

concept. All that is being claimed is that reproductive isolation is a characteristic of the species. It leaves open whether reproductive isolation or some other characteristic is definitive. The problem is that it does not satisfy the requirements for a definition. Furthermore, it cannot be tested against the Recognition concept.

Consider Dobzhansky's (1951:263-264) definition: "Species are accordingly, groups of populations the gene exchange between which is limited or prevented in nature, by one, or by a combination of several, reproductive isolating mechanisms." The claim here is that reproductive isolation is the definitive characteristic of species. The Recognition concept claims that a common fertilization system is the definitive characteristic of species. These concepts are incompatible and meet the normative requirements for definitions. They can also be tested against each other. One way they can be evaluated is in terms of their degree of universality.

Universality and the species problem

We have seen previously that there is a correlation between the position of an event along a causal chain and the level of universality of the definition derived from this event. Universality and consequently causal definitions are desirable in science. In this section I assess the level of universality of various concepts inferring their position along the speciation chain as an indication of their adequacy. In table 4-1 the concepts are rewritten in the form of conditionals. I then determine whether the conditional holds true for all possible situations to test its degree of universality.

Table 4-1. Species concepts in the form of conditionals.

Concept	Conditional	Position along Causal chain
Taxonomic	If X has $A_1, A_2, \dots, A_n$ then it is a B where A_1-A_n are morphological characteristics.	3 rd
Isolation	If X & Y are potentially able to mate but do not, they belong to different species.	2 nd
Recognition	If X has $S_1, S_2, \dots, S_n$ then it is a B where S_1-S_n are components of the fertilization system.	1 st

It can be seen that the taxonomic conditional does not hold true for all possible situations. It often happens that two species have biological reality, i.e. have different distributions, mating behaviour, physiology etc. and yet are extremely difficult to distinguish between on morphological criteria (e.g. *Anopheles gambiae* complex). The Morphological Species Concept, then, is inadequate.

The isolation conditional, although it does much better, also does not hold true under all possible situations. It could not apply in the hypothetical situation of there being only one species on earth. The conditional is such that it requires at least two species to exist for it to be supported. The isolation concept fails the universality test just because it is relational. There are two ways of reading isolation in the above conditional.

Isolation could be viewed as an effect of two species having different fertilization systems. The other view is that isolation is causative. Here the conditional would read: 'X & Y belong to different species because they are unable to mate'. This statement sounds reasonable if X & Y are two closely related mosquitoes with genitalia that do not match. However, Paterson (pers. comm.) says that few would want to argue that humans and mosquitoes are different species *because* they are unable to mate. Thus in this form the conditional falls far further short of applying under all situations.

What of the recognition conditional? It holds true under a greater range of situations than the previous two conditionals. Two species may be morphologically indistinguishable, differing only in the chemical signals used in their courtship. SMRS theory would give them separate species status. The conditional would hold true even in the event of there being only one species existing on earth. On the grounds of greater generality the Recognition Concept wins over the others. We have come now to the third step in the multi-cornered approach.

Step 3: Developing multi-cornered predictions

The way this is done is as follows: Logical connections are established between particular hypotheses H_1 and H_2 and mutually exclusive predictions P_1 and P_2 .

It is not necessary that the predictions be forward-looking (Williams 1985). It is important that the hypotheses H_1 - H_2 be clearly distinguished from one another. Otherwise it will be difficult to establish whether a particular observation has confirmed or refuted one of the hypotheses. The predictions P_1 - P_n should be mutually exclusive, since this enables us to go back and adjudicate between our hypotheses.

Testability between alternative species concepts is augmented by requiring that definitions be causal. This is so because each definition will then imply a different sequence of steps in the speciation process. Testing the adequacy of particular views of species becomes in part a matter of ascertaining the correct sequence of events in speciation. I say in part because each view has many implications, one of which is a particular sequence of steps in the speciation process.

A number of predictions of the Recognition Concept have been supplied (Paterson 1978, 1981, 1986). It is noted that not all these are of equal value. Of one prediction it is said that it "is not in absolute conflict with the isolation concept" (Lambert and Paterson 1984) But most of the predictions are multi-cornered. Five of these are given in table 4-2.

Table 4-2. Some predictions of the Isolation and Recognition concepts of species.

Recognition Concept	1. The fertilization system will vary little geographically. 2. The fertilization system will tend to remain stable in time. 3. The complexity of the fertilization system will not depend on the proximity of other species. 4. Species that have little gene flow between populations will still remain stable. 5. Speciation will occur in allopatry.
Isolation Concept	1. The fertilization system will vary geographically as much as any other character. 2. The fertilization system will not remain stable in time. 3. The complexity of the fertilization system will depend on the proximity of other closely related species. 4. There will be substantial gene flow between populations. 5. Speciation will occur in sympatry or by reinforcement.

Lack of space forbids me to follow all the logical consequences of every view of species. Instead I will consider three: the Morphological Concept, the Isolation Concept and the Recognition Concept with the object of emphasizing the logical connection between these and one particular feature of speciation- its sequence. It will be necessary, in doing this, to discuss the temporal aspect of the speciation process:

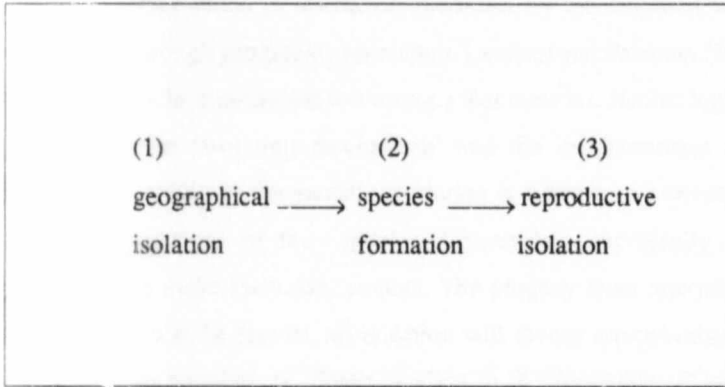
The temporal aspect of the speciation process

Speciation can be viewed as a causal chain because it involves a number of causally connected events. Hull (1974) has described some of the properties of causal chains and this will be helpful to us in understanding speciation and the species problem. One important property of causal chains is that they have a temporal aspect. Causes by definition never follow their effects. Consequently, there is a precise order or direction of events along the chain. The various species concepts imply different sequences of events in speciation, and thus different modes of speciation. To show this I will consider three species concepts in turn:

The Recognition Concept

The Recognition concept of species is closely tied to the allopatric model of speciation. Paterson says of this concept that there are no problems accommodating it to allopatric speciation (Paterson and Macnamara 1984). Under the Recognition Concept the acquisition of a new Fertilization System by a population is a prior event to reproductive isolation. Reproductive isolation is an effect. A consequence of this isolation is the setting up of independent phylogenetic lines since any change in one line will not be registered in another. Morphological divergence may only arise after a number of speciation events. In the case of sibling species there is reproductive isolation without a change in morphology. Morphological divergence, then, is contingent upon speciation (or

sub-speciation). The order of events in the allopatric model of speciation is as follows:



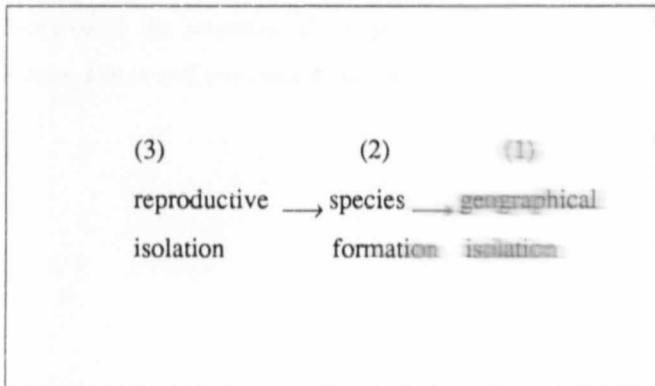
It is important to note that the Recognition Concept of Species does not state merely that a fertilization system is an important property of species, but that acquisition of this system is the primary event with reproductive isolation merely an effect. The Recognition concept is thus logically tied to the allopatric model of speciation. As a result, testing this concept becomes in part a matter of discovering what sequence of events actually occurs in speciation. Other species concepts imply different sequences, providing us with a multi-cornered test.

The Isolation Concept

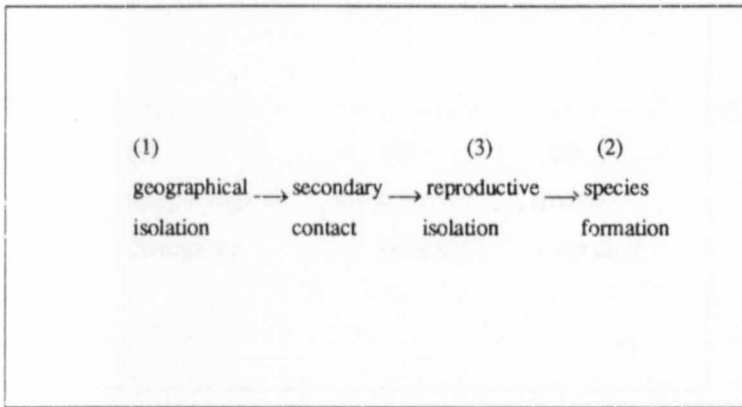
If the Isolation Concept is a definition in terms of causes, then speciation is contingent upon reproductive isolation. There are several modes of speciation in which this would be the case. One of these is sympatric speciation. Bush (1975a) says: "In sympatric speciation premating reproductive isolation arises *before* a population shifts to a new niche" (*Italics mine*). Mayr (1963:451) says that "according to the theory of sympatric speciation the splitting of the gene pool is caused by ecological factors, and whatever spatial isolation of the thus

formed populations ensues is a secondary, later phenomenon." Thus, geographic isolation is contingent upon reproductive isolation and speciation.

Another mode of speciation predicted by the Isolation Concept is reinforcement through geographic speciation. Lambert and Paterson (1984) have said that it cannot be emphasized too strongly that there is a distinct logical nexus between the term 'isolating mechanism' and the reinforcement model of speciation. According to this model, speciation is a two step process. Initially, allopatric populations of the species differentiate genetically. The two populations then make secondary contact. The progeny from interpopulational crosses are likely to be less fit, so selection will favour reproductive isolation between the two populations, finally leading to the formation of two species (Ayala *et al* 1974). Sympatric speciation and reinforcement have in common that speciation is contingent upon reproductive isolation. Note that this order of events is in contrast to that found in the allopatric model. Two sequences predicted by the isolation concept are:

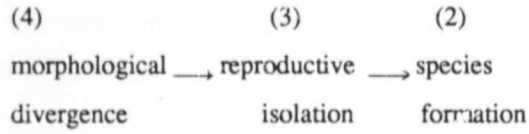


or



The Morphological Concept

If morphology is considered the primary criterion of species rank, then a distinct mode of speciation is predicted. For, the implication is that reproductive isolation and speciation are secondary consequences of morphological divergence. This would be the view of the mechanical isolationist. Here morphological divergence causes a block to gene flow; differences in the structure of the genitalia between the two species causes isolation. The causal sequence will be as follows:



Two important points emerge. First, the Morphological Species Concept implies a specific sequence of events in speciation. Second, this mode is a subset of sympatric speciation or speciation by reinforcement.

Since we have required that species definitions be in terms of causes a link has been established between the concepts and speciation. This has allowed for the development of multi-cornered predictions as follows:

- H₁ (Recognition -----→ P₁ (1 - 2 - 3)
Concept)
- H₂ (Isolation -----→ P₂ (3 - 2 - 1 or 1 - 3 - 2)
Concept)
- H₃ (Morphological -----→ P₃ (4 - 3 - 2)
Concept)

This step, which is an important step in the empirical testing of species concepts has not been consistently practiced by species biologists. This is evidenced by the following:

a) In major works on evolution such as Mayr's (1963) 'Animal Species and Evolution', White's (1978) 'Modes of Speciation' and 'Evolution' by Dobzhansky et al (1977) there is no discussion on the consequences for speciation of particular concepts of species. In particular it has not been emphasized that the Morphological Species Concept implies a distinct mode of speciation as compared to both the Recognition and Isolation Concepts of species.

b) At this late date Lambert and Paterson (1984) still have to stress the logical connection between particular views of species and speciation.

An interesting question is why there has been the tendency to ignore the connection between species and causal sequence. One reason is that to see this connection requires that the previous step be performed: species concepts must be adequately delimited. As we saw, the Biological Species Concept has not been unambiguously defined. We come now to the final step of the multi-cornered approach.

Step 4: Adjudicating between alternatives

Introduction

The object of the multi-cornered method is to bring alternative theories, concepts or hypotheses into a confrontation with each other and the real world; to let the world be the judge of which hypothesis is the victor. More realistically,

fights between hypotheses may involve a number of rounds. In each round the goal is to have a different part of the world be the judge of which is the victor. In such a system we have a method for ensuring that the greatest possible demands are made on theories. Theories are subjected to severe tests. As we have come to the last step in this method it will be useful to outline the whole argument:

if H_1 then P_1

if H_2 then P_2

⋮
⋮
⋮

if H_n then P_n

P_j

therefore H_j

Step 4 can be divided in two parts. First, the necessary observation statement(s) P_j are gathered. P_j represents a particular observation statement. Second, the observation statements are used to decide between the alternative hypotheses H_1 - H_n . Since P_1 - P_n are mutually exclusive, affirming particular observation statement P_j implies the denial of all other predictions considered. In the previous section we saw that each of the species concepts considered implies a different sequence of events in speciation. In the fourth step the evidence on speciation is used to judge between the concepts.

The evidence

The evidence for and against different modes of speciation is a subject in itself and will be dealt with in the next chapter. Suffice to say that the only mode of speciation whose occurrence is unequivocal is allopatric speciation. Paterson (1981) has categorized it as a class I model i.e. one which has support from observed critical facts as opposed to a class II model which does not have

support from observed critical facts. Mayr (1963:449-480) has shown that the evidence for sympatric speciation is merely common, being accountable for in terms of allopatric speciation. The evidence suggests that speciation by reinforcement hardly if ever occurs in nature given the unlikely conditions it requires (Mayr 1963:472, Paterson 1978, Lambert, Centner and Paterson 1984).

But several other lines of evidence have been given which favour the Recognition over the Isolation Concept (Lambert and Paterson 1984). Some of these are: the number of cases in which the complexity of the courtship is clearly not dependent on the presence of other closely related species; the little geographic variation found to occur in the SMRS of particular species (Lambert and Harper 1985); and the stability of species (Mason 1964).

The evidence, then, discriminates against the Isolation Concept and for the Recognition Concept. One would expect the Recognition Concept to be accepted over the other. This is not so. Leading evolutionists such as Mayr and Dobzhansky have favoured the Biological Species Concept, stressing isolation as the most important property of species. Paterson (1981) has even accused Dobzhansky of playing down the logical inconsistency between the Isolation Concept and the known fact of allopatric speciation.

Why has this happened? I do not believe that the problem lies with a lack of the right kind of data. The data is there. In order to adjudicate between alternatives, the significance of this data must be appreciated. This in turn is dependent on considering the collective evidence, rather than each line of evidence in isolation, for then it becomes easy to explain away the conflicting evidence through the addition of *ad hoc* hypotheses.

It is also dependent on careful defining and reasoning. If common evidence is not recognized for what it is, a concept will appear to be adequately supported, and there will seem to be no need to consider alternatives. If species

concepts are not adequately delimited, the logical connectedness of these concepts to particular views on the speciation process will not be realized. If this logical connectedness is de-emphasized, the full significance of discriminatory evidence will not be recognized. And again it will become easier to explain away the conflicting evidence through the addition of *ad hoc* hypotheses.

Notes

1 In order to avoid this problem, Kripke (1977:66-101) has proposed that we separate definition and reference. In his causal theory of reference he has sought to provide a means of reference that is independent of an item's conceived properties. Reference is realized by a causal connection rather than by associated descriptions. One merit of the theory is that it allows one to be mistaken about an item's properties, and yet correctly refer to that item.

CHAPTER 5: METHODOLOGY AND SPECIATION

Introduction

We saw in chapter 4 that species biology is characterised by pluralism and polemics. It is not surprising to find speciation biology in a similar state considering the close relationship between species and speciation. There are a great deal of data on speciation but it has not been integrated into a single unifying mechanism. White (1978:16) identifies 7 modes of speciation, many of which are mutually exclusive. Mayr (1963:428) describes 9 different modes. Paterson regards this as a bad state of affairs arguing that there is a loss of "generality with every distinct mode of speciation admitted..".

From the outset it should be specified in what sense, if any, the various modes can be said to be competing. It could be objected, and rightly I think, that there is no *a priori* reason why speciation should not occur in several modes. The fact that the occurrence of allopatric speciation has been unequivocally established does not mean, of course, that sympatric speciation does not occur. The conflict is over the importance and prevalence of the various modes. It is at this level at least that controversy exists. Thus White (1978) says: "... it seems impossible today to deny the reality of sympatric speciation, at least in many groups of insects." Paterson (1981) objects: "I am afraid I cannot accept this assertion."

It is the thesis of this chapter that inadequate method may be a significant contributor to this state of affairs. My aim, therefore, is to evaluate the methods used in population biology according to the criteria established in my

second chapter. Paterson (1981) has complained of conflation between species concepts. It will be argued that an analogous conflation has occurred with regard to method; that distinct methods have sometimes been confused. In addition, further methodological principles of benefit to Population Biology will be suggested. Since the main objective is to discuss points of method, I will not give a detailed account of all modes of speciation or compare the variants of these modes. We will be concerned chiefly with allopatric and sympatric speciation and speciation by reinforcement, although one would expect the principles to apply to tests involving other modes of speciation. First it will be necessary to give some background to speciation.

Background to speciation

Traditionally evolutionary change has been divided into two kinds: anagenesis or evolution within a single population and cladogenesis or the divergence of populations into different species. Speciation refers to the latter process- the origin of species. The importance of this process has recently become more apparent as several biologists claim that most evolutionary change occurs at speciation. (Paterson 1985,1986, Gould and Eldredge 1977, Eldredge and Gould 1972). There is no doubt that the origins of species has an genetic explanation. As we have seen the controversy is over the importance of particular modes of speciation.

Modes of speciation have been classified in several different ways. Mayr (1963:428) distinguishes two broad categories- instantaneous and gradual speciation. Under the former he includes single mutations in asexual organisms and chromosomal modes. The latter category he further divides according to geographical considerations. Geographic speciation (= allopatric speciation) occurs when a population is split into two by a geographical barrier, and, through

genetic differentiation evolve into separate species. Sympatric speciation occurs when two populations undergo genetic differentiation without being geographically isolated.

Templeton (1981) feels that it is better to classify modes according to population-genetic rather than geographical criteria. Accordingly, he and Mayr (1978) define 'allopatric' in terms of dispersal barriers rather than purely geographically.

One important difference between several of the modes is the sequence of steps in the process. Mayr (1963:451) has said that the allopatric and sympatric models of speciation differ "in the sequence in which the steps of the speciation process follow each other." "In sympatric speciation premating reproductive isolation arises *before* a population shifts to a new niche". (Bush 1975a, *italics mine*). The claim here is that populations develop intrinsic reproductive barriers while in sympatry. Eventually individuals from the two populations will be unable to mate and consequently will be different species.

Under the allopatric model a daughter population becomes geographically isolated in a new habitat. The reproductive isolation arises fortuitously *after* this event, and as a by product of adaptation to the new habitat. The reinforcement model of geographic speciation is a two stage process (Ayala *et al* 1974). Initially, allopatric populations of the species differentiate genetically. The two populations then make secondary contact. The progeny from interpopulation crosses are likely to be less fit, and so, it is claimed, selection will favour reproductive isolation between the two populations, finally leading to the formation of two species. In chromosomal models of speciation, karyotypic changes initiate divergence (White 1978:169) whereas the alternative view is that these changes are contingent upon speciation (Paterson 1981). We can turn now to evaluating method according to the steps involved in the multi-cornered approach.

Step 1: Recognising common evidence

The first case that we will consider is the evolution of the neuropterans *Chrysopa carnea* and *C. downesi*. Tauber and Tauber (1977a) have claimed to have found evidence for sympatric speciation. The title of their paper reads: "Sympatric speciation based on allelic changes at three loci: evidence for natural populations in two habitats." They say: "... we report experimental evidence herein that disruptive selection can act through habitat differences in the speciation of non-host-specific animals." Hendrickson (1977) thinks otherwise, pointing out that the evidence is equally consistent with allopatric speciation. Let us examine the evidence and its interpretation in some detail. The object is to determine whether this evidence is common or discriminatory.

The evidence. *C. downesi* is dark green and univoltine (producing a single brood in a season). From hybridization tests its colour was found to be the result of the semi-dominant G allele in the homozygous state. *C. downesi* is camouflaged against the conifers it lives on. Its univoltism is due to the presence of recessive alleles d_1d_1 and d_2d_2 . *C. carnea* is multivoltine. In the reproductive phase the adults are light green and camouflaged in their grassy habitat. At the end of the breeding season the adults move to the senescent foliage of deciduous trees, while changing their colour to between a pale green and a reddish brown. Thus they remain camouflaged.

The interpretation. Tauber and Tauber interpret the evidence as supporting sympatric speciation. They propose that *C. downesi* evolved from a *C. carnea*-like ancestor through a two step process. In the first step selection is supposed to favour the establishment of the allele G in the ancestor (we will ignore the question of how the gene would spread after arising). This form would be at an adaptive advantage in the conifer habitat. The heterozygotes would be intermediate in colour and thus disadvantaged. They claim that through disruptive selection a 2-allele polymorphism would be maintained. In the second

step selection favours the establishment of the alleles $d_1d_1d_2d_2$ in the ancestor. The selection would favour univoltinism in the incipient *C. downesi* because food and competitors would be present throughout the year. The process is represented as follows:

$$ggD_1D_1D_2D_2 \rightarrow GGD_1D_1D_2D_2 \rightarrow GGd_1d_1d_2d_2$$

But, as Hendrickson (1977) has pointed out, the title is misleading since their evidence can be accounted for in terms of allopatric speciation. According to this model a small population would have become isolated in a conifer habitat. Subsequent to this isolation the population undergoes the allelic changes leading to the formation of *C. downesi*. Both models predict the same set of allelic changes but would predict a different timing for these changes. In sympatric speciation the changes begin while the populations are in sympatry. In allopatric speciation the changes occur when the populations are in allopatry.

Tauber and Tauber have done some useful research in discovering the probable allelic changes that occurred in the evolution of *C. downesi*. But that is all. They have no evidence regarding the timing of these changes and consequently they cannot discriminate between allopatric and sympatric speciation. In claiming that they can they have not recognised their evidence for what it is- common evidence.

Let me suggest a few reasons why this has happened:

1. The authors do not clearly distinguish between the evidence and their interpretation of the evidence.

After giving the evidence they say "... we *propose* that *C. downesi's* speciation from a *C. carnea*-like ancestor occurred in two two steps..." (emphasis mine). The term 'propose' suggests that they recognise that this is interpretation. This is fine. But then they begin to speak in the past tense creating the impression that the evidence is that sympatric speciation has in fact occurred: They write: "*Thus* the population *was* subjected to disruptive selection which produced and maintained a stable, two-allele polymorphism..." (italics mine). Such use of language makes it easy to slip into thinking that the common evidence is actually discriminatory.

2. The authors do not have a clear understanding of the distinction between common and discriminatory evidence. This is evident from an inconsistency in their claims. The language of their title, as we have seen, shows that they believe that their evidence discriminates against allopatric speciation. However, note their choice of words in the summary: "... such gene substitutions *can* occur, in the absence of geographic isolation, as a result of disruptive selection..." (italics mine). The use of 'can' is revealing. It suggests a more modest claim than that found in the title; that their claim is merely that allopatric speciation is not alone in being able to account for the allelic changes.

It is also evident from their not responding relevantly to Hendrickson's criticisms. To respond relevantly they would need to speak in comparative terms. Instead, much was made of the fact that their observations "... precisely fit the predictions ..." of sympatric speciation (Tauber and Tauber 1978). Of course, the observation that X has fur precisely fits the hypothesis that X is a dog, but it precisely fits the hypothesis that X is a cat as well. Their statement does not, then, speak to the issue.

3. The absence of appropriate terms is also a factor. We use the term 'evidence' in at least two senses (common and discriminatory), often relying on the context to indicate which is meant. Part of the disagreement between Tauber and Tauber and Hendrickson is the result of each using the term 'evidence' in a different sense.

Another case is Littlejohn's work on the premating isolation in the *Hyla ewingi* complex. This case is often cited in textbooks (e.g. Dobzhansky et al (1977:182)) because it is thought that it clearly demonstrates reproductive character displacement. Littlejohn (1965) was able to demonstrate that the two species studied, *H. ewingi* and *H. verreauxi* had similar mating calls when in allopatry but showed divergence when in sympatry. One explanation is that the mating calls are premating isolation mechanisms which arise through the direct action of selection for these mechanisms. The second explanation is that the premating isolation is an effect arising incidentally from adaptive processes operating in the allopatric populations.

Littlejohn favours the former explanation. He suggests, "that the marked differences between sympatric populations have resulted from the direct action of selection for increased reproductive efficiency, i.e. the slight differences present in the allopatric populations have been reinforced in the sympatric populations". The basis for this decision seems to be the difference in the mating calls which he established between the two species in allopatry and sympatry. But, by his own admission, this difference is expected from both explanations. For, he regards the problem as whether the ethological isolation "...arises incidentally...or whether through the direct action of selection for the isolation effect itself." Thus Littlejohn bases his decision on common evidence.

Futuyma and Mayer (1980) cite a number of cases where the evidence used to support a particular model is consistent with alternatives. One of these is the evolution of host races in the fly genus *Rhagoletis* which is believed by some

(e.g. Bush 1975b, White 1978) to be convincing evidence of sympatric speciation. Before the 1860's *R. pomonella* was only known on hawthorn. Subsequently, it has been reported on cultivated apple and cherry (Futuyma and Mayer 1980). Bush's (1974) model has been criticised on several grounds by Paterson (1981) and Futuyma and Mayer (1980). For our purposes the most interesting criticism is that the evidence relied on by Bush and White is insufficient to allow one to choose between Bush's hypothesis and alternatives.

The central argument for sympatric speciation reads: "The sympatric origin of host races in *Rhagoletis*- and hence of species, because there can be no doubt that these host races are potentially incipient species seems to be as firmly established as any case of allopatric speciation has been" (White 1978).

Paterson points out that this fact can be alternatively interpreted as *R. pomonella* increasing its number of hosts. As it is *R. pomonella* lives on 16 species of host plant apart from apple and cherry (Bush 1974). To exclude this possibility one has to know that host choice has a genetic basis (Paterson 1981). This is not known, or at least was not known, in the 1970's (Futuyma and Mayer 1980).

A further supposed line of evidence is the significant difference in size and ovipositor length between flies collected from apple and hawthorn at one locality (Bush 1974, 1975b). As Futuyma and Mayer remark, this difference *may* indicate genetic divergence and hence a stage in sympatric speciation, but this is only one alternative. The available evidence does not exclude the possibility that this difference is a phenotypic response to different environments.

Mayr (1963:449-480) lists several lines of evidence that have been used in the past to support sympatric speciation. After a detailed examination of this evidence he says: "A re-analysis of all five reported reputed proofs of sympatric speciation - sibling species, speciation in monophagous groups, speciation in

parasites, species swarms in lakes, and the instantaneous splitting of fossil lineages- thus shows that they are consistent with the theory of geographic speciation". Two of these "proofs" will be examined to show that each is a case of relying on common evidence.

The occurrence of species swarms is a line of evidence that was used much in the past to support sympatric speciation (Mayr, 1963:504). Species swarms are collections of many closely related species in a small area. In the case of lakes the argument has been that since there are no external barriers, speciation must have been sympatric (Worthington 1954). But species swarms may be the result of multiple invasions. Another possibility, for which considerable evidence exists (Fryer and Iles, 1972), is that the lakes have undergone contractions and expansions thus creating the external barriers necessary for allopatric speciation. Since many of the species of cichlid fishes of Africa are littoral, external barriers between populations do exist in the form of harsh shoreline habitats. Thus the initial reliance on species swarms can be interpreted as a case of mistakenly giving common evidence discriminatory status.

A line of evidence that has, in the past, been thought to unequivocally establish the reality of sympatric speciation is the sympatric occurrence of sibling species (Wieser 1958, Kohn 1958). The reasoning is that this coexistence represents the final stage of their speciation in sympatry. But, as Mayr (1963:452) emphasizes, the assumption is that species originated where they were found. Allopatric speciation can accommodate this evidence by proposing that the sympatry is secondary.

White (1978) has written an influential book on speciation. After a lengthy discussion of sympatric speciation he concludes: "...in spite of the rather woeful lack of evidence as to the genetic processes involved, it seems impossible today to deny the reality of sympatric speciation, at least in many groups of insect" (pg 260). What would be interesting, would be to examine the lines of

evidence White considers to be favourable to sympatric speciation, and to determine whether these are of the discriminatory or common kind. These lines are (pg 231-232):

1. The existence of "biological races", "host races," "ecological races," or "allochronic races" of a species within the same territory.
2. The occurrence of speciation on very small oceanic islands, where geographic isolation could not occur.
3. The results of laboratory experiments on "disruptive selection," some of which seem to provide a plausible basis for sympatric speciation.

The problem with the first and second lines of evidence is that they can be easily reinterpreted under the allopatric model. Two populations may be in the same territory or on the the same small oceanic island but actually never come into contact to interbreed (This point is developed later). They would be effectively allopatric. I conclude that these lines of evidence are common to both modes of speciation. Paterson (1978) has shown that experiments on disruptive selection are fundamentally flawed. This is because an alternative outcome, that of one of the populations going to extinction, is artificially prevented. These experiments do not, then, establish sympatric speciation over the alternative of extinction of one of the populations and therefore only provide common evidence.

The practice of relying on common evidence is not confined to the support of sympatric speciation. In the case of stasipatric speciation authors have often supported the model on the basis of a correlation between fixation of chromosomal rearrangements and speciation. Lewis (1966), for example, writes: "evidence that speciation occurs as a result of saltational reorganization of chromosomes,...comes from the observation that adjacent populations,... may differ greatly in chromosome arrangement and sometimes in basic chromosome

number." But this sort of evidence is common. To show a correlation between fixation of a chromosomal rearrangement and speciation is to show merely that these steps occur in the speciation process. But the dispute is not over what the steps are in speciation but over the causal sequence. Paterson writes: "there certainly appears to be a correlation between speciation and the fixation event, but there is no reason to believe that the fixation of the rearrangement has *caused* the speciation to occur". (Paterson 1981:116, *Italics mine*). Mayr(1978) and Templeton(1981) would agree with this verdict.

Step 2: Distinctly defining the alternatives

Introduction

Mayr (1976a:500, 1978) has repeatedly stressed the need for conceptual clarity in Evolutionary Biology. My object is to show that this need is apparent in the area of speciation; that there are a number of definitions of key terms such as 'sympatric' and 'allopatric' and that because of the ambiguity over what is meant by these terms the testing of alternative modes of speciation is hindered. Paterson (1981) has remarked that if products of speciation cannot be recognised without ambiguity then there is no possibility of ever testing a model of speciation. Normative principles for defining mentioned in the previous chapter will be applied, and some of the definitions given to the above terms will be evaluated.

At the outset it is necessary to emphasize the importance of this subject. It is sometimes said of a distinction that it is merely a semantic difference. The implication is that the meaning of terms is not really important. I hope to show here that how we interpret matters of fact depends in part on the meaning we give to particular terms. Yet there are a number of sometimes rather different definitions for the term 'sympatric' for example.

Variations in the meaning of 'sympatric' and 'allopatric'

The definitions of the terms 'sympatric' and 'allopatric' can be classified into two categories. These will be called the genetical and non-genetical definitions. The non-genetical definitions are expressed in spatial rather than genetical terms. An example is Futuyma's (1979:502): allopatric refers to "... a population or species; occupying a geographical region different from that of another population or species". Similarly Rivas (1964) suggested that the term 'sympatric' be reserved for species within the same geographical area, whether or not they occupied the same macrohabitat. Consequently, sympatric speciation would be defined as "the acquisition of species status by a group of organisms without their being geographically isolated" (Dillon 1973:309).

For some authors the genetic criterion is fundamental. For instance Mayr (1978) considers it better to define 'allopatric' "... in terms of dispersal barriers rather than purely geographically." For him (Mayr 1963:449,451) sympatric speciation is "the origin of isolating mechanisms *within the dispersal area of a single deme*" i.e. a local population. (italics mine). Others authors include both genetic and non-genetic criteria in their definitions but regard the genetic criterion as fundamental. Thus Futuyma (1979:507) wrote that 'sympatric' refers to "two species or populations occupying the same geographic locality [non-genetic criterion] *so that* the opportunity to interbreed is presented" [genetic criterion].

In the next section we will see that the variation in the meaning assigned to 'sympatric' and 'allopatric' leads to drastic consequences for the testing of modes of speciation.

Consequences for testing

One case that *prima facie* supports sympatric speciation is the evolution of the Mallophaga (bird-lice). Clay (1949) reports that one finds closely related species of Mallophaga in restricted and isolated geographical areas. Clay holds to a more or less genetic understanding of 'allopatric'. For her the different species of Mallophaga are unlikely to ever come into contact to interbreed. She regards the host species as analogous to islands because of the low level of migration between them. She says: "... although , in general, the Mallophaga are host specific there are cases of immigrant parasite species establishing themselves on a new host."

For White (1978) that there is *some* migration is sufficient to regard the species as sympatric. He wrote (White 1978:244) that: "Different sympatric host species that come into sufficiently close association (by sharing roosting places, nesting areas, dust baths, or the like) to permit migration of the parasites are emphatically *not* analogous to oceanic islands- they are alternative ecological niches within the same geographic area, habitat, or *patria*."

We see that even though both authors, to some degree at least, are viewing the allopatric/sympatric distinction from a population genetics criterion, each interprets the evidence differently. The source of their difference is *not* over how much migration occurs. Both agree that it is low. It exists over how much migration they will allow to call the situation sympatric. Their disagreement is not over what the facts are, but over what they mean by sympatric or allopatric. This sort of thing has happened many times (Mayr 1963:461-468), but below we will look briefly at just a view more instances.

Under Dillon's definition species swarms in lakes would be *prima facie* evidence for sympatric speciation because here we have many and often closely related species occupying the same geographical area. If, however, the definition of allopatry (and hence of sympatry) were altered to include microallopatry, then

the same phenomenon could be expected under allopatric speciation (Fryer and Iles 1972). Here again we find that the interpretation of evidence depends on the meaning of terms.

Another example concerns speciation within a single island. It is thought that the fact that this occurs supports sympatric speciation. Behind this thinking is the view that populations are sympatric by virtue of being on the same island. Thus White (1978:244-245) writes: "If major geographic barriers are a *sine qua non* for speciation, speciation should be impossible on small oceanic islands..." Much depends on how strictly we define 'sympatric'. White (1978:247) regards the existence of many species of beetles on Saint Helena as "overwhelming evidence for non-allopatric speciation." But then he asks (1978:247): "was this speciation sympatric in the *strict sense* It is possible that very minor geographic barriers, on an extremely local scale, may have provided some temporary isolation in some instances" (my italics). If 'sympatric' is defined strictly then this may not be a case of sympatric speciation. Again we see the close relationship between semantics and testing. The sense in which we use terms is therefore important. It is strange, then, to find White later say that this is "emphatically not a field that should be encumbered by sterile semantic arguments as to the meaning of terms."

Theories contain terms. Defining the alternatives distinctly must involve giving strict meanings to these terms. We have seen above that this is not been done properly. Judging from White's statement the importance of this step is even being played down. Are there any principles that can help us in defining terms? In the previous chapter we saw that there were. It was argued that definition should be causal, ontological and universal (or at least have the highest possible degree of universality). In the next section definitions of the terms 'allopatric' and 'sympatric' will be evaluated according to these principles.

An evaluation of definitions

The principle of ontology suggests that we need to distinguish between whether two populations are sympatric from the point of view of the organisms or whether from the viewpoint of man. It is very possible that two populations are effectively allopatric whereas a human observer would have difficulty perceiving it as such. The following statement by White suggests that he confused these issues: "It is possible that very *minor* geographic barriers, on an extremely local scale, may have provided some temporary isolation in some instances" (*italics mine*). But minor to whom? What to humans may be a minor barrier may be major to a flightless beetle. The biologically important criterion is whether the populations are presented with the opportunity to interbreed (Futuyma 1979:507). In other words, a useful *indicator* of sympatry is geographical proximity but this should not be the definition of sympatry just as morphological dissimilarity is a useful indicator of species status but should not be used in defining 'species'.

One problem with definitions that rely on purely geographical criteria, then, is that this is not the most biologically meaningful or fundamental way of defining allopatry or sympatry. Mayr (1978) has agreed that it "would seem advisable to define allopatric in terms of dispersal barriers rather than purely geographically."

A related way of evaluating a definition is to determine how far it will support counterfactuals. One can evaluate Futuyma's (1979:502) definition of allopatry in this way by expressing it in the form of a conditional: If X and Y occupy A and B respectively then they are allopatric, where X and Y are different populations or species, and A and B are different geographical regions.

Imagine a country (call it Smogaria) in which all *human* males become infected with a disease which renders them sterile. Other *countries*, fearing the spread of the disease, forbid all Smogarians to tread on their soil. For the same

reason the Smogarian tourist industry becomes non-existent. The Smogarian government, concerned that they might not have a next generation, calls for aid. And aid comes from the U.S.A. in the form of refrigerated sperm parachuted onto the island. The U.S.A. and Smogaria are separate geographical regions but the populations are effectively sympatric because of the transfer of sperm. Thus the above conditional does not satisfy the universality test.

A definition that does satisfy the criterion of universality is Key's (1981:430). His object was to sharpen Futuyma's (1980) definition. It reads as follows:

"Allopatry- a distributional relationship in which two populations occupy territories separated by a region that neither crosses and which is free from any intergrades or hybrids between them."

or in the form of a conditional:

'If X and Y occupy A and B respectively and neither crosses a region C separating them where C does not have any hybrids between A and B.'

According to this conditional the 'U.S.A.-Smogaria' case is really sympatric because there will be intergrades between the two populations. It is worth noting why this conditional satisfies the universality criterion. It is because it is expressed not just in geographical terms. Since it includes a population-genetic criterion it is able to cover the hypothetical situation above.

However, I do not think this makes Key's definition acceptable. In light of the previous chapter we can see that Key's definition is unnecessarily complicated because it includes both the fundamental and the less essential. We have seen that definitions should contain that single criterion thought to be the decisive one.

Futuyma's (1979) definition also does not satisfy this test. He wrote that 'sympatric' refers to "two species or populations occupying the same geographical locality (non-genetic criterion) so that the opportunity to interbreed is presented (genetic criterion). This definition is interesting because the 'so that' reveals what Futuyma believes to be the more fundamental criterion- the genetic one.

Conclusions

We have seen that there are a variety of definitions of the terms 'allopatry' or 'sympatry' in the literature and that as a result there are differences in the interpretation of evidence on speciation. While discussion has been restricted to two important terms this conclusion may apply more broadly. For example, In the case of the evolution of the the morabine grasshoppers, what Bush (1975a) regards as parapatric speciation, Grant (1981:151) calls "allopatric speciation in sedentary organisms."

In agreement with Mayr it is concluded that definitions of 'allopatry' or 'sympatry' that are merely in distributional terms are inadequate, and that it is better to define these purely genetically.

Step 3: Developing multi-cornered deductions

In this section cases of apparently successful science will be contrasted with those cases that were apparently unsuccessful. The object is to show that the degree to which successful science is practiced is, in part, dependent on the degree to which the predictions of hypotheses are multi-cornered. Developing these sorts of predictions involves drawing as many deductions as possible that are different between the various modes of speciation. We shall find that the

above principle has to be tailored to some special features of Evolutionary Biology.

Before we go further it is necessary to discuss an objection that some might have about applying this step to Evolutionary Biology. Their reasoning would be as follows: testing hypotheses through their predictions is standard scientific procedure. Evolutionists cannot predict. They cannot say beforehand when a species will speciate or what it will speciate into. Thus, the scientific method cannot properly be applied to Evolutionary Biology.

Ghiselin (1969:27-28) and Williams (1985) have shown that this predictionist thesis is gratuitous; that it is based on a misunderstanding of what logicians mean by prediction. The term 'prediction' in common parlance carries along with it the idea of a forward looking. When logicians use the term they mean deduction. It is not necessary, for the testing of hypotheses, that deductions be forward looking.

The argument expressed above reflects an interesting methodological bias toward the hard physical sciences. Philosophers of science (e.g. Ghiselin 1969:27-29) have repeatedly pointed out that it is relatively easy to predict in the forward looking sense in the hard sciences, because it is relatively easy to control the relatively small number of background conditions. In evolutionary biology, however, it is impossible in practice to control all of the potentially vast number of background conditions. Hence the difficulty in predicting in the forward looking sense.

Testing is still possible in evolution through the use of retrodictions or backward looking predictions (Ruse 1973:100-102, Popper 1980). We have seen in the first chapter that, from the perspective of demarcation, it is irrelevant whether predictions or retrodictions are used. The reason is that one can exclude

hypotheses with either. The result is diminishing theoretical diversity which is characteristic of scientific disciplines.

The nature of evolutionary biology necessitates the use of retrodictions. There are a potentially large number of background conditions involved in the speciation process. Because it is impossible in practice to control all these, it is necessary to look back from our modes of speciation and predict what conditions or stages are necessary for a particular mode of speciation to occur.

In the next section I wish to describe some normative principles which may be useful in the application of step 3 to the biology of speciation. My one thesis is that it is essential to understand the specific characteristics of the speciation process if we are to practice this step properly. In the previous chapter the speciation process was described as a causal chain. It was noted that causal chains have particular properties (Hull 1974), and that understanding these properties may help us in understanding speciation. Now I will list some of these properties showing how these affect how we apply step 3.

Normative principles in testing modes of speciation

Speciation is a historical process, and, as Ghiselin (1969:28-29) shows, an examination of conditions is indispensable in historical explanations. This creates a complexity in the process which is heightened by the relation between cause and effect not being universally reciprocal. A single or particular condition may be necessary but not sufficient for a particular outcome. For example, the occurrence of two populations in sympatry is a necessary prerequisite for sympatric speciation but it is not sufficient. Coupled to this sympatry the model requires, amongst other things, a stable polymorphism.

This fact implies some important things about how we test modes of speciation. Because a number of conditions are necessary for a particular mode

of speciation to occur it is unlikely that a model would stand or fall upon a single condition. This point needs to be emphasized. It is tempting to think that the occurrence of a necessary condition for a particular mode of speciation, implies the occurrence of that mode of speciation. Mayr (1978) has reported that this distinction between necessary and sufficient conditions for speciation has not always been kept in mind. One way of ensuring multi-cornered predictions is to specify a set of conditions that must be met for a particular mode of speciation to occur. We may not be able to ask for a *single* multi-cornered condition. We can ask for a multi- cornered *cluster* of conditions. A multi-cornered cluster is a set of conditions such that if they occurred, one and only one particular mode of speciation would result. In summary, then, the development of multi-cornered conditions requires the specification of a set of conditions because of the complex nature of the subject material.

A second point is that evolution is a historical process. This means that to correctly interpret a case it may be necessary to know, for example, the past distributions of populations. Evidence on this is unfortunately often difficult or impossible to obtain.

A third point has been made forcibly by Ghiselin (1969) and Williams (1973). In evolution it is often necessary to make predictions about patterns in sets of phenomena, rather than about individual events. In what follows these principles will be explained and applied.

Applying normative principles

Since modes of speciation differ in their sequence of events, any predictions regarding sequence are likely to be multi-cornered to some extent. One way this can be done is to set up experimentally a presumed stage in speciation in the field, and then observe the outcome. This has in fact been done. Lewis, working

on *Clarkia* set up two populations in sympatry. Although, the deductions were not spelt out, table 5-1 shows their form.

Table 5-1. The deductions in Lewis's (1966) argument.

Conditions	then	Outcome
Sympatry, heterozygote disadvantage	then	speciation by reinforcement.
Sympatry, heterozygote disadvantage	then	extinction.

The deductions are multi-cornered because two different outcomes are expected from the alternatives modes. Note that the predictions in this example are forward looking. It could be objected that Lewis' experiment does not really discriminate against speciation by reinforcement because he did not provide the special conditions required for this mode of speciation to occur (see p105). The objector is right. This experiment shows three things: that extinction is a viable alternative to reinforcement; that in this instance reinforcement is discriminated against; and that to make general statements about the occurrence of one or other mode it is important to establish the conditions required for these modes.

To establish the conditions necessary for a mode to occur it is necessary to construct mathematical models. This is a second way in which multi-cornered predictions can be developed. Here a stage in the evolutionary process can be represented mathematically and the outcome followed algebraically. In describing the construction of a multi-cornered deduction it may be helpful to contrast it with one that is not. Consider the following argument:

"If the gene pools of the two populations are sufficiently different, progenies from interpopulational crosses are likely to have less fitness than progenies from intrapopulational crosses. Mating preferences are affected by genes. Alleles that decrease the probability of mating with individuals of a different population will, then, be selected for, while alleles increasing the probability of intrapopulational mating will be favoured by natural selection. Eventually, the process may result in two reproductively isolated populations, and thus two different species" (Ayala 1974 *et al*).

The problem with this retrodiction as Paterson has shown is that heterozygote disadvantage can lead to an alternative outcome - elimination of the rarer population or chromosomal arrangement. Since the same condition (heterozygote disadvantage) is retrodicted from two outcomes, this retrodiction

is not multi- cornered, but common. It is necessary but not sufficient for reinforcement to occur.

We have seen that since speciation is a complex process it is unlikely that one can find a single multi-cornered deduction. In the deduction above the other conditions necessary for speciation by reinforcement to occur have been ignored. One has to determine what cluster of conditions are necessary for a given outcome. In a multi-cornered deduction a set of conditions are specified such that if they occurred the only outcome would be one particular mode of speciation.

Paterson and McNamara (1984) argue that purely verbal arguments often appear plausible, whereas if they were expressed mathematically they would not. With this in mind let us look more closely at the argument of Ayala *et al.* Note the use of the term 'may' in the argument. This might suggest that all that is being said is that reinforcement is a possibility, and who could argue with that? But by only mentioning reinforcement one is left with the impression that this is the most likely outcome without this actually being said.

What are the conditions relevant to speciation by reinforcement? Below are a few:

- a) heterozygote disadvantage- for the reason given by Ayala *et al.* above.
- b) size of parental populations- these have to be maintained to prevent extinction of rarer population or chromosomal rearrangement (Paterson 1978).
- c) number of niches (Maynard-Smith 1966).
- d) whether there is habitat selection or not (Maynard-Smith 1966).

e) the stability or potential for change in mate recognition systems, henceforth denoted by k . If k is too low reinforcement is unlikely to occur (Lambert, Centner and Paterson (1984)).

This is not an exhaustive list. Each condition described above may be affected by a large number of sub-conditions. For example, there are many factors which affect population size and the constant k . Also the outcome of a set of conditions or sub-conditions depends on an interaction between factors. Lambert *et al* report that k may depend on "the amount of variation, co-adaptation of signals and responses and the complexity of the repertoire of courtship behaviour". They also state that the outcome is dependent on an interplay between forces favouring extinction and those favouring divergent systems of mate recognition. It is not obvious, then, what conditions are necessary for a given outcome. Because of the complexity of causal relations it is essential to formulate mathematical models in drawing the logical connections between conditions and outcome. A purely verbal statement is insufficient.

This has been done in part by Maynard-Smith (1962). He showed that for disruptive selection to lead to a stable polymorphism (which is necessary for speciation by reinforcement) you would need the populations occurring in the two niches to remain constant in size. The beauty of this model is that it links the probability of occurrence of a stable polymorphism to a condition that can, and in fact, has been determined (as we shall see later). His predictions are thus to some extent multi-cornered. Later he showed that given a stable polymorphism you could get speciation by reinforcement if there was imprinting or conditioning. Maynard-Smith is drawing logical connections between sympatric speciation and conditions that are both decisive for the model and which can be determined.

Lambert, Centner and Paterson (1984) went deeper and showed that a critical factor is k - the potential for change in the fertilization system. If k is low the

probability of extinction of the rarer population or chromosomal rearrangement is greater than the probability of speciation. Using computer simulation they could determine the minimum value of k required for speciation by reinforcement to occur and obtained a value of .15. Their deduction is multi-cornered and is broken down in table 5-2.

Table 5-2. The predictions of Lambert et al (1984).

Conditions		Outcome
$k < .15$, sympatry	then	extinction of one population.
$k > .15$, sympatry	then	speciation by reinforcement.

The deductions are multi-cornered because two different sets of conditions are retrodicted from the two outcomes. Again, the beauty of such a deduction is that one can easily estimate k from selection experiments (which has been done) and use the data to decide between the alternatives.

Let us examine one more approach to developing multi-cornered predictions- the use of distributional studies. The purpose here is to determine what it is about this procedure that makes it work. Ghiselin (1969:148) says that confirmation of geographic speciation has come for the most part from these sorts of studies. The theory implies that there will be a correlation between the amount of speciation and the presence of geographic barriers; that speciation will be greatest in those groups that have difficulty in dispersal in a particular environment. Table 5-3 expresses Williams's (1973:521) deductions.

Table 5-3. Williams's (1973:521) deductions.

"If allopatric speciation is the prevailing mode...	then	... the majority of the incipient species pairs existing today will have the two members of the pair living sufficiently far from each other to be outside each others dispersal range..."
"If sympatric speciation is the prevailing mode...	then	...less than half of the incipient species pairs found today will be found with the two members of the pair living sufficiently far from each other to be outside each others dispersal range..."

Author Anderson Michael Laurence

Name of thesis Aspects Of Scientific Methodology With Special Reference To Evolutionary Biology. 1988

PUBLISHER:

University of the Witwatersrand, Johannesburg

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