mutations arise in
either or both species that make their carriers averse to mating with the other
species. The nonmutant individuals of A that cross with B will produce a progeny
inferior to the pure species. Since the mutants breed only or mostly within the
species, their progeny will be superior in fitness to that of the nonmutants.
Consequently, natural selection will favor the spread and establishment of the mutant
condition."

In a careful population genetical treatment of the subject, Felsenstein (1981)
shows that the evolution of reproductive isolation may not be as straightforward as
Dobzhansky (1970) suggests. Felsenstein considers a two-locus haploid subdivided
population model, in which the fitness of genotypes follows the order BC > Bc = bC >
bc in subpopulation I, and bc > bC = Bc > BC in subpopulation II. For certain
parameter values, this model yields a stable equilibrium in which bc and BC genotypes,
averaged over both subpopulations, have a higher fitness than bC and Bc genotypes.
According to Dobzhansky (1970), this is the situation in which the evolution of
reproductive isolation between bc and BC genotypes should be straightforward.
Felsenstein then introduces a third locus, which causes the individual to mate
assortatively with probability d, and randomly with a probability (1-d). Complete
reproductive isolation (in other words, speciation) occurs when an allele coding for d
= 1 is selected.

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Felsenstein shows that the results of the model depend on the details of assortative mating. In some cases (which he terms "one-allele" models) the evolution of reproductive isolation is straightforward, while in others (termed "two-allele models"), assortative mating at times does not evolve, even though the ecological situation would appear to warrant it. Finally, Felsenstein demonstrates that most previous models of reproductive isolation (e.g Maynard Smith 1966, Endler 1977, Dickinson and Antonovics 1973, Balkau and Feldman 1973, Caisse and Antonovics 1978) fall into one of the two categories.

Although Felsenstein's (1981) study is a major contribution to the subject, the way in which assortative mating is modelled involves a number of unstated assumptions that are biologically unrealistic. For example, all of the above cited models require that the requisite proportion (d) of the appropriate genotype can always be found, that every genotype has a constant fitness (at least within a subpopulation), that the process of evaluating mates for the proper type is cost free, and that mating with the wrong type prevents also mating with the right type. Interestingly, the designs of laboratory experiments on the evolution of reproductive isolation often incorporate these same assumptions.

Recent work by behavioral ecologists indicates that an economy of mate choice exists, such that an individual may preferentially choose a mate on the basis of body size (Perrone 1978), territory quality (Howard 1978, Lenington 1980) or offered resource holdings (Thornhill 1979). Moreover, mate searching and intrasexual conflict may incur considerable costs to individuals (Parker 1970, 1978). Thus, it is probable that the assumptions of reproductive-isolation models are often violated in nature. Therefore, we suggest that despite heterozygote disadvantage, and in addition to the factors identified by Felsenstein (1981), organisms may be selected to mate with the "wrong" genotypes because of economic benefits or high costs of selective mating. In these cases, the evolution of species isolating mechanisms is not straightforward, even given a permanent stage of so-called "incipient speciation", in which heterozygotes produce relatively unfit offspring. It is possible that many populations possess the necessary genetic differentiation for speciation, but are prevented from speciation by the economics of mate choice.

This note briefly explores some of the implications of optimal mate choice for the process of speciation. As a starting point, our models assume a stable population of two types, A and B, in which intertype matings produce offspring of lower fitness than intratype matings. We then consider a variety of ecological situations and ask whether the optimal mating behavior includes intertype mating. If it does, then an allele coding for complete reproductive isolation will likely be selected against. In other words, speciation will not occur.

We show that depending on the situation,
1) The polymorphism can remain totally intraspecific.
2) Mating preferences can evolve that cause switches between complete isolation and complete interbreeding, depending of the circumstance. That is, two types may act as "good species" but with occasional "hybridization". This hybridization is not maladaptive, as is implied by the use of the phrase "a breakdown of isolating mechanisms"; rather, it is an adaptive choice on the part of the individuals involved. One might even speak of optimal degrees of hybridization.
3) Conflict situations can exist in which it is advantageous for one sex to "speciate", but not for the other.
4) Other conflict situations can exist in which it is advantageous for one morph of the polymorphism to mate assortatively, but not for the other. Often, the more common morph will be selected to be selective while the rarer morph will be selected to mate randomly.

The models presented here are not explicitly genetic. A more rigorous analysis would use the subdivided population model of Felsenstein (1981), or Pimm's (1979) model of density-dependent competition as a starting point, and then replace the simple rules of assortative mating used in these models with a more complicated rule, more cognizant of the economics of mate choice. Such a model is beyond the scope of the present paper. However, there are good reasons (discussed below) for thinking that the conclusions derived here will also hold in an explicitly genetic model.

OPTIMAL MATE CHOICE

In many ways, the decisions facing an individual searching for mates of variable quality are similar to those facing an individual consumer searching for food items of variable quality. Ecologists have developed a theory of optimal foraging (based on the premise that fitness is related to foraging behavior) that predicts how a consumer should choose its food (reviewed by Pyke et al. 1977, Krebs 1978). When an optimal forager confronts a given food item, it must decide whether to capture and eat it, or to use the time required for capturing and eating it to search for a better item. In the theory, items are ranked according to their quality, defined as the energy value ($\underline{e}$) of an item, divided by the time required to capture and eat it ($\underline{t}$). The most important conclusion of optimal foraging theory from our standpoint is that the consumer accepts all items from the highest quality item down to a certain cutoff point in quality, below which it ignores all items (even if they are common). When the abundances of different food types are stable, a given food type is thereby either always accepted or always rejected.

Two major points of the theory are worth emphasizing.
1) Since the quality of an item is defined as e/t, the rate of return for the item (e/t), not its absolute quality ($\underline{e}$), is the important parameter.
2) As high-quality items become more available, the optimal forager becomes more selective. Thus, whether a given item is accepted or not depends not on its own abundance, but on the abundance of more desirable items.

In an elaboration of the basic theory, Hughes (1979) has demonstrated also that in special cases where each item must be individually evaluated for quality, there is a cost even for rejected items, and selectivity declines.

Although many details of optimal-foraging theory remain to be worked out (Krebs, 1978; Pyke et al. 1977), the ability of animals to follow its predictions, at least in crude form, is well supported by laboratory and field work (Werner and Hall 1974, Goss-Custard 1977; Krebs et al. 1977). At least some animals are also able to make optimal decisions about mates (Parker 1978, Parker and Stuart 1976, Jackson 1980). Thus, it seems within the capacities of animals to make optimizing decisions.

Much of the apparatus of optimal-foraging theory may be applied directly to optimal mate choice. Consider an individual encountering a variety of prospective mates at random. A mate's quality can be characterized by an expected number of offspring, each of which will have an expected fitness. These fitnesses combined are the analog to optimal-foraging theory's $\underline{e}$ value. However, each mating also requires a certain amount of time, perhaps followed by a period of parental care or a refractory period during which eggs and sperm are regenerated. The total time during which additional matings cannot take place is the analog to optimal-foraging theory's $\underline{t}$ value. The optimal mater must determine whether it is more profitable to copulate with a given potential mate or use the time to search for a higher quality mate. the analogy with optimal foraging theory is sufficiently strong that it seems unnecessary to rederive the mathematics for this application. See Schoener (1971) and Charnov (1976a,b) for treatments of optimal-foraging theory.

To place optimal-mating theory in the context of speciation, consider a population composed of two types, A and B, at a total density of N and in proportions p and (1-p). Intratype matings produce a number, k, of offspring, each with a fitness of 1. Intertype matings produce a number, sk, of offspring ($0 \leq s \leq 1$), each with a fitness of u ($0 \leq u \leq 1$). The expected fitness of intertype matings is therefore usk, or qk, where q = us. This is a symmetrical situation in which intratype matings are superior (in terms of expected fitness) to intertype matings. Yet, as in optimal foraging, the rate of return for the mating is the important value (not its absolute quality), and the acceptability of a given type of mate depends on the abundance of more desirable mates. Where the optimal mating decision includes only intratype matings, reproductive isolation evolves. But where high-quality mates are very costly to attain or low in abundance, or when the low-quality mate does not jeopardize

opportunities for gaining higher-quality mates, the optimal mating decision may include intertype mating; thus, reproductive isolation will not evolve. These considerations seem to be underrepresented in the speciation literature.

   The following sections briefly explore some of the implications of optimal mate choice for speciation.

1) "Trivial" Speciation and Adaptive Hybridization: Optimal mate choice has an interesting all-or-none property: Depending upon the encounter rates, a given type should be either always accepted or always rejected by the optimizing individual. The status of the given type changes when the encounter rates change. Thus, consider a locality at which individuals encounter their own type at a sufficient rate that intertype matings never occur. In other words, the two types act as "good species". Yet merely by reducing the intratype encounter rates, a point may be reached where types suddenly interbreed! As encounter rates fluctuate through time or space, the types alternate between being "one species" and "two species".

   Those who think that speciation is a fundamental evolutionary event will doubtless object to calling this trivial form of reproductive isolation "speciation". But if the population were studied during its "2-species" phase, it would conform in every way to the "reproductive" concept of species (Mayr, 1963), and could not be distinguished operationally from "real" species, however traditionally defined. Furthermore, if high encounter rates persisted for a number of generations, the types could remain reproductively isolated long enough for selection or drift to increase their incompatibility. Then when the encounter rates did decline, the e/t value of intertype matings might be low enough that the types could become "good" species, by any definition.

2) Other Determinants of Fitness: As the model stands, each individual has a choice of two mate types, with fitness values k and qk, respectively. But in nature fitness is rarely determined by just a single factor. Now consider the situation in which the mean fitnesses from intra- and intertype matings are k and qk, respectively, but with a variance around the means. For example, mate quality might depend on body size or territory size, where there is no correlation between these attributes and genotype at the particular loci under disruptive selection. As before, the optimal mater should accept all potential mates from the most profitable down to a cutoff point, below which all others should be rejected. With variance in fitness, however, individuals of the other type can easily fall within the accepted range. For example, a large female of the "wrong" type may be more profitable than a small female of the "right" type.

   An example is illustrated in figure 1. Here, k = 100, q = 0.75, and the variance in fitness equals twice the mean. If the two types are equal in abundance (p = 0.5), then the frequency distributions of fitness for "own" type and "other" type are represented in the top figure. Each type has a roughly three-fold range in fitness, which is not unrealistic for many species. The acceptance range of the optimal mater will depend on its overall encounter rate with potential mates. The vertical line in the figure represents a possible cutoff point. Notice that in this example, the optimal mater is rejecting a substantial proportion of its own type (0.25). Nevertheless, a fairly large number of the other type fall within the acceptance region. An individual that categorically rejected intertype matings would not be selected in this situation.

   In figure 1 (bottom) the proportion of the other type among accepted mates is plotted against the frequency of one's own type. This figure was obtained by altering the relative sizes of the frequency distributions in 1 (top), while retaining the cutoff point. When an individual's own type is in a frequency of 0.1, almost 70% of the individuals in the acceptance region are of the other type. When an individual's own type is at a high frequency (say, 0.7 or 0.8), the other type still constitutes an appreciable fraction of the desirable mates. Under this circumstance, the optimal mater should usually reject, but not categorically exclude, mates of the other type. (Note the asymmetry in optimal mating strategies for two types whose frequencies differ, as mentioned earlier.)
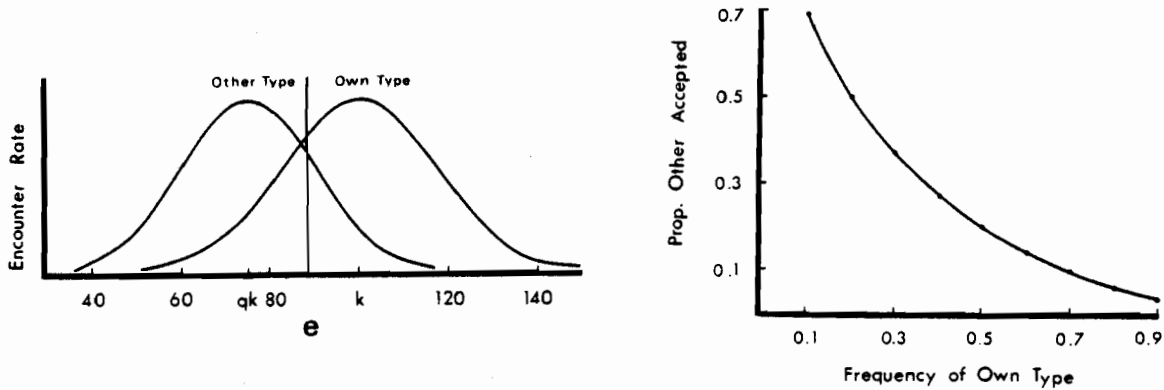
Figure 1. Top; fitness of prospective mates for "own" type (right hand
distribution) and "other" type (left hand distribution). The optimal mater
accepts all prospective mates to the right of the vertical line, which includes a
significant proportion of the other type. Bottom; the proportion of the other
type among accepted mates (y axis), depends on the frequency of one's own type
(x axis). See text for explanation.

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To summarize, most models of reproductive isolation somewhat artificially assume
that all potential mates of one's own type will yield a higher fitness than all
potential mates of the other type. When this assumption is violated, as it sometimes
must be when mate quality is multifactorial, then speciation becomes less likely.
Grant and Grant (1979) provide a possible example of this as a factor limiting
speciation, using a similar argument based on the mating options available to
individuals.

3) Cost of Choosing: In optimal foraging, if there is a finite recognition time
(such that all prey encountered are examined prior to acceptance or refusal), then
low-quality items may be accepted even though higher-quality items are abundant (see
also Hughes, 1979 and Janetos, 1980, for a rigorous treatment of this point). That
is, the cost of choosing lowers the e value of items and selectivity declines.
Similarly, in optimal mating anything that makes "comparative shopping" for mates
costly will decrease selectivity, and thus decrease the likelihood of speciation.

For example, consider the situation in which either evaluating a potential mate
or mating exposes an animal to predators, decreasing expected fitness by a factor of
(1-c). If the first potential mate encountered is accepted regardless of type,
expected fitness is

$$(1-c) \; [pk + (1-p) \; qk].\tag{1}$$

Now consider an animal that rejects the first potential mate if it is the other type,
but accepts any second potential mate encountered. The expected fitness here is

$$(1-c)pk + (1-c)^2 \; (1-p) \; [pk + (1-p) \; qk].\tag{2}$$

Mate selectivity is advantageous only where term (2) is greater than term (1) which
reduces to

$$q < \frac{(1-c)p}{1-(1-c)(1-p)}\tag{3}$$

The same inequality (3) serves to compare the expected fitness of an animal that
is selective up to the (N+1)th mate with that of one selective only up to the Nth.
Thus, if the inequality is satisfied, the optimal mater continues to reject potential
mates until it encounters its own type. (This model assumes that time is not
important.)

As a numerical example, compare the case where p = 0.1 and c = 0.05 to that where p = 0.1 but there is no cost (c = 0). In this simple model, when there is no cost, it is always advantageous to be selective (q < 1); yet when the cost is 0.05, selectivity is advantageous only for q < 0.65. Thus, the cost of choosing has made the conditions for speciation more stringent.

Now consider the case where c = 0.05 as before, but p = 0.9. Here, q must only be lower than 0.94 for selective mating to evolve. Notice that assortative mating is more advantageous for the type in high frequency (0.9) than for the type in low frequency (0.1).

4) <u>Conflicts of Interest Between Types and Sexes</u>: As demonstrated in the last two sections above, situations may exist where reproductive isolation is advantageous for only one of the two types. Where such conflicts of interest exist, optimal mating theory predicts that the more common type should evolve towards speciation while the rarer type should evolve counter-adaptations to speciation. This is in contrast to many other discussions of speciation, which assume that reproductive isolation should evolve more strongly in the rare morph (e.g. Watanabe and Kawanishi 1979). These arguments generally assume that mate choice is cost-free.

As with all conflicts of interests, the eventual outcome is difficult to predict. In some animal groups, forced matings are common (e.g. dung flies, Parker 1978; scorpion flies, Thornhill 1980; ducks, Barash 1977) or mate sequestering (e.g. roe deer, Lincoln <u>et al</u>. 1970; elephant seals, Le Boeuf 1972). It is also possible that a type can evolve to be phenotypically indistinguishable from other types, a form of mimicry that could also prevent mate choice. For these cases, speciation would not occur if against the interest of only one type (but see below). However if forced matings are not possible, and if the types can be distinguished phenotypically, then speciation should occur even if in the interests of only one type.

Additionally, it is possible for a conflict over speciation to exist between the sexes (see also Parker 1974, 1979, pp. 138-142). For instance, consider the common situation in which a female invests more time and energy in each offspring than does a male. Using the optimal-foraging analogy, each parent receives the same benefit from the mating (e), but at very different expense (t). Hence the e/t ratio differs for the sexes, and the male has a lower threshold of acceptability in terms of absolute expected fitness than does the female. Once again, the outcome should depend on details of the mating system, and in particular on the opportunities for free choice versus forced matings and deception. The expectation that males can often be less choosy than females is well borne out by observations of <u>Drosophilia</u>, in which males, unlike females, frequently attempt to mate with species other than their own (Merrell 1954, Von Schilcher and Dow 1977, but see Spieth 1974, Wood and Ringo 1980). Nonetheless we are unaware of any papers that rigorously relate patterns of animal speciation with mating systems.

Although the possibility of conflicts over speciation suggest a variety of interesting evolutionary consequences, only one will be mentioned here. Consider a situation in which females can exercise free choice, and the two types are phenotypically distinguishable. Encounter rates are such that it is in the interest of females to discriminate, but not males. The evolution of sex-limited traits causes the male types to become phenotypically indistinguishable. Females cannot discriminate male types, so speciation does not occur and mating is random. Now, imagine that an allele arises that causes the female to prolong the length of time she requires a male to display before she allows mating. Using the optimal-foraging analogy, this allele increases t for a male choosing to pursue the female. Thus, the female is less profitable for a male than other females of the same type. It is a tenet of optimal-mating theory, however, that all potential mates above the cutoff point are equally acceptable. Hence, in a practical sense, the mutant female is <u>not</u> less desirable than others of her type to the male, provided her e/t falls above the cutoff point. Furthermore, a male of the female's own type will gain a higher expected fitness (<u>e</u>) than will a male of the other type, such that a range of t values exists that will place the female <u>above</u> the cutoff point for her own type but <u>below</u> the cutoff for the other type. In other words, even though the female cannot

distinguish between male types phenotypically, she can force assortative mating by manipulating the $\underline{t}$ value for optimizing males. Speciation occurs, but only in tandem with prolonged courtship displays.

DISCUSSION

Because speciation is of central interest to evolutionary biology, it is often treated as an adaptation not qualitatively different from other adaptations, such as body size, feeding rate, or fecundity. But speciation is a property of populations, not individuals. Unless group selection is to be invoked, speciation is best thought of not as an adaptation in itself, but as a coincidental byproduct of adaptation on the level of individuals (Williams 1966, see also Littlejohn 1981). We have noticed a subtle form of naive group-selectionism in much of the speciation literature. For example, if two "species" hybridize over parts of their ranges, the hybridization is often attributed to a "breakdown in species isolating mechanisms". This phrase strongly connotes a maladaptive behavior, which the hybridization may well be. However it also may be a behavior that has evolved because it is very adaptive for at least some individuals, with species made or broken as a coincidental byproduct.

Thus, our model offers a potential explanation for the enigmatic failure of reproductive isolation to evolve in stable hybrid zones (Hunt and Selander 1973, Yang and Selander 1968, Moore 1977), for temporal or spatial fluctuations in the degree of hybridization noticed in sympatric populations (Short 1969, Hunt and Selander 1973, Yang and Selander 1968), and for the remarkably sharp boundaries of some hybrid zones (Moore 1977). It predicts that the genetic differentiation necessary for speciation exists in some groups which are prevented from speciating until the economics of mate choice change. Conflicts of interest between types and sexes provide possible explanations for the common phenomena of asymmetrical genetic introgression between hybridizing populations (Hunt and Selander 1973, Yang and Selander 1968) and asymmetries between the sexes in tendency to hybridize.

The greatest weakness of our models is that they are not explicitly genetic. For example, only the two "pure" types are treated, and the fate of the hybrids is not considered in detail. However, even though such a traditional population genetical-treatment will be worthwhile, it is unlikely that the major conclusions will change. To see this, consider a type of assortative mating discussed by Endler (1977, p. 142), following O'Donald (1960), in which one locus codes for three genotypes (AA, Aa, aa) with the usual fitnesses (W_1, W_2, W_3), while another locus codes for assortative mating. In particular, assume that the presence of a dominant B allele causes an individual to mate assortatively with its own genotype on the A locus (i.e. AA with AA, Aa with Aa, aa with aa) with a frequency of d, and randomly mate with a frequency of (1-d). The recessive b allele mates randomly with a frequency of 1. Endler shows that in this model the B allele spreads to fixation whenever

$$W_1 + W_3 - 2W_2 > 0 \qquad (4)$$

In other words, reproductive isolation evolves whenever heterozygote disadvantage exists. Now assume that there is a cost for mate choice, which lowers the fitness of BB and Bb individuals, but not bb individuals, which mate randomly. Can this have any other effect than to retard or prevent the spread of the B allele? Similarly, assume a second factor that bestows high fitness on individuals, independent of their genotype at the A locus. Again it is hard to imagine that a genotype that assortatively mates according to this second factor in addition to the A locus would not be selected over a genotype that categorically mated only with its own genotype. One might argue along with Felsenstein (1981) that this is in an artificial model of assortative mating. Felsenstein's "two-allele" models show that reproductive isolation may not evolve even when condition (4) is satisfied. However, if we take his model and include additional costs of assortative mating, along with benefits of mating with other genotypes, then we can only expect the conditions for reproductive isolation to become even more stringent. In short, there is every reason to expect that a more traditional population-genetical analysis of the economics of mate choice will make roughly the same conclusions arrived at here.

Another criticism that can be brought against these models is that they require sophisticated behaviors on the part of the organisms. Individuals must assess both the quality of the prospective mate, plus their chances for obtaining future mates if the present one is rejected. It is certainly likely that some species may not be capable of such behaviors. For these cases, a coarser model of adaptation is more suitable, in which individuals make unconditional decisions to mate or not mate with a particular type. However, in view of abundant evidence from the behavioral literature that at least some species rely on economic considerations in choosing mates, we feel our approach is appropriate. This brief treatment points to several important variables that seem underemphasized in the traditional speciation literature.

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