SPECIATION AND THE RECOGNITION CONCEPT

THEORY AND APPLICATION

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The Johns Hopkins University Press

Baltimore and London

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Printed in the United States of America
on acid-free paper
04 03 02 01 00 99 98 97 96 95 5 4 3 2 1

The Johns Hopkins University Press
2715 North Charles Street
Baltimore, Maryland 21218-4319
The Johns Hopkins Press Ltd., London

A catalog record for this book is
available from the British Library.

Library of Congress Cataloging-in-Publication Data

Speciation and the recognition concept : theory and application / edited by David M. Lambert, Hamish G. Spencer.
p. cm.
Includes index.
ISBN 0-8018-4740-0 (hc : alk. paper). —
ISBN 0-8018-4741-9 (pbk. : alk. paper).
1. Species. 2. Sex recognition (Zoology). I. Lambert, David M. II. Spencer, Hamish G.
QH380.S64 1994
575.1'3—dc20 94-27980
CIP

MINOT STATE UNIVERSITY OLSON LIBRARY

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1

Species as Habitat-Specific, Complex Systems

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THE SPECIES CONCEPT has often been construed as an epistemological "chameleon" able to take on whatever meaning happens to be convenient in a given subfield. This tradition is reflected by the many species definitions bearing descriptive prefixes, like **chronospecies**, **morphospecies**, or **taxospecies** (terms defined in the glossary at the end of this chapter). The contrary view, which I share, is that all species should be the same kind of ontological entity and that all speciation should denote one particular kind of process. I will compare the major ontological concepts that have been debated recently (e.g. Otte and Endler 1989; Kimbel and Martin 1992): the **Isolation** (= "Biological," Mayr 1963), **Recognition** (Paterson 1978, 1985), **Phylogenetic** (Cracraft 1983), and **Cohesion** (Templeton 1989) species concepts. Table 1.1 compares the concepts in terms of the character divergence regarded as necessary for speciation.

It is largely a semantic matter which kind of entity should bear the venerable name *species* and what the names for other kinds of organismal groups should be. But the conceptual distinctions should be made and honored by different names of some kind. I will explore four questions that I regard as fundamental to the natural organization above the level of organisms:

1. Does a given concept require a species to have the *status of a complex system* (see Simon's [1962] definition in the next paragraph), by virtue of consistent, heritable among-organismal interactions? Or does it approach species and species' characters, respectively, as no more than aggregates of organisms and of organismal characters related by descent?

2. Is each species required to have a unique **habitat specificity**, that is, a unique combination of **resources** that it can use?

Table 1.1. Character divergence required for speciation under the Recognition (Paterson 1985), Isolation (= "Biological" [Mayr, 1963]), Cohesion (Templeton 1989), and Phylogenetic (Cracraft 1983) species concepts

	Required character divergence						
Species concept	Prefertilization system		Postfertilization system		Habitat adaptation		Any other
Recognition	X						
Isolation	X	or	X				
Cohesion	X	or	X	or	X		
Phylogenetic	X	or	X	or	X	or	X

3. Does a concept require speciation to result in *irreversible lineage branching?* Or does it allow species to be ephemeral with species-specific characters that either disappear or merge with those of the sister-species when the two come into secondary sympatry?

4. Is each species required to be a *monophyletic group* (*sensu stricto,* Nelson 1971) of organisms?

The concepts are characterized according to these four criteria in Table 1.2. I also discuss the operational problems of using each of the concepts to diagnose species.

Should Species Be Construed as Complex Systems?

One definition of a dynamic system is that of Caswell et al. (1971:4): "a collection of objects, each behaving in such a way as to maintain behavioral consistency with its environment which may include other objects in the system." This includes such a broad range of phenomena that "species" under

Table 1.2. Comparison of the implications of the Phylogenetic, Cohesion, Isolation, and Recognition species concepts

	Do species require:			
Species concept	Complex system status?	Unique habitat specificity?	Irreversible branching?	Monophyly?
Phylogenetic	No	No	No	Yes
Cohesion	No	No	No	No
Isolation	Yes	No	No	No
Recognition	Yes	Yes	Yes	No

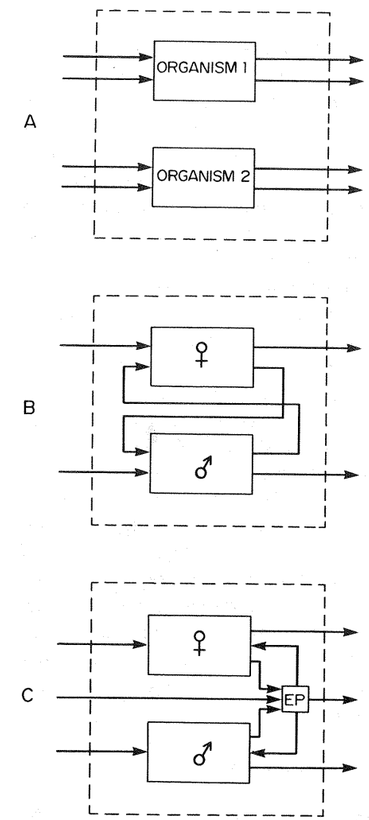


Fig. 1.1. Block diagrams representing organisms as subsystems within two kinds of organismal groups, or systems. *a,* The simple asexual case: organisms do not interact with each other, only with the environment. *b,* The complex biparental sexual system: males and females not only each have inputs from and outputs to the environment, but also interact with each other. *c,* Male-female interactions result in an emergent property, the Specific-Mate Recognition System (Fig. 1.2), that interacts with the environment.

all concepts qualify as systems. I will focus more narrowly on the complex system discussed by Simon (1962:86) as "a system made up of a large number of parts that interact in a nonsimple way. In such systems, the whole is more than the sum of the parts, not in an ultimate metaphysical sense, but in the important pragmatic sense that, given the properties of the parts and the laws of their interaction, it is not a trivial matter to infer the properties of the whole. In the face of complexity, an in-principle reductionist may be at the same time a pragmatic holist." Figure 1.1a represents a system, the subsystems (here organisms) of which interact only with the environment and not with each other. I am concerned here with complex systems (Fig. 1.1b,c) in which the causal influences acting between environmental inputs and outputs involve not only the subsystem states, but also emergent properties of the system resulting from particular interactions between subsystems.

Living entities clearly include complex, hierarchically structured systems. In fact, one of the most striking and quintessential attributes of life is its **hierarchy** of subsystems (or stable subassemblies, *sensu* Simon 1962) nested and interacting within larger systems, and so on, at levels of increasing complexity. If there is any biotic phenomenon, besides reproduction and resulting genealogy, that definitely needs representation in biological formulations and concepts, it is this one. Of course, the complex-system hierarchy *is* prominently acknowledged by the most basic concepts we have. A "gene" made up of certain base pairs is different from a collection of those same base pairs, because the gene consists of those base pairs *and* a particular arrangement and interaction of those base pairs relative to one another. "Cell" and "metazoan organism," referring to two kinds of complex systems each of interacting subsystems, are also keystone concepts, which are real to all biologists and for the most part unambiguously and uniformly defined.

Groups of Organisms as Systems

When it comes to entities arising from organization *among* organisms the meanings of the few terms we have are hotly disputed. This failure with respect to systems *above* the organism level is unprecedented for biology. I suggest that the overwhelming reality and importance of hierarchy in biology is one good argument to reserve the familiar term *species* for a kind of complex system existing above the organism level.

Many of the actions organisms do by which they stay alive are purely or largely direct transactions with the physical environment. For instance, when oryx antelopes of the species *Oryx gazella* thermoregulate during the heat of a day in the African deserts, by panting that sets up countercurrent cooling of arterial blood on its way to the brain (Taylor 1969), in one sense it is true that the *species* is thermoregulating. But it is true only in the sense of a simple

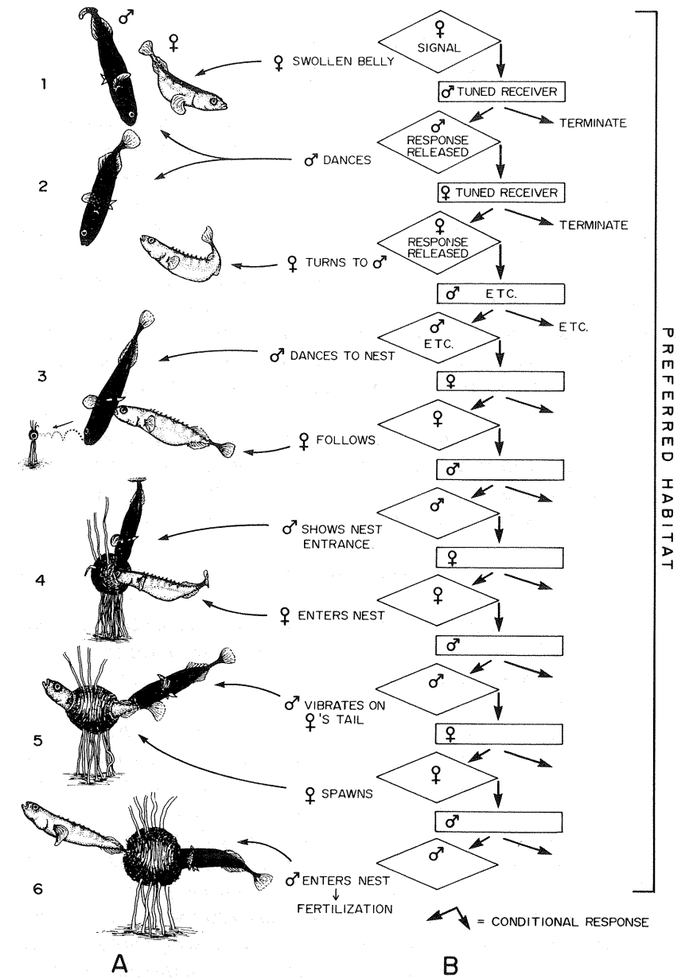


Fig. 1.2. *a,* The Specific-Mate Recognition System (SMRS) of *Pygosteus pungitius,* the ten-spined stickleback. *b,* Schematic illustration of the form of the SMRS as a coadapted signal-response reaction chain. (Adapted from Morris 1970[*a*] and Paterson 1985 [*b*].)

summation of the organismal behaviors (Fig. 1.1a, if one thinks of the larger system as *Oryx gazella,* the subsystems as oryx antelopes, the inputs as temperature, and the outputs as cooler brains, altered metabolism, behavior, etc.): The species *O. gazella* is not acting as a complex system with respect to thermoregulation. Many other activities, such as locomotion, feeding, and excretion, belong in this category, at least in many instances in many lineages.

Yet there are other cases of behaviors that depend on *among*-organism interactions. Where an entire lineage shares genetically based interactive behavior of this kind, with broadly predictable results in terms of population structure, variation-composition, and distribution, the lineage acts as a complex system, and those results are correctly termed heritable emergent properties of the lineage. (See Schull [1990], who explored species as massively parallel distributed processing systems, indeed as intelligent systems, with emergent properties based on mutation and recombination rates, on interdemic variation, and on the "species' norm of reaction" based on all the reaction norms of the component organisms.)

The most striking among-organismal organization is evident in biparental sexual reproduction [Fig. 1.1b,c and Fig. 1.2]. Because sexuality versus asexuality has featured prominently in species debates, let us briefly consider different reproductive modes.

Reproductive Modes

The distinction that is particularly relevant is that between (1) lineages that never have biparental sexual reproduction and (2) lineages that at least sometimes have biparental sexual reproduction.

A lineage of kind 1 (represented by Fig. 1.1a) is not a complex, among-organismal, reproductive system (although, of course, those organisms may interact in respects other than reproduction, such as by colony formation and by subdivision among them of feeding and defense roles and may constitute complex systems with respect to those interactions). Lineages with reproductive modes of kind 1 include the following (see glossary definitions from Bell [1982] and extensive discussions in Ghiselin 1974*a;* Williams 1975; Maynard Smith 1978; and Bell 1982): all lineages with obligate parthenogenetic **thelytoky** in either of its guises, **apomixis** and **automixis**, which are all uniparental modes (except biparental **gynogenesis**), and lineages that always use uniparental sexual modes such as obligate self-fertilizing hermaphrodites.

Lineages with reproductive modes of kind 2 follow the scheme in Fig. 1.1b,c at least some of the time. They comprise all those with obligate **amphimixis** (i.e., with syngamy between biparentally produced gametes); all lineages with parthenogenetic **arrhenotoky** (because although the haploid males are from unfertilized eggs, diploid females are produced from fertilized eggs); and all lineages with **heterogony** (with cyclical parthenogenetic life cycles in which one or more thelytokous generations are followed by an arrhenotokous or amphimictic generation).

Prevalence of Reproductive Modes

Many have objected to a sexual reproduction criterion for species on the grounds that several kinds of populations (those of kind 1) would be excluded from species status. (See review in Templeton [1989] who sums up his objection as the problem of "too little sex".) Thus, it is of interest what proportion of differentiated forms of life is in fact of kind 1, that is, that never engaged in biparental sex.

I have not found in the literature any estimated numbers of obligate self-fertilizing hermaphrodites. But Maynard Smith (1978) addressed such estimates for the other, larger category among reproductive modes of kind 1, namely that of obligate parthenogenetic thelytokes. He noted that "existing parthenogenetic populations must be descended from many hundreds of different ancestral lineages. Yet, with one important exception (the bdelloid rotifers), in no case does a major taxonomic group (subfamily or above) consist predominantly of thelytokous populations" (p. 53). On the same page he gave the example of the twenty-eight known thelytokous varieties of psocids (Insecta: Psocoptera) which "belong to thirteen different families, and in twelve of the twenty-eight cases there are sexual and parthenogenetic forms of the same nominal species." He concluded that a fundamentally similar picture is found in plants. It seems that thelytokous forms crop up in phylogenetically isolated positions, that these forms have hardly ever diversified after origin, and that *obligate* thelytoky may be rare. In fact, the major reviews (Ghiselin 1974*a;* Williams 1975; Maynard Smith 1978; and Bell 1982) suggest that the vast majority of distinct lineages among the highly diversified metazoans at least at some times engage in biparental sex.

Lineage as a Complex System due to the Fertilization System among Organisms

Figure 1.1b represents two kinds of subsystems, male and female, that share a fertilization system (the male-female interaction linkages in Fig. 1.1b) to constitute a larger system. The fertilization system of many taxa in which males and females remain in proximity is simple. In contrast, most mobile organisms have additional signal-response interactions that serve to bring sexual partners together for mating—the subsystem of the fertilization system that Paterson (1978) has termed the **Specific-Mate Recognition System** (SMRS). Among SMRSs, one can further note widely differing degrees of com-

plexity. At one end of the spectrum are the minimal signal-response interactions of, for instance, the chemical recognition system found by Wiese and Wiese (1977) between mating types of the green alga *Chlamydomonas moewusii*. At the other extreme are some elaborate vertebrate SMRSs that include olfactory, auditory, tactile, and visual (color and behavioral) signals. In Figure 1.2 the form of the SMRS as a coadapted signal-response reaction chain is schematically illustrated (b) and exemplified by the moderately complex SMRS of *Pygosteus pungitius*, the ten-spined stickleback (a). (This and other courtship sequences are analyzed in Morris [1970]. Note that Fig. 1.2 shows the "classical" version of the courtship reaction chain in *P. pungitius*, while in reality most responses of either sex can be released by more than one action by the opposite sex. Yet Morris points out that the range of possible sequences that lead to fertilization is severely constrained.)

I suggest that a lineage of biparental organisms that share a unique fertilization system is itself a system, with both "vertical" linkages among organismal subsystems (by chains of ancestry and descent through time) and "horizontal" linkages (by interactions at particular times). To acknowledge the larger entity (here the species *P. pungitius*) as a system does not require that the linkages between male and female subsystems must be activated at all times. Inputs from the environment, together with the internal states of the subsystems, at some times result in a positive signal along the interaction linkages and at other times in a zero signal value, as is well known in nature for sexual systems. For instance, even in an obligate biparental sexual form like *P. pungitius*, reproduction is suppressed in environments that are unsuitable for SMRS function (as will be elaborated on below, after Morris 1970). In heterogonic lineages, such as *Aphis fabae* and many other aphids, many parthenogenetic generations can intervene between episodes of sexuality; and experimental manipulation of variables like temperature and photoperiod can elicit the switch from one reproductive mode to the other (Bell 1982). But the temporary absence of positive signals along the SMRS interaction linkages does not disqualify the lineage from constituting a sexual system.

Figure 1.1c represents the notion that the interactions among the subsystems can result in emergent systems properties. (I here mean the operational concept of emergence used in mathematical modeling of dynamic systems about which, for instance, Caswell et al. (1971:39) wrote: "It is an unfortunate fact that emergent properties have sometimes been given an almost mystical character in the literature. They *are* real phenomena, which do arise to confront anyone studying a complex system.") Fully elaborated sexual reproduction as a whole is a synapomorphy emergent at the lineage level that characterizes a huge living clade (if those who argue that it evolved only once are correct). Each unique SMRS, such as the stimulus-response reaction chain of the ten-spined stickleback (Fig. 1.2) and including all of its genetic and phenotypic components, is a complex emergent property, subdivisible into component emergent properties, of a particular lineage system, although particular SMRS components may be shared by clades over millions of years.

The sexual system has had enormous consequences for evolution, through its effects on the variation distributions within and among lineages and on rates of lineage diversification and extinction. While sexual lineages have massively diversified into the vast majority of distinct metazoan phenotypes on earth, asexual lineages characteristically have remained undiversified from their phylogenetically isolated origins (Williams 1975; Maynard Smith 1978; Arnold et al. 1989). As Maynard Smith (1978:54) puts it: "The facts fully support the . . . view that parthenogenetic varieties are doomed to early extinction." If evolutionary impact is considered a criterion for what should be encompassed by our favorite biological concepts, then the unique sexual systems among organisms are good candidates for species status.

Species Concepts in Relation to Complex Systems

The Phylogenetic Concept

The requirement under the Phylogenetic Concept that species be strictly monophyletic is based explicitly on nested homologies at the *levels of organisms and their constituents*. Whereas organismal characters that participate in sexual systems are used to deduce organismal genealogies, emergent characters of among-organismal systems are excluded. The set of phylogenetic species includes both asexual and sexual monophyletic groups of organisms. Thus, whereas this concept brings a strong hierarchical approach to deducing organismal genealogy, it ignores hierarchy in the systems sense by leaving out levels of organization above that of organisms.

An example within my family partly illustrates this species concept. My grandmother was born with the mutant phenotype of an abnormal left lower rib morphology. By chance assortment of alleles it happens that all her descendants so far bear this phenotype. Thus, we are a "smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (Cracraft 1983). Thus, I gather that under the Phylogenetic Concept we are a species. Yet, as we happen to live in different parts of the world without interactions (all our interactions, including sexual ones, are with "nonspecifics"), we are not a system of interacting subsystems. If we are a "species," we are likely to be an extremely ephemeral one.

The Recognition Concept

In contrast to the Phylogenetic Concept, the Recognition Concept focuses squarely on systems properties above the organismal level: the crux of the recognition species, and the phenomenon we can look at in nature to study it,

is the system of "horizontal" linkages of interactions among sexual partners (Fig. 1.2). By virtue of strong stabilizing selection on the fertilization system (Paterson 1978, 1981, 1985), it also has potential stability through long time along the "vertical" linkages of ancestry and descent.

As mentioned above, the SMRS is an important subpart of the fertilization system in mobile organisms. Although entire clades of species may be characterized by individual components of the SMRS, such as a pheromonal, auditory, color, or behavioral phenotype of the male or female, a recognition species can be diagnosed only by the complete system based on a combination of such characters that is unique to a given cluster of related biparental organisms. (See example in Fig. 1.2. I emphasize that the choice of the fairly complex example in Fig. 1.2 should not be mistaken for "vertebrate-centric" bias against taxa with the rudimentary fertilization systems, which would not do justice to Paterson's [1978] intent. He has consistently argued that his concept applies equally to taxa, like many plants and the *Chlamydomonas* algae mentioned above, with simple systems.)

Paterson argued at length (convincingly, in my view) that divergence in the *post*fertilization system on its own (see Table 1.3) is highly unlikely to initiate

Table 1.3. Mayr's (1963:92) classification of "isolating mechanisms" augmented from Templeton (1989)
(The term *isolating mechanisms* is in quotes to indicate that it is inappropriate [Paterson 1978].)

Prefertilization isolation[a]

1. Premating isolation
   a. Ecological (habitat and temporal) isolation: potential mates do not meet because they mate in different habitats (or use different pollinators, etc.) or in different seasons
   b. Ethological isolation: potential mates meet but do not mate
2. Postmating but still prefertilization (prezygotic) isolation
   a. Mechanical isolation: copulation attempted but no sperm transfer takes place
   b. Gametic mortality or incompatibility: sperm transfer occurs but egg is not fertilized

Postfertilization (postzygotic) isolation

3. a. F1 inviability because zygote dies or produces a hybrid of reduced viability
   b. F1 sterility because hybrid is fully viable but partly or completely sterile
   c. F2 or backcross hybrid breakdown due to reduced viability or fertility
   d. Endoparasitic or cytoplasmic infection of a population results in fertility or viability breakdown after matings with uninfected individuals, although infected individuals are interfertile

[a] Under Paterson's (1978, 1985) Recognition Concept (1) prefertilization isolation (1*a*–2*b*) results as an incidental effect of divergence of the prefertilization system; and (2) in motile organisms the character subset of the fertilization system of especial importance is the Specific-Mate Recognition System (SMRS), underlying (1*b*) and, provided one accepts "lock-and-key recognition" during copulation and "gametic recognition" as part of the SMRS, also (2*a*) and part of (2*b*).

new separate branches on the "tree of life." Therefore, the species concept should focus on the causal network that matters: the *pre*fertilization—or simply fertilization—system. To my knowledge he was the first to argue this "to the hilt" of its consequences for branching in the sexual biota. In doing so he particularly had to address the logical and biological shortcomings of the Reinforcement Model of speciation according to which "isolation mechanisms" (Table 1.3) evolve by selection for isolating function (as espoused by Dobzhansky 1935, 1937; Ayala et al. 1974). Since the publication (Paterson 1978) many have quietly come to a closely similar conclusion on the improbability of reinforcement speciation (e.g. Mayr 1982; Lande 1979; Futuyma and Mayer 1980; Templeton 1981, 1989; Carson 1982; Butlin 1989).

The Isolation Concept (Biological Species Concept)

The elements of the Isolation Concept of species date from Dobzhansky's (1935, 1937) analyses and also Mayr's (1942, 1963; but see Eldredge, this volume). These were seminal in replacing the **typological species** concept with the neo-Darwinian synthesis of species as sexually reproductive units. This synthesis deserves credit for demolishing the idea of species as classes with defining essences (see Mayr 1970; the notion of species as logical individuals was later argued extensively by Ghiselin [1974*b*] and Hull [1976]).

It is curious that, while this tradition explored the implications of a reproductive system, especially for population variation, it focused strongly on its *negative* consequences—reproductive isolation—rather than on the system itself. Its central theme has been the importance of isolating *mechanisms* and how they could evolve by selection. Both prefertilization and postfertilization divergence to reproductive isolation are regarded as separately sufficient for speciation (Tables 1.1 and 1.3); thus, the idea of among-organismal systems is implicit in this concept (Fig. 1.1; Table 1.2), but in a negative sense. If species are to be construed in terms of sexual systems then, as Paterson has remarked (pers. comm.), it is as curious to construe them in terms of an "isolating function for hybridization avoidance" as it would be to view sex as being "for celibacy avoidance." It is hardly surprising that many speciationists (e.g. Templeton 1989) have come to agree with Paterson (1978) that this concept, although long known as the *Biological Species Concept,* is more appropriately termed the *Isolation Concept.*

The Cohesion Concept

The Cohesion Concept represents Templeton's (1989) effort to include all asexual and sexual forms (see the glossary for an outline of his ideas). He did not define cohesion more explicitly than genetically based "phenotypic cohe-

sion." Among the "cohesion mechanisms" that promote phenotypic similarity by descent among organisms, he included very diverse phenomena: gene flow that promotes (while its absence preserves) genetic identity, the fertilization system *and* the postfertilization developmental system (and, thus, isolating mechanisms), genetic drift in monophyletic groups of organisms, natural selection for **niche** adaptation, and a variety of constraints on evolutionary change.

Table 1.4 gives my interpretation of how Templeton (1989) would apply his criteria of "genetic" and "demographic exchangeability" to decide on species status in different cases of two populations. *Case 2:* For two or more sexually reproducing populations to belong to the same species, "genetic exchangeability" between them is not sufficient on its own in this view. They have to be "demographically exchangeable" as well by virtue of a common "fundamental niche." For instance, the members of a **syngameon** (a syngameon is equivalent to a recognition species), because they are not demographically exchangeable, are separate cohesion species although they share genetic exchangeability. *Case 3a:* Demographic exchangeability can be sufficient on its own to decide species status without any reference to genetic exchangeability, as in the case of the "asexual species" recognized under this view. *Case 3b:* Yet, demographic exchangeability between two populations does not guarantee conspecificity. I gather that Templeton would recognize two sexual populations that still share a common habitat but have diverged postfertilization systems (i.e., that have lost genetic exchangeability) as two species.

In sum, the cohesion species clearly does not *require* an among-organismal interactive system; for instance, the consequences at the population level (genetic identity) of selection at the organism level or of drift are enough.

Table 1.4. Number of cohesion species recognized in different cases of two populations[a]

Demographic exchangeability between two populations	Genetic exchangeability between two populations	
	Yes	No
Yes	1. One Species	3a. Asexual: one species 3b. Sexual: two species
No	2. Two Species	4. Two Species

[a]This table represents my interpretation of how Templeton [1989] would apply his criteria of "genetic and demographic exchangeability" to decide on species status.

Does a Species Need a Unique Component of Habitat Specificity?

The strong association in nature of distinct organisms with different combinations of climatic and other habitat variables (Darwin 1859) must surely be a prime candidate for the basis of a species concept. One can argue that species status should necessarily imply a unique relationship to habitat (note the subtle difference between a **habitat** and a **niche**). Before I compare the four species concepts in this respect, I raise five points regarding habitat specificity and the resources that organisms can use. In one way or another these points are relevant to all species concepts. In discussing these five points, when I refer to "species" I here have in mind not a particular bias with respect to problematic units (such as syngameons and sibling species), but those many units in the systematic literature the species status of which seems to enjoy widespread consensus.

Habitat Specificity as a Tolerance Range Based on Genetic and Ecophenotypic Variation

The habitat specificity of a species, with respect to a particular habitat variable (such as mean annual rainfall, temperature, or soil nutrient status) is always a *range* of tolerance within which life and reproduction can occur and outside which it is impossible for that species. The same is true for an organism's habitat specificity.

The habitat tolerance range of a species may be influenced at three levels: (1) genetic and phenotypic variation in resource use *among populations*, (2) *among organisms* within each population, and (3) the environmental tolerance range *within each organism*, resulting (3*a*) from the varied environmental tolerance of any particular phenotype or (3*b*) from the varied phenotypic expressions possible from a single organismal genotype in different environments. The latter (3*b*) is also known as the norm of reaction (see Stearns [1982] for numerous examples). Many lineages have broad reproductive norms of reaction, switching facultatively between different phenotypes, and from sexual to asexual reproduction, depending on environmental cues (Stearns 1982; Bell 1982). The nature and breadth of a norm of reaction itself are genetically based and can evolve (Stearns 1982). Thus, a species' habitat specificity is ultimately genetically based.

Estimation of Habitat-Specific Limits

The limits, with respect to variables such as temperature, rainfall, substrate, food, and vegetation cover, of a species' habitat specificity can in principle be quantified. For instance, Caithness (1990) used multivariate discriminant-

function methods and bioclimatic profile matching (Nix 1986) to estimate such limits for each of seventy-three African antelope species, in terms of twelve temperature- and rainfall-related variables.

Also, the relative importance of different habitat variables to a given lineage can be estimated. For instance, Greenacre and Vrba (1984) used correspondence analysis on antelope census data, from areas representing different ecosystems across subsaharan Africa, to investigate the relative causal influences of habitat components on the biogeographic patterns. This method is objective in not presuming any causal structure underlying the data. Instead, any nonrandom structure is revealed afterward by comparing the resulting distribution of taxa and areas along the axes with "supplementary" environmental variables for each game area. In our study these included mean annual rainfall and temperature, soil nutrient status, and vegetation cover coded from low to high proportions of woodcover compared to grasscover. We found (Fig. 1.3) that the vegetation cover codes plot in almost perfect ascending order against axis 1: among the variables we considered, *gross vegetational physiognomy* (i.e., not defined by plant species but by wood-to-grass proportions) was pinpointed as primary in the habitat specificities of the antelopes.

Long-term Heritability of Habitat Specificity

Within broad limits, components of habitat specificity can be heritable and characteristic for entire clades through millions of years. For instance, the cladistic relationships in Figure 1.3 (based on mitochondrial DNA [J. Gatesy pers. comm.] and skull characters [e.g. Vrba 1979; Vrba et al. 1994]) suggest this for vegetational habitat specificities in antelope taxa. Note that all eight species in the reduncine clade (*Kobus, Redunca*) are in the open woodland part, and all seven in the alcelaphine clade (*Alcelaphus*, etc.) are in the open grassland part of the vegetation spectrum. Each clade is known since at least five million years ago. The main point is that hypotheses of long-term constancy (due to heritability within and among species) of components of habitat specificity are testable cladistically: The distributions of species' habitat specificities among taxa are expected to form hierarchically nested sets and subsets just as those of the more conventional phenotypes do. There is already considerable support for the notion that species and clades can have long-term habitat fidelity (e.g. Vrba 1987, 1989, 1992).

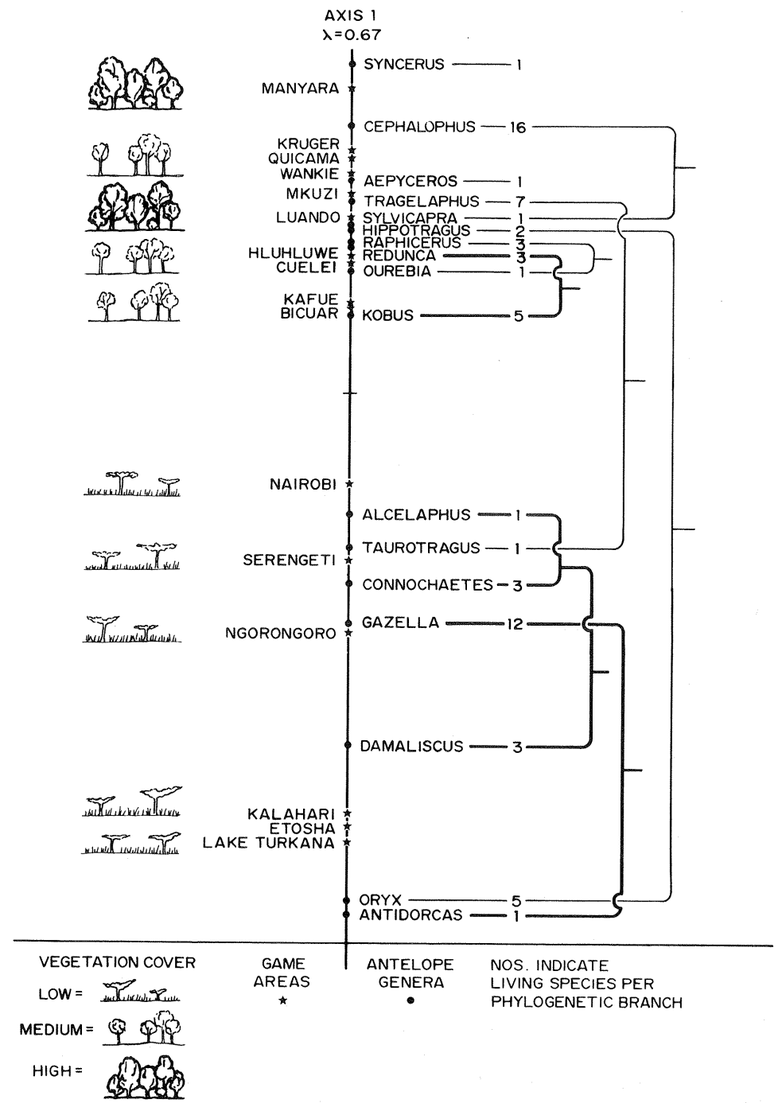


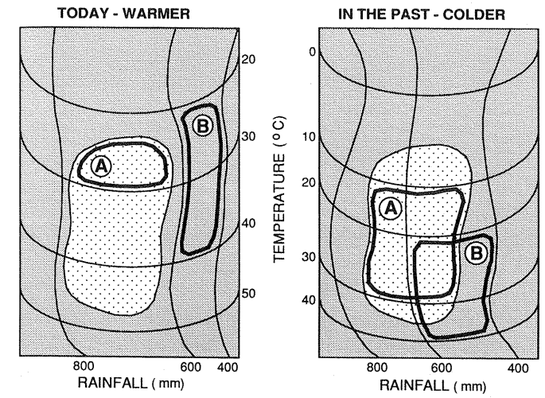
Fig. 1.3. Axis 1 from a correspondence analysis (Greenacre and Vrba 1984) showing generic antelope frequencies in sixteen African game areas (*center*) to be strongly influenced by the habitat-variable vegetation cover (*left*). Cladograms (*right*) suggest that vegetation habitat specificities have been heritable characteristics (synapomorphies) for some clades through millions of years.

A Species' Habitat Specificity as a Unique Combination of Resource Ranges

It follows from the previous observation that a "unique habitat specificity" of a lineage or species is likely to involve only one or a few habitat components and often displacement of tolerance-range limits relative to those of related species while maintaining range overlap. Herein lies the reason, I believe, for the observations (e.g. Huntley and Webb [1989] for North American trees; Bush and Colinvaux [1990] for Central American forest communities; Coope [1979] and Coope and Brophy [1972] for beetles; Sutcliffe [1985] for European mammals) that, while species' habitats and geographic distributions during past climatic changes underwent large-scale shifts, they did not always shift in perfect "lockstep," so that the ecological associations of taxa were different to some extent in the past (even in the Quaternary) from those today. This is hypothetically depicted in Figure 1.4 in which two extant species, *A* and *B*, are compared with respect to three habitat variables. *A* and *B* differ but overlap in tolerance of temperature, rainfall, and substrate. *A* is more generalized with respect to mean annual rainfall and *B* with respect to substrate. As a result, *A* and *B* are allopatric today, but were partly sympatric during a past colder period. The main point here is that each species has a particular tolerance range for each habitat component that may or may not overlap or be identical to that of other species and a *combination* of such ranges for all its requirements that is unique.

Paleoclimatic Implications for Species' Habitats and Distributions

It is now generally accepted (e.g. Berger et al. 1984) that Earth's paleoclimate has cycled periodically between global cooling and warming, although not always accompanied by polar ice changes as during the Plio-Pleistocene. Three dominant cycles have been documented (the Milankovitch cycles): of roughly 100,000-, 40,000-, and 23,000-year periodicities. The best evidence for these astronomically caused cycles, from the Plio-Pleistocene, shows that the cycles were accompanied not only by large-scale expansion and retreat of ice at the poles (Denton 1985; Hays et al. 1976; Shackleton et al. 1984), but also by major climatic and vegetational changes in the land tropics (reviewed in Rind and Peteet 1985). These cycles, in some form, must have accompanied the entire history of life (see Olsen [1986] for the Triassic; Park and Herbert [1986] for the Cretaceous). So far we have data only for small parts of the fossil record. These show that over longer periods (one to several million years apart) the "background" Milankovitch cycles underwent major changes in mean and mode. Some have argued (review in Vrba 1992) that tectonic changes precipitated these major displacements of the Milankovitch cycle curve. (Note that these hypotheses suggest a causal role for tectonism only with respect to the *changes*



HABITAT VARIABLES	TOLERANCE RANGE	
	SPECIES A	SPECIES B
TEMPERATURE	10°-30°C	20°-40°C
RAINFALL	400 - 800 mm	400 - 600 mm
SUBSTRATE	ONLY	AND

Fig. 1.4. Components of the habitat specificities of related species showing commonly overlapping ranges. Hypothetical species *A* and *B*, due to overlapping specificities for three habitat variables, have disjunct distributions today, yet had sympatric ones in the past.

in the nature of the Milankovitch cycles—the basic cycles are known to result from astronomical changes [e.g. Broecker and Denton 1990].)

The Milankovitch climatic amplitudes were large, at least for some periods and areas, relative to the habitat adaptations of most extant species (Vrba 1992*b*). And the less frequent changes in cyclic mean and mode must have been even more strongly felt by the biota. Thus, climatic and habitat changes of large scale swept back and forth over continents and in the oceans with periodicity about, for instance, 1/20th of the duration time of the average species of terrestrial mammals (about two million years, from observation of the African record). Much evidence shows (Vrba 1993) that most known species survived many climatic cycles by the passive response of geographic shifting and vicariance of their distributions, while maintaining habitat fidelity. This was by far the most common response of lineages (the rarer re-

sponses were extinction or evolution of novelty with or without lineage branching).

Most species occur today in a vicariated state, often with numerous allopatric populations. Many have cited this as a problem for species concepts (for instance, it is a barrier to species diagnosis under the Isolation Concept; see below). It has also been argued to negate system status for groups the organisms even if they share a common fertilization system, that is, for recognition species. Miller (1978:24) wrote: "The individual members (organisms) of a given species are commonly units of widely separated concrete systems. The reason the species is not a concrete system is that, though all its members *can* interbreed and interact, they do so only locally."

I suggest that the new paleoclimatic evidence necessitates a revision of our preconceptions based on the vicariated populations that we see today. Consider that each of all new species (under all concepts here considered) is expected to have originated as a single population, which spread initially in contiguity. Vicariance and allopatry followed only later with an extreme climatic change. But during regular background Milankovitch cycling, any one such climatic (for instance, cold) extreme is only one in a series of similar, regularly recurrent extremes, which is also true of the soon-to-follow (in geological terms) alternate (warm) extreme. Thus, in terms of "species time" or "lineage time," allopatry is an evanescent (yet recurring) phenomenon, with reconstitution of geographic distribution to sympatry in most cases soon to follow. The often-quoted metaphor "the gavotte of the chromosomes" in genetics applies analogously in biogeography as "the gavotte of the geographic distributions." The genetic metaphor describes the idea that the signal values of interaction linkages between different chromosomes are sometimes zero and at other times positive, as they alternate between quiescent separation and interactive contact on the cellular time scale. The analogous phenomenon occurs between males and females in populations and between populations sharing a fertilization system, on the organismal and species time scales, respectively.

Miller (1978) argued that a committee that meets once a year using the same committee rules or charter from year to year (with perhaps a total duration of that charter of twenty years with a turnover of members) is a good system. By analogy, a mammal species' population that resumes contact under the same "charter" (undiverged fertilization system) with other conspecific populations every 100,000 years or less must also be a good system (quite apart from the argument that the same system can exist in allopatry, such as Alaska, Hawaii, and the rest of the United States under a central governmental system; see Ghiselin [1974*a*] on individuality). This new perspective of a constant renewal of interactive linkages, a regularly recurring opportunity for mingling of sexual gene pools with potential obliteration of populationwide genetic divergence (given an intact fertilization system), casts a new light on more than one aspect of the species debate.

Species Concepts in Relation to Habitat Specificity

The Phylogenetic Concept. The Phylogenetic Concept does not require a species to have unique habitat specificity. Recall that under this view a species is "the smallest diagnosable cluster of individual organisms, within which cluster there is a parental pattern of ancestry and descent, beyond which there is not" (e.g. Nelson and Platnick 1981; Cracraft 1983). For example, any unique, small, selectively neutral modification to a protein that diagnoses a clade *A* of organisms, even if they exist in sympatry and with a habitat use identical to that of organisms in the sister-clade *B*, is sufficient to proclaim *A* as a species. Habitat relations do not feature at all under this concept.

The Cohesion Concept. The Cohesion Concept does directly address habitat specificity, in the guise of "demographic exchangeability": "complete demographic exchangeability occurs when all individuals in a population display exactly the same ranges and abilities of tolerance to all relevant ecological variables" (Templeton 1985:15). However, in this concept habitat specificity, or demographic exchangeability, is only one possible route [albeit a frequent one] to species status. Thus, the cohesion species does *not require* unique habitat specificity, because demographic exchangeability between two populations does not guarantee conspecificity. Recall Case 3*b* in Table 1.4: Templeton would recognize two sexual populations that still share a common habitat but have diverged postfertilization systems, that is, that have lost genetic exchangeability, as two species.

Templeton (1989) contributed significantly on the question of evolutionary forces that promote phenotypic uniformity—cohesion—in both asexual and sexual populations. His discussion of how drift and cohesion relate is especially interesting. He points out that (1) demographic exchangeability implies that the probability of a neutral or selectively favorable mutation going to fixation is exactly the same regardless of the individual in which it occurs; that (2) for the case of neutral alleles, "the rate at which genetic drift promotes identity-by-descent depends only on the neutral mutation rate and is therefore equally important in both small and large populations . . . predictions [which] are equally applicable to [sexual and] asexual organisms"; and that (3) in the neutral case, "making *only* the assumption of demographic exchangeability, it is inevitable that at some point in the future all the alleles will be descended from one allele that presently exists" (Templeton 1989:16).

Nevertheless, in spite of the strong stress on habitat relations, the cohesion species is so all-encompassing in its definition that it ends up without a consistent relation to this habitat criterion.

The Isolation Concept. The isolation species is also not necessarily specific for a unique habitat range. Numerous cases have been reported of postfertilization-

isolated sister-"species" that mate freely (with heterozygote disadvantage) in hybrid zones in which both kinds of organisms use the same resources in the same habitat.

The Recognition Concept. To diagnose a recognition species *requires* only documentation of a unique fertilization system (Table 1.1). Yet, Paterson's (1978, 1981, 1985) specifications of a *system among organisms* and of conditions required for evolution of a new system (i.e., for speciation) have far-reaching *necessary* consequences, including that each species is uniquely habitat specific.

Miller (1978:1027) identified one of the quintessential characteristics of living systems as follows: Living systems "can exist only in a certain environment. Any change in their environment of such variables as temperature, air pressure, hydration, oxygen content of the atmosphere, or intensity of radiation . . . produces stresses . . . under [which] they cannot survive." For a recognition species this environment is the habitat-specific tolerance range in which the fertilization system can function. One can distinguish the tolerance-range limits for particular resources that this system requires—the system habitat specificity—from those limits needed by all life activities of organisms other than fertilization interaction—the economic habitat specificity (following Eldredge's distinction; 1985 and this volume). For example, Morris (1970:31) reports that the habitat conditions required for breeding of ten-spined sticklebacks (Fig. 1.2) "are profuse fresh vegetation of a type in which nests can be built, water which is not very fast moving (as this would cause too much movement of the weeds and endanger the nest), water which is well oxygenated and of a particular pH, and water which does not dry up in the possible high temperatures of late spring and early summer." He notes that breeding is absent or rare in other areas where the fish are nevertheless found, "for example the River Kennet in Wiltshire [is] in most places too swift-flowing for breeding purposes." Similarly, for many of the heterogonic lineages, such as the aphids mentioned earlier, the evidence indicates differences in habitat variables between the parthenogenetic and sexual phases (Bell 1982).

The crux of the recognition species' unique habitat specificity lies in the necessary conditions for evolution of a new system (speciation; Paterson 1985). Because the fertilization system comprises a coadapted signal-response reaction chain (Fig. 1.2), (1) it can only be changed by selection of small mutational steps involving male and female subparts in turn; and (2) an environmental change, acting on a population in allopatry from the parent sock, is *required* to set such divergence in motion. Unless the old habitat changes, strong stabilizing selection on the system obtains. Thus, one prediction for any two sister-populations is the equation: distinct fertilization systems = distinct habitat specificities. This can be tested in principle and without much difficulty in cases where habitat variables can be experimentally controlled (again, the stickleback research of Morris [1970] and others is a case in point).

This central implication is often missed by those who discuss the Recognition Concept. For instance, Templeton (1989:14) wrote: "the isolation and recognition concepts . . . have elevated a single microevolutionary force—gene flow—into the conclusive and exclusive criterion for species status." This is untrue for the Recognition Concept. It stresses that natural selection for a particular fertilization system can maintain single-species status across allopatric populations for long time periods, provided those populations are all subject to the same range of habitat conditions to which that species is adapted. Thus, gene flow here is irrelevant.

This new theoretical element on habitat specificity constitutes one of the fundamental differences between these two concepts: although both acknowledge prefertilization divergence as a cause of speciation, Paterson added a new focus on a recognition *system* that can change only in an environment different from the parental one. In contrast, the more traditional concept permits a wide variety of conditions under which "isolation mechanisms" can evolve, including divergence in the absence of habitat difference.

Species Concepts in Relation to Lineage Branching

What concerns me is not the extensive gray area that surrounds the actual process of lineage splitting before species divergence is unambiguously complete (particularly, of sexually reproducing lineages), but rather the expected long-term fate of incipient or newly arisen branches on the tree of life. For all incipient species branches there are favorable environments (their habitats) with respect to which environmental change represents habitat deterioration. Under all concepts, such onset of adversity may wipe out "young" species soon after origin. But the concepts differ sharply in their expectations of species longevity in the face of persistent favorable conditions.

One of the most highly corroborated and spectacular phenomena of life is its branching genealogy. In my view, a species concept should directly address that branching pattern. Any part of a given species concept that includes "species" that must, in terms of its own premises (including recently accumulated evidence on the implications of those premises), remain "stillborn buds" or tiny offshoots soon to be resorbed by the parent stem is irrelevant to the tree of life. I suggest that a reasonable requirement of any species concept is that it should be "economical" in being restricted to branches that *can* take off with "habitat luck" and that do so irreversibly.

The Phylogenetic Concept. Asexual phylogenetic species fulfill the "economical" requirement. But the sexual species do not. Recall the evidence that global

paleoclimatic cycles resulted in large-scale changes in the geographic distributions of most taxa (Vrba 1992). For the moment, let us accept as species those taxa generally agreed to be species in the literature. Take, for example, a mammal species of two-million-years duration (average for mammals; average durations in many other groups were much longer [e.g. Stanley 1979]). If that mammal species had moderate tolerance to the cyclic changes, responding only to particularly severe extremes (which were about 100,000 years apart during part of the Pleistocene), then episodes of maximal vicariance and maximal recoalescence of its distribution might have recurred only with periodicity about 1/20th of the duration time. If that species was highly stenotopic and responsive to either the cold or the warm extremes in all cycles, then during its lifetime its distribution would have undergone nearly one hundred episodes of maximal vicariance and maximal recoalescence.

Thus, for most sexual taxa we may expect that phases of allopatric divergence (speciation under the Phylogenetic Concept) were more or less evanescent phenomena. "Diagnosable clusters" recurrently lost their genotypic distinctiveness as sympatric sexual interactions resumed: precisely during phases of maximal spread of their optimal habitats, their monophyletic identities ceased to exist. The Phylogenetic Concept recognizes even groups that are diagnosable by only minute genetic differences as species. Thus, one can expect from many to numerous phylogenetic species to exist (in actuality most will not be noticed, as argued below) within the average recognition species. Thus, the vast majority of all sexually reproducing species under the Phylogenetic Concept are not expected to be irreversible branches of the tree of life.

The Isolation Concept. Under the Isolation Concept some species, those with diverged fertilization systems, are expected to be irreversible branches. But species isolated only by postfertilization divergence are unlikely to lead to branches. As Paterson has pointed out since 1978 [1981, 1982, 1985, 1986], both theoretical and experimental results strongly suggest that postfertilization isolation is not an *initiating* cause of divergence of the fertilization system. Of course, in some cases of an allopatric population that is already postfertilization-isolated, the fertilization system may diverge independently, causally influenced not by reinforcement but by habitat change. But most such isolation species are expected to be the stillborn buds, mentioned above, that can never maintain branch identity when in sympatry with the parent species. Many evolutionists have come to an essentially similar conclusion (e.g. Mayr 1982; Lande 1979; Futuyma and Mayer 1980; Templeton 1981, 1989; Carson 1982; Butlin 1989). A category that is still cited by many as valid speciation via postfertilization isolation is speciation by polyploidy, particularly in plants. But, in my view, Paterson (especially 1981:117–118) has convincingly countered these arguments as well.

The Cohesion Concept. Asexual species under the Cohesion Concept are irreversible branches. So are sexual cohesion species evolved by divergence of the prefertilization system. But, among the several completely different kinds of species recognized under this concept, some fail the criterion of true and irreversible branching. Thus, Templeton (1989) includes two isolation species, distinguished only by postfertilization divergence, as two species because they lack "genetic exchangeability" (Table 1.4).

The Recognition Concept. All recognition species, once launched to the point where hybridization is negligible or has ceased, are necessarily implied to be irreversible branches with distinct durations that hold as long as appropriate habitats survive. If one focuses on the *system* as that which confers species identity, then the same species can continue even after giving off a branch with a distinct system and ends once its system ceases to exist.

Species Concepts in Relation to Monophyly

The Phylogenetic Concept. The Phylogenetic Concept is the only concept that claims that each species (from speciation to terminal extinction) must be strictly monophyletic based on nested homologies at the levels of organisms and their constituents. Bonde (1981:28), an adherent of this concept, reasoned the need for this criterion as follows: "If in the classification species have to be basic units (taxa) and phylogenetic relationships shall be precisely expressed in the system, then the ancestral species must cease to exist at speciations. Only in this way *all parts* (e.g. "chronosubspecies" or single fossil specimens) *within a species have exactly the same phylogenetic relationship to any* (part of) *other species in the system*" (italics in original). That is, even if the ancestral stem [*A*] is precisely the same as one of the descendent branches (*A′*, the sister-branch being new species *B*) in every respect, this concept requires that the ancestor, *A*, become "extinct" at the speciation event, and that descendant branch, *A′*, be recognized as a new species. In this view, the alternative of recognizing the persistent ancestral lineage (*A-A′*) as the same species before and after giving off branch *B*, is unacceptable because it makes species *A-A′* paraphyletic. Recent arguments have gone further and suggested that there is no such thing as an ancestral species at all (e.g. Nelson 1989) or that all possibly ancestral lineages (for which only plesiomorphies are known) are metataxa or metaspecies and not species (Donoghue 1985; De Queiroz and Donoghue 1988, 1990). Thus, the species in this view is always a terminal taxon, as implied by its being a smallest diagnosable monophyletic group.

It is worth asking: precisely *what* is monophyletic in such a phylogenetic species?

The asexual case is clear: if a mutant gene *X* first appears in organism *A* and is

transmitted to all its descendants, then *A* and those descendants are a monophyletic lineage characterized by *X*. Of course, as soon as an offspring appears with a new diagnostic gene *Y*, the previously recognized "species"—the *X*-organismal cluster—becomes paraphyletic and loses its species status.

The situation is more complex in the sexual case. A sexually out-crossing lineage can never be monophyletic at the organism level. Take the case of a dominant allele *X* which arises in a female (of genotype *Xx*, phenotype *X'*) which mates with a non-*X* male (genotype *xx*, phenotype *x'*), in a population in which *X* eventually becomes fixed. Let us call the initial state, from mutation onward but previous to fixation, stage 1. During stage 1 there is indeed a smallest diagnosable (by gene *X*) cluster of organisms. Is this, under the Phylogenetic Concept, "species *X*"? If so, species *X* is of course nonmonophyletic at the level of organismal lineages. Even given the unlikely events that all F1 offspring of the mutant-*X* mother have *X*, and *X*-bearing individuals mate only with each other, and all further descendants of the mutant-*X* mother have *X*, one would still need an "immaculate conception" in the mutant-*X* mother to have a monophyletic *X*-cluster of organisms.

Let us call stage 2 the period that starts from fixation and lasts until a new mutant or immigrant destroys the *XX*-homozygosity of the population. Does "species *X*" start only with the population fixed for *X* at stage 2? I presume that, under the Phylogenetic Concept, this is what *has* to be claimed: the monophyly buck stops here in the sense that this first (or stem) unit of a new species, an "Eve-population" fixed for a diagnostic character, must be declared immune to investigation of its phyly. And this indeed seems to be what adherents do claim (e.g. Wheeler and Nixon 1990).

But how, when looking at variation in nature or in museum collections, does one recognize such an Eve-population? Wheeler and Nixon's (1990:77) stance on this is simply one of cladistic fiat: "species are the smallest terms analyzed by cladistic methods," and "in cases where cladistic analysis is possible . . . we are dealing with distinct species and not with infraspecific units." But I agree with De Queiroz and Donoghue's (1990:88) reply: "Wheeler and Nixon (1990) . . . wish to distinguish between inconstant 'traits' in populations [such as *X* in the stage 1 population in my example] and constant 'character states' of 'species' . . . present 'in all individuals of a terminal taxon.' But how is one to distinguish between variable traits and constant character states unless one recognizes beforehand the unit ('terminal taxon') within which the organisms bearing these attributes, whether variable or constant, occur?"

Similar problematic observations on monophyly apply to all cladistic analyses of sexually out-crossing lineages, and therefore also to the Cohesion Concept of biparental species and to the Isolation and Recognition concepts.

But these differ from the Phylogenetic Concept in claiming criteria for species other than strict monophyly.

The Recognition Concept. The Recognition Concept focuses on a *system* to diagnose a species. System status at a higher level does not depend on strict monophyly of subparts, but on the rules by which the subparts interact to constitute the system. For a new fertilization system to originate, at least one new male and one new female phenotypic and genotypic character pertaining to system interaction must evolve. As long as the system remains intact the species endures, even if it has in the interim given rise to one or more daughter species.

In sharp contrast, the Phylogenetic Concept insists that a sexual species cannot be allowed to persist as the same species after giving rise to a daughter species as it would then become paraphyletic. I would have reservations about this argument even if there were not the ambiguity on monophyly during the species' origin (mentioned above). Consider the same argument, but shifted to a lower level (in Vrba [1985] this is explored in relation to species as individuals, *sensu* Ghiselin [1974*b*]; the argument has more force if species are systems): instead of focusing on the species as the system with organismal subparts, focus on the metazoan organism as the system with subparts that are cells, and, within cells, genes. For instance, at the birth of my child some of the gene (and cell) lineages in my body became paraphyletic (quite apart from the fact that my genome was polyphyletic to start with); and yet I remain the same system. I repeat, system status at a higher level does not depend on strict monophyly of subparts, but on the rules by which the subparts interact to constitute the system. To say that a parent species must cease to exist once it gives off a branch, and be recognized as a new species if it persists without change after branching, is like saying that I ceased to exist at the birth of my daughter and since then must be named as a new individual.

Epistemology, with Special Reference to Extinct Species

I find the Cohesion Concept the most difficult species concept to apply. In attempting to encompass all groups of living organisms, it pays the heavy price of multiplied operational problems. First, the practical diagnosis of those cohesion species (including asexual clones and sexual syngameons) defined only by demographic exchangeability is unclear. How can one decide that too much or too little demographic exchangeability is present in a given case? Second, the diagnostic problems variously faced by the two sexual concepts of species, whether Recent or extinct, all apply to genetically exchangeable cohesion species as well.

The definition of the Isolation Concept is relational, as has often been

pointed out (e.g. Ghiselin 1974*b*; Paterson 1981; Vrba 1985). Just as one can diagnose a "sister" only in relation to a sibling, so one can diagnose the boundaries of an isolation species only by evidence of reproductive isolation from a sister-species. Consequently, species status of allopatric populations presents a problem. If it is true that populations that are isolated only by postfertilization divergence are shortlived (Paterson 1978; Mayr 1982; Lande 1979; Futuyma and Mayer 1980; Templeton 1981, 1989; Carson 1982; Butlin 1989), then the predictions under this concept for systematic patterns in the recovered record of extinct species are expected to be quite similar to those of the Recognition Concept.

All the species concepts share the operational problem of norms of reaction, as all insist that speciation is a genetic event. The norm of reaction of most organisms (Stearns 1982) can result in different ecophenotypic expressions of the same genotype in response to different environments, and it is difficult to distinguish (especially in the fossil record) such ecophenotypic differences from genetically based ones. A large proportion of populations that would be judged as different phylogenetic species based on phenotypic diagnosis are likely to represent geologically ephemeral ecophenotypes. The same holds for many populations that appear to be separate species, of differing demographic exchangeability, under the Cohesion Concept. For instance, many or most cohesion species within syngameons may fall into this category. I suggest that the Recognition Concept is least vulnerable: the strong stabilizing selection on the fertilization system as a whole (Paterson 1978, 1981, 1985) is also expected to result in narrow norms of reaction for the components of this system. For the male *and* female SMRS characters (Fig. 1.2) both to change ecophenotypically in a changed environment, such that the SMRS still functions, would require the highly improbable situation that both change in a precisely covarying way. Selection is expected to remove reaction norms that result in any other kind of change. (The hypotheses that SMRS characters should have narrower variances and narrower norms of reaction are both testable. Lambert and Levey [1979], for instance, found support for the first hypothesis in *Drosophila melanogaster;* but I have not seen any tests of the second one.)

Next, I will consider some general issues in relation to paleontology. Then, because the problems and virtues of the Phylogenetic and Recognition concepts with respect to fossils jointly subsume those of the Cohesion and Isolation concepts, I will concentrate most of the remainder of my remarks in this section on the former two.

General Remarks on Operational Approaches to the Fossil Record

I think that we all agree on three issues relating to species, whether Recent or extinct:

1. We wish to study, name, and incorporate in our analyses of processes, those different kinds of entities, out there in nature both today and in the past, that are distinct and coherent entities.

2. As evolutionists we require that the biotic entities on which we focus our research energies should maintain coherence, manifested as stability of combinations of character states, at least through modest periods of time. (As a paleontologist I suggest that we should think in terms of at least 300,000 to one-half million years during which certain combinations of character states, including apomorphic and plesiomorphic states, must be consistently shared by a collection of organisms for that collection to qualify as a meaningful biotic entity.)

3. Such long-term stability implies a basis rooted in heritable characters and processes. The Phylogenetic Concept stresses the vertical genealogical linkages resulting from reproductive processes, while the other three concepts variously add emphases on horizontal linkages resulting from sexual and ecological processes; but all focus on processes. This agrees, for instance, with Michaux (this volume) who supports a species concept based on processes that lead to the coherence of the entities that we can see sufficiently clearly so as to be motivated to recognize them as biologically important.

Using these three criteria of meaningful coherence, stability through at least modest time intervals, and a basis in evolutionary processes, we can address two questions that have been often debated in relation to species in the fossil record:

Should we have a different concept for "species" in the fossil record? The answer has to be a resounding *No* if we consider that there is only one tree of life reflecting one history and one unified set of processes. While we can in principle recognize the presence of several different meaningful kinds of living entities (such as minimal clades, habitat clones, and species, in my usage), we should seek to comprehend them in both the modern and the extinct biota wherever the data allow us to do so. Turner (this volume) reviews the old acceptance that the "bread and butter species of the paleontologist" (morphospecies, or in more modern usage, a phylogenetic species, namely, "bread and butter" in the sense that the species concept is easy to apply) should differ from the biospecies (traditionally the isolation species). I agree with his conclusion that to argue for a different paleontological "species" is absurd. Further, as I point out below, *all* species concepts to varying extent lack "bread and butter" quality in application to the fossil record, as all require estimation of the truth and none is free of difficulties.

The second question is closely related to the first. *Should we hesitate to use a species (or other) concept just because it is difficult to apply to (and test in) most of the fossil record?* That is, should our articulation of concepts be subservient to an

epistemological requirement that they should be testable in all or most of the fossil record? Again, the answer must be *No,* unless we want to argue that some of the great hypotheses of process in biology and geology were invalid at the time of their articulation simply because of then-current difficulties of testing them (or, for that matter, that they are invalid today because of persistent absence of relevant data from most of the geological record). For instance, if such subservience to the shortcomings of the geological record is taken seriously, then Milankovitch had no business to articulate his astronomical model of climatic cycles in the 1920s, as critical tests were only possible half a century later (review in Broecker and Denton 1990). And the Milankovitch hypothesis would still not be respectable, as it has only survived falsification in a minute fraction of the geological record. However, it has been supported in all cases in which testing is possible to date. (The same is true of many other major biological and geological hypotheses.) Thus, in my view, paleontologists use the same general concepts that have been found internally consistent and testable elsewhere in biology; and they may add some of their own that are first raised by, and tested in, the paleontological record. The intrinsic merit of a particular concept does not depend on the number of instances in which it can be tested, provided it is testable in principle and testable somewhere out there in the reality of obtainable data. If phylogenetic and recognition species, for instance, are judged to be meaningful entities, then let us recognize these distinctions theoretically and test for the existence of each where we can.

The Phylogenetic Concept. At first glance, the Phylogenetic Concept is easiest to apply to the fossil record, but upon closer examination there are conceptual problems. A concept can claim to have a good operational criterion for diagnosing species if that criterion succeeds in recovering units that preserve the theoretical meaning of species under that concept. I agree with De Queiroz and Donoghue (1988, 1990) that the ease of erecting some kind of cladogram or other does not save the Phylogenetic Concept from some problems in this respect.

Let us allow, giving the benefit of the doubt, that a unique character (discovered in some population or fossil collection) of a cluster of organisms—no matter how small—heralds the "clean beginning" of a new phylogenetic species. There still remain theoretical and operational difficulties with "quick and messy endings" in one of two ways. First, such a character-clade ceases to exist as a species as soon as a new character evolves within it. In epistemological terms, with every discovery of a new character, the status of species changes, that is, the concept is defined relationally and provisionally, pending exhaustive character analysis. Second, because we must expect repeated separations and reunions of populations over geologically short time intervals given cyclic climatic changes, hybridization must often result in a second kind of messy

ending as recombination of character sets "fudges" previous species boundaries. Such "species genealogies" may be conceived to look more like an unusual piece of knitting than a diverging tree.

When one views life's genealogy in hindsight, there are relatively few species under this concept: only terminal autapomorphic branches are species, the vast remainder being metataxa (Donoghue 1985) banished from species status by their paraphyly.

The Recognition Concept. One problem in dealing with the extant biota is that the systematic character distributions of SMRSs in particular, and of fertilization systems in general, remain relatively little studied. It has also been held against this concept (and the Isolation Concept) that all lineages that never exhibit biparental sexual reproduction are excluded and that numerous cases exist in nature in which varying levels of hybridization blur species boundaries. On the positive side, all recognition species eventually do have definite beginnings of irreversible branches (unlike some isolation species) *and* "clean endings" (unlike most phylogenetic species). They also have a clear and testable diagnosis in principle (unlike some cohesion species), are not defined relationally, and, thus, are diagnosable in allopatry.

Because the Recognition Concept focuses on a particular and complex process among organisms, it entails a range of predictions for patterns including paleontological ones. Paterson's (1978,1982) arguments predict not only particularly narrow variances in a species' SMRS characters in space and time, relative to other phenotypic characters, but also a pattern of punctuated equilibria, primarily in SMRS characters, and by pleiotropy also in other phenotypic characters (predicted independently, Paterson and James [1973] and Paterson [pers. comm.] of the articulation by Eldredge and Gould [1972]).

Insofar as the *skeletons* of extant survivors are found to include characters of the SMRS, this hypothesis is testable by examination of the fossil record of that monophyletic group. Consider that in cases where mating communication is primarily visual, a breakdown of communication between populations (speciation) should involve a shift in morphology (Vrba 1980, 1984). In such groups, rates of morphological change and speciation, under the punctuation model, should be positively correlated. Even relatively closely related species of visual "communicators" might be expected to be morphologically distinct. This explanation may be appropriate for the morphological differentiation between chimpanzee and man (King and Wilson 1975) and other higher primates, in speciose groups of *Haplochromis* (Fryer and Iles 1969) and the homoallozymic *Drosophila heteroneura* and *silvestris* (Carson 1976). Conversely, uniform species' flocks (e.g. minnows, Avise and Ayala [1976] and some fruitflies) may have an SMRS dominated by olfactory, auditory, or other nonvisual signals. The observation that frogs, with their bias toward auditory communica-

tion, include many sibling species would support this argument. Among mammals, particularly numerous sibling species have been recorded for rodents. Distinctive auditory and behavioral SMRSs have been reported for morphologically identical rodent species (Gordon and Dennet 1979).

The implication for the paleontologist is obvious (Vrba 1980): in monophyletic groups including extant species whose visual communication involves skeletal characters (e.g. Vrba 1984), the probability of successfully estimating species and species diversity patterns in the fossil record may be good. In contrast, it is hopeless in the case of groups of species that are sibling in terms of their hard parts. *The problem of extinct sibling species is shared by all species concepts.* In judging distinct fossil morphologies as species, the Recognition Concept of species requires the argument that the relevant morphologies are good symptoms of differing fertilization systems. I argue below that this argument is not as difficult to defend as is often claimed.

A Proposal for Paleontological Procedure

Two implications of the fossil record are important to the species issue. The first is a positive aspect, a strong and unique advantage relative to other data sets: the fossil record affords at least some direct evidence on the temporal persistence of any unique *combination* of morphological characters that we see in individual fossil organisms. Such a unique character combination might include at least one autapomorphy alongside a combination of plesiomorphies, or it might include only plesiomorphies relative to later cladistic branches, as expected of an ancestor. (Kimbel and Rak [1992] recently argued this and used the approach in conjunction with cladistic analysis to infer extinct species in the Plio-Pleistocene hominid record.) Long endurance of such a character combination of a sexual taxon allows certain inferences on process: the taxon did not interbreed with its sister-taxon of distinct character combination, either because allopatry alone (less likely, given what we know about paleoclimatic oscillations) or reproductive isolation in sympatry made it possible.

The second is the negative aspect of "gaps" in the fossil record—the low probability of preservation that excludes especially forms that are ephemeral in time and geographically rare. As already noted, most apparent novel combinations of phenotypes (which would be labeled phylogenetic species, if recovered) are small and evanescent in time, either because the population soon disappears altogether, or because the character combination dissolves upon each recurrent sympatry with the sister-taxon, or because of a changing norm of reaction. Included among these new ephemeral branches are those that constantly (in geological time) arise to rob ancestral taxa of their species status under the Phylogenetic Concept. We may infer that the gaps in the fossil

record act mainly to hide all these ephemeral new taxa from our view. As a result cladists record far fewer branches overall than were really present; yet among these recorded branches, a high proportion of apparent phylogenetic *species* are really metaspecies. They have survived as species under the Phylogenetic Concept simply because their ephemeral subbranches that eclipsed them into metaspecies status are invisible to us.

The basic systematic procedures in paleontology are in principle those used in neontology; yet there are practical differences in how they can be applied. This topic deserves much more thorough and rigorous treatment than I can give it here. I offer only a few comments, including the following pragmatic conclusion: *The vast majority of sexual fossil taxa of sufficiently long duration to find their way into a cladogram at all, and then to be recognized by some as phylogenetic species, are recognition species* (with the caveat, under either concept, that separate species that are sibling in terms of their hard parts will not be detected). The phylogenetic metaspecies is also a potential recognition species—an ancestral recognition species. Recall that recognition species are predicted to remain discrete lineages that share certain combinations of character states, through long time in the face of the frequently recurring episodes of sympatry that paleoclimatologists insist have been a pervasive feature of the history of life. Under this conclusion the gaps in the fossil record act as a "great leveler." Whatever their semantic preferences, I suspect that most biologists would like to reserve a term for those *long*-lasting distinct units among sexually reproducing lineages. By an artifact of the fossil record, the different conceptual schools end up agreeing on most such fossil lineages that they should be called species!

I suggest that paleontologists, like neontologists, can in principle erect both cladistic hypotheses, with minimal clades and metataxa, *and* hypotheses of recognition species in relation to those cladograms. The latter hypotheses arise from the genealogy, together with patterns of character combinations in organisms, taxa, and through time and are testable by additional character information.

I will illustrate some relevant points by my cladistic analyses of skull characters in the Pliocene-Recent antelope tribe Alcelaphini (a cladistic revision of Vrba [1979] is now in preparation with J. Gatesy and R. DeSalle, incorporating additional fossil taxa to make a current total of about forty, as well as cladistics of the mitochondrial DNA sequences of the living taxa which number at least seven). I have argued that in Alcelaphini (and other bovid groups), minimal clades are unlikely to contain hidden sibling species. This is based on analogy with living alcelaphines in which all sister-taxa, which in sympatry behave like separate recognition species by not interbreeding, are distinguishable by skull characters.

First, the alcelaphine cladogram indicated metataxa that are hypothetical

ancestral recognition species. An example is a *Damalops* sp., species 17 in Vrba (1979:Fig. 2), which is wholly plesiomorphic with respect to other cladistic branches from the same node as *Damalops* sp. or from higher nodes on the cladogram. *Damalops* sp. is known from numerous fossils, which consistently share a unique combination of character states (although they share no single autapomorphy) over half a million years. The hypothesis that this cluster of specimens represents an ancestor is falsifiable by future discovery of additional characters that disqualify it from such ancestry.

Second, there are extinct minimal clades that preserve a unique character combination (including at least one autapomorphy) for at least a few hundreds of thousands of years, which I hypothesize are terminal recognition species (such as *Parmularius angusticornis*).

Third, there are instances of clades, each containing at least one metataxon and one minimal clade, which I hypothesize to represent a single terminal recognition species. For instance, the taxon *Damaliscus niro* in Vrba (1979) has a combination of an autapomorphy (prominent, widely spaced transverse ridges on the horncores) with several plesiomorphies (one example is the wide spacing of the supraorbital foramina, an apomorphy of *Damaliscus*). This combination persists from 1.7 million years until the latest Pleistocene. *Within* this taxon, one set of specimens in an early stratum shares a subtly different horncore orientation from all others, making it a minimal clade within the larger clade; but this cluster is connected to other *D. niro* specimens in that stratum by intermediates, suggesting interbreeding, and is present in only that one assemblage, supporting the expectation based on interbreeding that it was an ephemeral manifestation. Hence, I suggest that the clade characterized by prominent, widely spaced transverse ridges on the horncores is the single recognition species *D. niro*.

Conclusion

I have examined the meaning of *species* under the Phylogenetic, Cohesion, Isolation, and Recognition concepts in terms of four phenomena: Does a concept require a species to have (1) *system status* through among-organismal interactions, (2) *unique habitat specificity,* (3) *irreversible lineage branching,* and (4) *monophyly?* These phenomena are fundamental to biotic organization and patterns at all levels of complexity. They should feature in distinctions that we make among different kinds of organismal groups.

One basic kind of organismal group is the "minimal clade" (minimally diagnostic character-clade; I suggest the possible abbreviation M-clade), termed *phylogenetic species* under the Phylogenetic Concept. Minimal clades, asexual or sexual, require study irrespective of the fact that most are very small and ephemeral.

A second important category is that of the obligately uniparental, habitat-specific clones—I suggest the term *habitat clones*—the evolution of which Templeton (1989) clarified, and which he regards as cohesion species held together by "demographic exchangeability." (*Habitat clone* here refers not only to obligate asexual but also to obligate uniparental sexual monophyletic lineages.)

A third fundamental unit is the "biparental sexual system" of the Recognition Concept, although most such systems are further subdivisible into minimal clades, and some are paraphyletic at the character level. Lineages that engage in biparental sexual reproduction at least sometimes differ crucially from those that never do so: the former have systemic organization *among* organisms while the reproductive system of the latter is confined to the organism level.

Between them, these three kinds of entities not only account for all of life but also refer to the basic kinds of living attributes.

I prefer to reserve the term *species* for the biparental system—the recognition species—because it requires three of the four criteria that I regard as fundamental biological phenomena (Table 1.2). The remaining criterion of character monophyly is violated once a recognition species gives rise to a daughter species. I argue that this requirement means as little when focusing on the species as a *complex system* as would the requirement that I became a new organismal system with a new name after incurring gene (and cell) paraphyly upon my daughter's birth. Eldredge (this volume) reviews questions by some systematists why species should differ from higher taxa (see Nelson 1989). The species under the Recognition Concept differs crucially in that it is a system among organisms, while clades of more than one species are not.

In addition to studying the boundaries in time and space of the species construed as a complex system, the relationship of the primary genealogical pattern of organismal character evolution—that is, of "minimal clades"—to the species must be addressed. Thus, I still agree with Avise et al. (1987:518) that "no longer will it be defensible to consider species as *phylogenetically* monolithic entities in scenarios of speciation and evolution" (see also Cracraft 1983, 1987; Nelson 1989). But I urge that we distinguish asexual from sexual lineages, and "minimal clades" from biparental sexual systems. The set of all groups of organisms that *look alike by descent* is divided by *differences in among-organism organization* too fundamental to squeeze them all into a single concept. Thus, I reject arguments that the term *species must* encompass all recognizable groups of organisms. As it is, among metazoans at least, the proportion of diagnosably different lineages that never use biparental sexual reproduction may be quite small (Maynard Smith 1978; Bell 1982).

Also, there is a common perception that to recognize only groups of a certain kind as species is to ignore other kinds—to deny the latter importance

and reality (e.g. Templeton 1989). But that argument has no force. Take the concept of a metazoan organism. In most cases each such an organism is (1) a clone of cells *and* (2) an organization arising from rules of interaction among those cells. To confer the name *metazoan* in recognition of the importance of the additional factor 2 does not rob the unicellular clone of reality.

What we call the distinct kinds of organismal groups may largely be a matter of semantic taste. But the term *species* is so strongly imprinted on the minds of biologists, and so much interwoven with evolutionary thought, that it should belong to a kind of group with particularly significant properties. I have suggested four such properties: complex system status, unique habitat specificity, irreversible lineage branching, and monophyly at some included level. Even if one wishes to fall back on preevolutionary thinking, the properties of an among-organismal system, and of unique habitat specificity, remain compelling. I find the nonfulfillment of three out of these four criteria by the phylogenetic species a major flaw in a candidate species concept; and the only required property, monophyly, leaves something to be desired when examined closely. For instance, a sexually out-crossing lineage can never by monophyletic at the *organism* level.

On the one hand, there is something satisfactorily clear-cut about focusing only on one kind of criterion—genealogy—and ignoring all other kinds of phenomena. On the other hand, the price paid for designating these little clades as "species" seems too high in my view. The vast majority of phylogenetic species are *very* small, meaningless in terms of interactions among the subparts and with the environment, and ephemeral in time.

The Cohesion Concept seeks to encompass all organisms in terms of a unified set of evolutionary processes, the "cohesion mechanisms." In this the concept fails in my view. "Cohesion" is not a particular property and is not clearly defined. This results partly because its two guises, genetic and demographic exchangeability, are extremely different phenomena and partly because demographic exchangeability is poorly defined. In the bid to qualify as "everyone's species concept" the cohesion species ends up not fulfilling any one of the four investigated conditions consistently.

The Isolation and Recognition concepts share the requirement of a sexual system in a species (Table 1.2). But there are major ontological and predictive distinctions that are much more fundamental than, as widely misinterpreted, simply "two sides of the same coin" (e.g. Templeton 1989). Paterson's concept has added distinct new theoretical elements to the older one: First, he clearly articulated a hypothesis of process that negates the initiation of a new species branch by postfertilization divergence alone (as affirmed under the Isolation Concept, via "reinforcement of prefertilization isolation," e.g. Ayala et al. 1974). In this respect the ontological consequences of the two models are clearly different: Given persistence of the incipient species' habitat, recognition speciation results in irreversible lineage branching, while some isolation speciation does not. We are dealing here with more than a mere matter of opinion on what to call the new branch initiated solely by postfertilization divergence—under the Recognition Concept *such branches are not there.* Second, although both concepts acknowledge prefertilization divergence as a cause of speciation, Paterson's focus on a recognition *system* whose change is limited to occur only in a changed environment is new. In contrast, a wide variety of conditions under which "isolation mechanisms" can evolve are part of the more traditional concept, including divergence in allopatry in the absence of habitat difference. Thus, while the recognition species implies a unique habitat specificity, the isolation species cannot afford this requirement.

All these differences arise in one way or another from the stress by the one concept on *recognition mechanisms,* while the other focused on *isolating mechanisms.* First, the stress on reproductive *isolation* unhappily brought postfertilization divergence to share center-stage in the speciation process with prefertilization divergence. Second, the stress on *mechanisms* conjured up the unfortunate connotation of selection for isolation function and necessitated the model of selective reinforcement in secondary sympatry of postfertilization isolation in allopatry. I use the word *unfortunate* because it is now widely recognized that such reinforcement for speciation is highly unlikely to occur (as argued early on by Paterson [1978] and subsequently by many others) and that, as there is no other model around of selection for isolating function, both the isolating properties of postfertilization divergence alone and the uncomfortable notion of isolating mechanisms are irrelevant to speciation.

Perhaps the time has come to lay to rest the "ancestral" Isolation Concept of species and to acknowledge fairly that it has evolved into the Recognition Concept, via replacement by new theoretical "apomorphies" of some old misconceptions. We owe Paterson a debt for pointing to the internal dynamics of the biparental fertilization system itself and to their evolutionary consequences.

Summary

I have compared species concepts in terms of four criteria based on fundamental biological phenomena: Does a concept require a species to have (1) *complex system status,* (2) *unique habitat specificity,* (3) *irreversible lineage branching,* and (4) *monophyly?* At least three kinds of organismal groupings deserve theoretical and terminological distinction: the minimally diagnostic clade (= phylogenetic species; Cracraft 1983), the biparental sexual system (= recognition species; Paterson 1985), and the obligately uniparental, habitat-specific clone (= one kind of cohesion species; Templeton 1989). What these should be termed is largely a semantic matter. I prefer to use *species* only for the recogni-

tion species, because it fulfills criteria 1 through 3, and criterion 4 is irrelevant to the species viewed as a complex system. Under the Phylogenetic Concept, only criterion 4 is claimed, but it is applied inconsistently. The cohesion species (Templeton 1989), in encompassing all organisms, is too broad to fulfill any of the criteria consistently. The Isolation (= "Biological" [Mayr 1963]) Concept, which requires only criterion 1 in a way that is now widely recognized as misleading, should be laid to rest.

Acknowledgments

I thank Hugh Paterson for sharing with me some of his deep insight into natural history and particularly for persevering through many hectic (but fun) arguments in showing me new perspectives on the subject of "the unknown and the unknowable"! I am grateful to John Gatesy and J. A. Grant-Mackie for very useful comments.

Glossary

Species Concepts

agamospecies - A species that reproduces only nonsexually.

chronospecies - The successive species replacing each other in a phyletic lineage which are given ancestor-descendant status according to the geological time sequence (paleospecies, successional species).

Cohesion Concept of Species - "The cohesion concept species is the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms" (Templeton 1989:12). Cohesion mechanisms may be classified as follows (after Templeton 1989:13):

I. Genetic exchangeability—The factors that define the limits of spread of new genetic variants through *gene flow.*
   A. Mechanisms promoting genetic identity through *gene flow:*
      1. Fertilization system—organisms are capable of exchanging gametes leading to successful fertilization;
      2. Developmental system—the products of fertilization are capable of giving rise to viable and fertile adults.
   B. Isolating mechanisms: genetic identity is preserved by the lack of *gene flow* with other groups.

II. Demographic exchangeability—The factors that define the fundamental niche and the limits of spread of new genetic variants through *genetic drift* and *natural selection.*
   A. Replaceability—*genetic drift* (descent from a common ancestor) promotes genetic identity.

   B. Displaceability
      1. Selective fixation—*natural selection* promotes genetic identity by favoring the fixation of a genetic variant;
      2. Adaptive transitions—*natural selection* favors adaptations that alter demographic exchangeability, constrained by:
         a. Mutational constraints on the origin of heritable phenotypic variation,
         b. Constraints on the fate of heritable variation:
            i. Ecological constraints,
            ii. Developmental constraints,
            iii. Historical constraints,
            iv. Population genetic constraints.

Ghiselin's (1974a) species concept - Species are the most extensive units in nature such that reproductive competition occurs among their parts.

Isolation Concept of Species (also called Biological Species Concept) - Species are groups of interbreeding natural populations reproductively isolated from other such groups (Mayr 1940, 1963). "Isolating mechanisms" determine a species' limits. Either prefertilization or postfertilization isolating mechanisms (Table 1.3) are sufficient.

morphospecies - A group of individuals that are considered to belong to the same species on morphological grounds alone.

Phylogenetic Species Concept - A species is the smallest diagnosable cluster of individual organisms, within which cluster there is a parental pattern of ancestry and descent, beyond which there is not. (e.g. Nelson and Platnick 1981; Cracraft 1983). No sexual reproductive linkages are referred to. Thus, a species can be a cluster of asexual organisms.

Recognition Concept of Species - A species is that most inclusive population of individual biparental organisms that share a common fertilization system (Paterson 1978, 1981, 1985).

taxospecies - A species based on overall similarity determined by numerical taxonomic methods.

typological species (nomenspecies) - 1. A species defined on the characters of the type specimen(s); 2. A species is an *eidos* (type) with an unchanging *essence* (from Plato's [428–348 B.C.] concept of unchanging essences of, and discontinuities between, each eidos and each other).

Other Terms

amphimixis - Occurrence of syngamy between gametes produced by different individuals of different gender.

apomixis - The absence of both meiosis and syngamy among organisms that reproduce by eggs.

arrhenotoky - Production of haploid males from unfertilized eggs and diploid females from fertilized eggs.

automixis - Syngamy between meiotically reduced nuclei descending immediately from the same zygote (with or without formation of gametes).

gynogenesis - Thelytoky requiring pseudogamy, that is, penetration of ovum by sperm without sperm genome contributing genetic information to zygote; a form of parthenogenesis.

habitat - Of an organism or species, includes places plus the resources in those places that are necessary for life of that organism or species. The *fundamental habitat* of a species includes all the places plus necessary resources in which a species can live (although it may not be present there); and the *realized habitat* at a given time includes all those in which it does live.

habitat specificity - Of an organism or species, refers to the resource requirements of that organism or species.

heterogony - Cyclical parthenogenesis: a life cycle in which one or more thelytokous generations are followed by an arrhenotokous or amphimictic generation.

hierarchy - In the sense of Simon (1962:87): "Hierarchy has generally been used to refer to a complex system in which each of the subsystems is subordinated by an authority relation to the system it belongs to . . . I use hierarchy in the broader sense . . . [to] mean a system that is composed of interrelated subsystems, each of the latter being, in turn, hierarchic in structure until we reach some lowest level of elementary subsystem . . . A hierarchy can progressively form, or evolve, as stable subassemblies [i.e., the subsystems] form at increasingly higher levels."

niche, fundamental and realized - The "role or 'profession' of an organism in the environment; its activities and relationships in the community" (Krebs 1978:623). "The ecological role of a species in the community; conceptualized as the multidimensional space, of which the coordinates are the various parameters representing the condition of existence of the species, to which it is restricted by the presence of competitor species" (Lincoln et al. 1982:167).

resources - (My concept of resources is close to Lincoln et al.'s [1982].): Any components of the environment that can be utilized by an organism in its metabolism and activities, including temperature; relative humidity; pH; salinity; stream flow velocity; substrate characteristics; places for living, nesting, and sheltering; light; inorganic ions and molecules; all kinds of organic foods (such as prey); and mates and other mutualist organisms in the same or different species.

Specific-Mate Recognition System (SMRS) - A subpart of the fertilization system that is particularly important in mobile organisms for bringing sexual partners together for mating.

syngameon - Larger units, containing phenotypically and habitat-differentiated populations that hybridize naturally and have limited gene exchange. This concept is much used by botanists, e.g., by Grant (1981), who defines the syngameon as "the most inclusive unit of interbreeding in a hybridizing species group."

thelytoky - Parthenogenesis in which syngamy and meiosis from the same zygote occur, or in which meiosis and syngamy are absent.

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2

Species Concepts and the Interpretation of Fossil Data

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PUNCTUATED EQUILIBRIUM (Eldredge and Gould 1972; Gould and Eldredge 1977) was not, despite what the subsequent debate seemed to suggest, exclusively about patterns of morphological change in the fossil record. A fundamental point was that these authors' views on morphological change were derived from their application of the Isolation Concept of species, combined with an allopatric model of speciation, to fossils. With one bold stroke Eldredge and Gould (1972) demonstrated to the paleontological community that fossil evidence does not "speak for itself." Fossil data, like any other, require interpretation, and the species concept the paleontologist employs is critical to this interpretation.

This crucial point raised in the punctuated equilibrium argument—that species concepts determine the way in which paleontological data are interpreted—was largely lost in the debate that followed. In 1979, Eldredge again argued that species concepts have logical priority in interpretation of data (Eldredge 1979). He outlined two approaches to the interpretation of fossil data based on distinct species concepts. These he termed a *taxic* approach, in which the biological reality of species is viewed as central, and a *transformational* approach, in which species are viewed as taxonomic conventions. He argued that instances of gradual transformation of morphology in the fossil record were routinely interpreted as examples of phyletic change in a species lineage and that this interpretation was dependent on viewing species as taxonomic conventions, that is, that species are defined solely in terms of gross morphology.

It was not that either he or Gould ever denied that examples of gradual character transformation existed, but rather that it was equally valid to interpret these transformations as a consequence of multiple speciation events

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3

The Species in Paleontology

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UNTIL THE EARLY 1970s there was broad agreement that the fossil record could be simply and directly married to natural selection, Mendelian inheritance, and molecular biology, to consolidate and extend the "modern synthesis" of Huxley (1942). The leading figure in efforts to integrate paleontology with evolutionary biology was undoubtedly Simpson (1944, 1953), but others such as Mayr, Dobzhansky, and Stebbins all described the construction of that greater synthesis, and their own roles as its architects, with infectious optimism. The clear implication was that only details need be added for a full understanding to emerge.

In a sense that was so, although it has always been evident that many of the details involve complex problems, as Mayr (1978) has stressed. But some of the details, far from being the decorations on the finished product envisaged by the architects, have proved to be part of the foundations. What was missing has turned out to be a clear understanding of what species are and how speciation actually occurs.

This gap in understanding, by its very nature, has been prevalent in both neontology and paleontology. Species are after all a common currency in both disciplines, even if speciation is something that the neontologist need generally consider only in theory. But its effect on ideas about evolution has been more insidious in paleontology, because it is there that we look for evidence of evolution as a fact of history. In contrast, it is from neontology that we derive our ideas about what species are, but if we are wrong it does not, at first sight, necessarily affect us too badly. We may, of course, fail to understand what separates an apparently homogeneous group into true species, each with different behavior patterns, and we may fail in our attempts to control pests, as Huxley (1942:156) clearly recognized in the case of malaria-transmitting mosquitoes (see Michaux, this volume). But if our idea of species is awry, one could

argue, we will still see the difference between a sheep and a sheepdog, or an alpaca and an aardvark, a point also essentially made by Huxley. We are unlikely to waste our time trying to persuade males and females from such different animals to mate, and in that sense it may seem to be of little overall importance to get the theory of what species actually are precisely right.

But if we apply an incorrect concept of species to the fossil record, and to our interpretation of evolution based on the deployment of speciation over time, other problems arise. We risk being seriously misled by a cumulative error in our understanding of the development of life. However much we may seek to avoid it, faulty ideas about evolution over geological time will feed back into our notions of microevolutionary mechanisms and complete the circle of arguments about tempo and mode.

In truth, the species has long been acknowledged as a problem in paleontology. For this contribution I shall chart what I consider to be some significant points in the development of ideas about it over the past several decades, without any pretense at dealing with everything ever written on the subject. In particular, I want to underline the fact that until the development of Paterson's Recognition Concept we really were stumbling in the dark, equipped with inadequate ideas of what constitutes a species, how speciation might actually take place, and how to integrate the theoretical process with the historical pattern of speciation in the fossil record.

Species and Paleontology

Some paleontologists have simply ignored the problems posed by the species, as Romer (1933, 1945, 1966) effectively did. By the time he wrote the third edition of his book on the vertebrates he was able to push the whole problem to one side with a passing reference to the "synthetic theory" available in works that the reader "would be well advised to consult" (1966:3). Others, in the spirit of the modern synthesis, have incorporated ideas from neontology into their own, at times extensive, discussions of the whole issue (see, e.g. Beerbower 1968; Kurtén 1968; Carroll 1988; Eldredge 1985*a*, 1989). But an indication of the persistent seriousness of the problem, and of the disparate views held by those active in the field, may be seen in the decision by the Systematics Association to hold a meeting in 1954 entirely devoted to the species concept in paleontology.

In his introduction to the resultant publication, Sylvester-Bradley (1956:1) argued that most paleontologists of the day recognized "two distinctly different sorts of species." The "biospecies" was the equivalent of the neontologist's species, which implied adherence to the definition given by Mayr (1942:120) as "groups of actually or potentially interbreeding populations reproductively isolated from other such groups." The second, what Sylvester-Bradley called

the "bread and butter" species of the paleontologist, was the "morphospecies." It is apparent from the other contributions that the confounding element in efforts to achieve a single "sort" of species fell into two, interrelated parts. The first was the time element and the resultant changes seen in the fossil record. The second was the fundamental problem of an inadequate definition of species that could apply to fossils, a problem simply exacerbated by the introduction of time into the discussion. But the overall view seemed to be that change within and between species in the fossil record was gradual in nature, just as it was held to be by classic population biology.

This view, of course, raised the problem of how to distinguish between species. While authors such as Rhodes (1956:40) argued that paleontological classification should strive to indicate genetic relationships, others disagreed fundamentally. Arkell (1956:99), in a wonderfully reactionary essay, saw only "a danger to palaeontology inherent in too much concern with the theoretical aspects of taxonomy," and felt that the units employed by the paleontologist must be arbitrary. He even argued (p. 97) that the only criterion for a taxon in paleontology was its "usefulness" in providing manageable groups and that different groups require different species concepts, conveying the forthright impression that he would be almost as happy classifying pieces of concrete as he would fossil organisms. Others again, such as Joysey (1956:86), took the view that chronological classification was essential. Indeed, Joysey was still championing such an approach nearly twenty years later, when he said, "I advocate that a continuous evolutionary sequence should be arbitrarily subdivided on chronological grounds" (1972:269). In his concluding remarks on the symposium, George (1956:124) strove to amalgamate genetic ("biological"), morphological, and chronological species into a single overall approach on the grounds that "there is no inherently 'right' way of achieving taxonomic integration."

All that was in 1954, and the debate might seem to be long behind us. But uncertainties over the nature of the species taxon in paleontology have continued to be reflected in the literature (Wiley 1978, 1979; Eldredge and Cracraft 1980; Vrba 1980, 1984*b*, 1985*a*; Tattersall 1986; Bock 1986). Moreover, the idea that fossil lineages can be divided somewhat arbitrarily into species at convenient points in the stratigraphy in the absence of other criteria has been repeated by others. Simpson (1961:165) and Mayr (1969:35–36) both lent their considerable authority to that view, and it was strongly implied by Kurtén (1968:238) in his discussion of mammalian evolution in the Pleistocene of Europe. Perhaps the most extreme statement of this position was made by Campbell (1979:569) in his survey of the problems of classification and nomenclature confronting physical anthropologists. As he put it then:

> It is clear that the boundaries of sequent taxa, be they genera, species or subspecies, should be conveniently agreed time-lines, rather than diagnostic mor-

> phological features such as the famed cerebral rubicon of Keith. This means that *both anatomy and dating are necessary to create the taxonomy of fossil lineages* [italics in original]. It follows that the development of a reliable chronology is one of the most important characteristics of the recent period of research, and as this paper will show, *new dates give us new taxonomy* [italics added].

I consider Campbell's statement extreme because I doubt if the suggestion that new dates should indeed give us a new taxonomy would find favor with many paleontologists. But the overall stance adopted is not so unusual. The result, at least until the end of the 1960s, was a reasonably coherent view of evolution held by paleontologists and neontologists alike, albeit with a few areas of obscurity about just what biological units the paleontologist actually employs. Although the details varied, the essence of most standard treatments of species in the fossil record was one of pragmatics and, at the risk of distortion, may be summarized as follows. It is impossible to know whether the organisms in question actually interbred on a regular basis (and therefore constituted what we would think of as a species), but some means of establishing taxa in the fossil record must be devised, and morphology (or rather the presence of morphological gaps) is the usual basis for decision making. The term *species* is used for the resultant groupings, but we should, of course, understand that this is done simply for convenience and that no precise parallel with the term *species* used for groups of living animals should *necessarily* be assumed. Evolution in the fossil record is therefore population biology plus time plus an inevitable (and apparently acceptable) measure of uncertainty.

Interpretations of the horse lineage offer perhaps the clearest example of the perspective. A trend toward monodactyly, greater size, and increased hypsodonty over several tens of millions of years are still frequently cited as a textbook example of the gradual nature of evolution at work, in line with the arguments put forward by Matthew and Chubb (1921), Romer (1933), and a host of other authors including, of course, Simpson (1944, 1951, 1953). A note of contradiction is introduced because change, in the conventional view, is expected to be gradual and cumulative, while absolute differences are expected to occur between taxa when speciation results from the accumulation of change over time, the usual paleontological dilemma. The various horse taxa are usually distinguished on the basis of detailed differences in tooth enamel patterning despite the overall assumption of a gradual and linear trend in evolutionary development (see, by way of example, the discussion by Churcher and Richardson [1978]). The mechanism for the actual process of speciation is never really made clear in such treatments, although seemingly correlated events such as chromosomal variations have increasingly been invoked as causal factors by some population biologists (Bush et al. 1977; Bush 1981) eager to incorporate newer ideas about an episodic pattern of change as discussed in the next section.

New Ideas, New Problems

The relatively coherent picture of evolution held until the end of the 1960s was seriously thrown out of focus when first Eldredge (1971) and then Eldredge and Gould (1972) argued that morphological gaps in the fossil record might point to the episodic nature of evolution and not to a series of preservational accidents. They suggested that phyletic gradualism, the slow and cumulative transformation of entire populations marred by an occasional break in the record, owed its dominance to intellectual inertia and an initial muddling of concepts by Darwin himself. In its place, they proposed that successive episodes of rapid change (punctuations) are followed by long periods of stable structure (equilibria).

These authors were led toward the idea of episodic change by the theory of allopatric speciation in small, peripherally isolated populations. Their emphasis on speciation in allopatry came about "because it is the allopatric, rather than the sympatric, theory that is preferred by biologists" (Eldredge and Gould 1972:94). Such a process, they argued, was incompatible with the idea of gradual change between species. But, although they highlighted the futility of much paleontological debate about how to reconcile the differences between biospecies and paleospecies, they stopped short of addressing the problem of the nature of species and the process of speciation from first principles. Unfortunately, the allopatric theory of speciation does not actually deal with the nature of species and offers a poor understanding of the process of speciation. Indeed, one of the major difficulties posed by speciation in allopatry was expressed by Mayr himself (1963:548) when he noted that isolating mechanisms, an essential part of the Biological Species Concept that underpins his theory of speciation in allopatry, "are *ad hoc* mechanisms. It is therefore somewhat difficult to comprehend how isolating mechanisms can evolve in isolated populations."

It is self-evident that any proposed character arising in allopatry cannot be an isolating mechanism, since it has not evolved in any sense to protect the "integrity of the species," and must be considered an *effect* in the sense employed by Williams (1966). But although Eldredge and Gould sought support from speciation in allopatry, they took no account of the difficulties posed by the requirement for isolating mechanisms to arise in such circumstances and restricted their concern to pattern rather than process. They were content simply to take what they needed from the idea of allopatric speciation and to argue (1972:94) that "a peripheral isolate develops into a new species if *isolating mechanisms* evolve that will prevent re-initiation of gene flow if the new form re-encounters its ancestors at some future time" (italics in original). As a result they left the way open for critics of punctuated equilibrium to argue that evolutionary biology could equally well predict a gradual pattern of change,

whatever theory of speciation was "preferred by biologists," as they put it.

Not surprisingly, the idea of punctuated equilibrium met with considerable opposition from members of a paleontological community firmly committed to the modern synthesis (see the discussion by Gould and Eldredge [1977] and Eldredge [1985*c*] and arguments put forward by Gingerich [1984, 1985] and by Hecht and Hoffman [1986]). Some of the criticisms even led Gould (1985:3) to characterize them as "distortions so obtuse that I can only regard them as willful." But a model of evolution rooted in the synthesis also continued to receive strong support from evolutionary biologists outside the paleontological community, in both specialist and popular treatments (Mayr 1978; Ayala 1978, 1983; Stebbins and Ayala 1981; Barton and Charlesworth 1984; Carson and Templeton 1984; Butlin 1987; Maynard Smith 1981, 1987; Coyne et al. 1988; Chandler and Gromko 1989).

The irony inherent in the proposal for punctuated equilibrium put forward by Eldredge and Gould is that it was rooted firmly in the ideas of the modern synthesis, which saw evolution by slow, progressive change within the species as a result of directional selection. Speciation was then expected to occur largely as a function of the time over which such within-species changes had accumulated and was itself seen as the product of the same slow, progressive change that from time to time spilled over into the production of a new species. Mayr's proposal for allopatric speciation did little to challenge that notion, since it simply argued for the divergence of geographically separated populations and the development of isolating mechanisms as part of the same overall process. When Eldredge and Gould challenged the intellectual inertia of phyletic gradualism they struck directly at the heart of the consensus view of evolution held by adherents of the modern synthesis, which may do much to explain the vehemence of the reaction. But they did so with a proposal that was not sufficiently radical in its departure from the accepted wisdom of the synthesis and that simply made the heretical suggestion that speciation might indeed be rapid and the gaps in the morphological continuity of the record therefore real. In so doing, of course, they also challenged one of the implicit beliefs of orthodox paleontology, the ludicrous notion that we are lucky to have such gaps; otherwise we should have no means of recognizing taxa in a world where gradual change prevails, as Eldredge and Cracraft (1980:116) have pointed out.

At the heart of the subsequent debate over punctuated equilibrium has lain a failure to separate within-species change from speciation. This stems in part from use of the term *stasis* to describe the periods between speciation events and from Eldredge and Gould's failure to deal with the nature of species and the precise mechanism of speciation. Critics of punctuated equilibrium have since felt that a demonstration of gradual change over time in a given species, expected under the terms of the synthesis, is sufficient evidence to reject the punctuationist interpretation in favor of phyletic gradualism. But the rate of

change within a species actually offers no answer to questions about the speed at which it became that species or eventually gave rise to another. The error that leads to a conflation of the two stems from an inadequate concept of the species itself, and once that is overcome the problem resolves itself. I shall return to this point in the next section.

I have suggested that the theory of allopatric speciation employed by Eldredge and Gould (1972) did not deal with the nature of species and gave at best a partial understanding of speciation itself. Gould (1980*a*:123) has since rejected the primacy of allopatric speciation and suggested the incorporation of sympatric models involving the fixation of chromosomal variants as isolating mechanisms. Eldredge (Eldredge and Cracraft 1980:126) has argued that, to the systematist, both parapatric and sympatric speciation might mimic the effect of allopatric speciation in peripherally isolated populations. Such proposals imply episodic change and can be fitted into the punctuated equilibrium picture of evolutionary tempo, although the causal connection between chromosomal rearrangements and speciation is open to very serious question (Paterson 1981), and speciation in sympatry has little theoretical or empirical support (Mayr 1963; Paterson 1981, 1985). But such shoring up of the edifice calls in question the strength of the original argument for punctuated equilibrium if the concept of the species and the model of speciation can be so readily altered or extended. In these circumstances both the extent and the inconclusive nature of the debate since 1972 have, with only modest hindsight, been entirely predictable.

More New Ideas, Fewer (or Different) Problems

A solution to the problems of understanding evolutionary tempo and mode in the fossil record has been provided by Paterson in various publications, most notably in 1985 and 1986. The essential point as made by him (Paterson 1985) when he stressed that "*any* view of species must be cast in genetic terms if it is to be useful in understanding the process of evolution" (italics added). That statement echoes those of the more perceptive participants in the 1954 meeting on species in paleontology. Arbitrary paleontological units, as advocated by Arkell (1956), may have their uses in some or other scheme for pigeonholing samples, but to argue that paleontologists deal with different categories of "species" is to remove any point of contact with neontology or, for that matter, with reality. The debate over tempo and mode in the fossil record concerns the deployment of speciation, not the appearance of arbitrarily defined units, as Wiley (1979:215) has stressed, and unless speciation is clearly understood to refer to genetic species the whole debate is pointless. Of course, the paleontologist may choose to operate outside the constraints of a genetic view of species, but then the whole business of studying fossils does indeed risk

becoming a form of stamp collection as implied by Gould (1980*b*).

Under the Recognition Concept, a species is defined as "that most inclusive population of individual, biparental organisms which share a common fertilization system" (Paterson 1985). The details of the Recognition Concept are adequately presented elsewhere. The point to stress here is that the fertilization system of a species will be stable because of the coadapted nature of its male and female components, the effect of stabilizing selection in the organism's normal habitat, and the large population size in normal circumstances. Stability is likely in components of the fertilization system that serve to bring mating partners together, what Paterson has termed the Specific-Mate Recognition System (SMRS). Speciation occurs when a new SMRS is produced by the action of directional selection on the original system in a small, isolated subset of the population in a different habitat, ensuring an inability to recognize and mate with members of the original population. In contrast, changes resulting from directional selection operating on characters unrelated to the fertilization system can occur at any time within the lifetime of a species and are effectively decoupled from those at speciation. Characters related to the fertilization system will therefore remain stable while the species persists, while others may change in response to selective pressures as the population becomes finely tuned to its new circumstances. But gradual changes resulting from such tracking of the environment say nothing about the deployment of speciation. The importance of all this for paleontology cannot be overemphasized. Speciation will be episodic, and the fossil record will show evidence of punctuated equilibrium rather than gradual change between species.

This view of speciation differs fundamentally from that incorporated in Mayr's Biological Species Concept, which underlay Eldredge and Gould's original argument for punctuated equilibrium. Species within the framework of the Recognition Concept cannot be arbitrary divisions of the morphological pattern over time in a lineage but are an effect of processes with a clear genetic basis. Because the Recognition Concept provides a robust explanation for stasis in species-specific characters, it also offers a better understanding of the equilibrium phases between the punctuations than that first proposed by Eldredge and Gould (1972:114). They suggested that the coherence of a species existing in nearly independent local populations might result from the species' origin "as a peripherally isolated population that acquired its own powerful homeostatic system." They argued for the reinforcing effect of such a homeostatic mechanism, but were unable to offer a concrete model for its action and could only suggest that "the answer probably lies in a view of species and individuals as homeostatic systems." We may now see that the effect of stabilizing selection on the signal and response chain of the SMRS is the key point in the argument for stasis and that it answers the call by Maynard Smith (1981) for an explanation of the phenomenon.

The extent to which the argument over phyletic gradualism versus punctuated equilibrium as the best description of evolutionary tempo and mode has been misplaced is now clear. Confusion has stemmed from an unfortunate use of the term *gradualism,* a misleading equation of the term *equilibrium* with stasis, and a failure to separate within-species changes from speciation events. As originally coined by Eldredge and Gould (1972:89), *phyletic gradualism* was clearly meant to mean gradual change between species in contrast with punctuated equilibrium. But because those authors themselves failed to distinguish within- from between-species changes clearly enough, confusion was set in train from the outset. *Gradualism* is also employed in the literature to describe the nature of accumulated intergenerational morphological change within a species, which simply must be gradual. *Equilibrium* as used by Eldredge and Gould referred to the continued existence of a species between the speciation event that brought it into being and any subsequent extinction. The term *stasis* has come to be regarded as synonymous with *equilibrium,* but it refers to the absence of any evidence for the operation of directional selection upon the species during its lifetime and not to the lifetime itself (see also Michaux, this volume). However, Eldredge and Gould chose to equate equilibrium with stasis and with an absence of change, and left the way clear for those who reject punctuated equilibrium based on a demonstration of gradual intraspecific change and the assumption that this implies phyletic gradualism. *Gradualism* and *punctuated equilibrium* are therefore not useful terms to employ for contrasting versions of the same thing, but should be used to describe totally separate phenomena, unless the distinction between speciation and within-species changes are to be blurred (as of course they usually are). Indeed, *phyletic gradualism,* seen from the perspective of the Recognition Concept of species, is a rather meaningless term. Geologically, a speciation event will always appear short, perhaps to the point of virtual invisibility. Efforts to demonstrate that evolution is gradual by producing evidence for a slow change in one or other character of a species in the fossil record simply say nothing about the deployment of speciation. Confusion over this point underlies the discussion by Carroll (1988) of evolutionary tempo and is evident in his conclusion (p. 575) that evolutionary rates are "certainly neither *gradual* nor *punctuational,* but *irregular* or *opportunistic*" [italics in original].

Of course, the Recognition Concept is not a panacea for the problems of identification that face the paleontologist. We are still left with the simple fact that fossils preserve only parts of an organism and that features of possible taxonomic value are often missing. The identification of species in the fossil record is therefore always going to present problems. Moreover, it follows from an acceptance of the Recognition Concept that the nature of the differences between species is unlikely to be absolute, since only those characters related to the fertilization system will *necessarily* change at speciation. Morphological

continuities will be enforced through phylogenetic inertia, and all change must be gradual from generation to generation unless we are to accept the notion of "hopeful monsters." Put most simply, paleontologists will detect speciations with greatest reliability in the fossil record when the fossils in question represent biparental organisms that bear characters of importance in the fertilization system of the species, such as the genitalia of insects, horn cores of the Bovidae, antlers of the Cervidae, or cranial ornaments in dinosaurs. They will have greater problems when they deal with families like the Equidae and Suidae, where many taxa are established on the basis of dental morphology (Turner and Chamberlain 1989). Continuities and partial preservation of tissues aside, sibling species are simply not amenable to recognition in the fossil record, and there may very well be an overall tendency to underestimate the number of true species in certain families or even orders (see also Vrba, this volume). This problem has been discussed in relation to the Hominidae by Tattersall (1986), although there are grounds for thinking that we may be able to approach the problem in a sensible manner if we adopt the perspective of the Recognition Concept (Turner 1986; Turner and Chamberlain 1989).

To date, acceptance of the value of the Recognition Concept of species in both neontology and paleontology has been slow. In the field of paleontology there has been some initial appreciation of the benefits (Vrba 1980, 1984*a,b*, 1985*a,b*, this volume; Turner 1985, 1986; Turner and Chamberlain 1989), and there is now evidence of interest among a wider circle (Crompton 1989; Tattersall 1989) beyond those former colleagues and students of Paterson who have applied his ideas to their own work. In a most significant step, Eldredge (1985*a,b*) has devoted increasing attention to the topic and presents (1989) a lengthy discussion of the SMRS in his latest book on the subject of macroevolution, which includes a clear statement of the difference between speciation and within-species changes. But although Eldredge's incorporation of Paterson's ideas affords considerable insight and addresses many of the issues discussed above, his analysis of developments appears somewhat flawed. One gains from it no sense that the Recognition Concept offers a radical alternative to the concept of species and the mechanism of speciation employed in the original formulation of the punctuated equilibrium model. Instead, the idea of the SMRS is simply incorporated into the argument for periods of stasis being interrupted by episodes of speciation, with the claim (1989:119) that disruption to the SMRS was covered in the original discussion of rapid adaptive changes in small, peripherally isolated populations presented by Eldredge and Gould (1972) and indeed went beyond the conclusions reached by Paterson. I find that part of the argument difficult to sustain.

In contrast, most if not all of the criticism of the Recognition Concept has

been from the neontological perspective and appears to have been based largely on an unshaken acceptance of the continued validity of the modern synthesis and the Biological Species Concept (e.g. Coyne et al. 1988) and, in some cases (for instance, Raubenheimer and Crowe 1987), a seeming inability to grasp the point at issue. Paterson (1981, 1982, 1985, 1988) and others (e.g. Masters and Spencer 1989) have demonstrated the illogicalities inherent in many of the criticisms, but a revolution in thought is still seemingly required on the issue. The clear value of the concept in the paleontological context may be the best hope of producing that revolution.

Acknowledgments

I thank David Lambert for inviting me to contribute to this volume in honor of Hugh Paterson, whose ideas have done so much to shape my own views on species in the fossil record. I am grateful to Ian Tattersall and Lars Werdelin for constructive comments and to The Leverhulme Trust for research funding.

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4

Kinji Imanishi's Biological Thought

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PROF. KINJI IMANISHI (1902–1992), since the 1940s a father figure in Japan for many different fields related to biology and anthropology, is now known to the West through articles by Sibatani (1983*a*,*b*), Imanishi (1984), and Halstead (1985, 1988). These articles are all related to his evolutionary theory on which he published many books and articles during the last period of his academic activity (e.g. Imanishi 1977, 1980, 1984, 1987). This was long after his retirement around 1966 from the chair of anthropology at the Institute for Human Sciences, Kyoto University, and from his duties as President of Gifu University around 1971. Because Imanishi took a strong anti-Darwinian or antiselectionist stance when articulating his thought on evolution, and because this coincided with the explosive growth of debate about evolution in the West since 1972, his name has been associated, mainly in the West but also in Japan in recent years, with the image of an unorthodox, and even nonscientific, theorist on evolution.

However, before he returned, toward the end of his academic activities, to the initial point in biology where he started his career as research scientist, he had worked in various fields of scientific pursuit, each time within a minority circle (Ogushi 1985). Indeed, through his work in such "marginal" areas he founded a number of new schools of research, some of which have by now risen to internationally acclaimed positions. These aspects of Imanishi's contribution to Japanese science are less well known than his position on evolution, but without acknowledging these it would be unjustified to generally criticize Imanishi's work and his insights into biology.

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6

Toward Operationality of a Species Concept

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A VAST AMOUNT has been and continues to be written about species concepts. I draw from this fact two conclusions: evolutionary scientists agree that the notion of a species is important yet continue to disagree on how a species should be defined. This chapter addresses the discrete issue of whether it is possible to devise an operational approach to defining the "interbreeding" or "mate recognition" criterion of the species concept for sexually reproducing organisms.

On Defining the Sexually Reproducing Species

Most biologists probably believe the sexually reproducing species to be well defined, perhaps even operationally defined. This section presents species definitions, explains what operationalism in biology means, shows why the widely accepted definition of the sexually reproducing species is neither clear nor operational, and reviews some possible approaches to making it operational.

Species Concepts and Evolution

The Latin root of the word *species* refers to outward appearance as in shape and form. Therefore, it is not surprising that early naturalists called organisms that looked alike "a species." In the task of pigeonholing living things, biologists assigned names to such species and began assembling similar species into larger groups. Our ability to "see" similarities and differences has been extended to traits ranging from molecular composition to animal behavior, but the similar/different criterion remains at the heart of most practical sorting of organisms into species. It is difficult to conceive of a meaningful alternative to

similarity/difference in classifying asexually reproducing organisms and those known only from the fossil record.

The advent of Darwinism altered the conception of higher taxonomic categories without fundamentally affecting the species notion. Groupings of species had to be based on similarities that reflected common ancestry rather than just any similarities. Although it would be perfectly logical to group together bats with those species of insects and birds that fly (the majority, although not all, insect and bird species fly), such a grouping would not reflect phylogeny. Bats have a more recent common ancestor with other mammals than with either birds or insects, and both insects and birds have more recent common ancestors with nonflying animals than they do with one another. Although the contemporary school of taxonomy called phenetics essentially rejects evolutionary criteria for defining higher categories, most modern systematics is explicitly phylogenetic in purpose. Despite this change in the nature of classification, no similar revolution in how we define species occurred until the middle of the twentieth century.

It is almost always possible to find precursors to any major conceptual breakthrough in the history of biology, but the recognition that a different sort of species concept is possible for sexually reproducing organisms is rightly attributed to Ernst Mayr. In one of the earliest, if not the very first, explicit statements on the subject, Mayr (1940) stated that species are "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (see also Mayr 1942). Variants of this definition are still echoed in virtually all modern textbooks of biology (e.g. Campbell 1990; Starr and Taggart 1992; Purves et al. 1992).

There are a few semantic problems with the quoted definition that have occasionally been circumvented by restatements. For example, breeding is most clearly viewed as an activity of individuals rather than populations. Another minor problem is the pleonasm created by the unnecessary specification of reproductive isolation from other such groups, which are obviously of the same species if there is interbreeding. Therefore, with no injustice to the original intent, one could say that species of sexually reproducing organisms are *naturally occurring groups of actually or potentially interbreeding individuals.*

This species definition for sexually reproducing organisms has stood the test of a half-century so well that apparently only Paterson (e.g. 1980, 1981) has tried seriously to reorient it. Paterson has emphasized the criteria used by individuals to recognize a mate: a Specific-Mate Recognition System (SMRS). He sees this SMRS as the fundamental property of a species, established at the time of speciation and essentially unaltered thereafter. Lest too narrow a view be taken of this notion, it is easily extended to recognition among gametes for plants and those animals that shed gametes into the environment without coming together for spawning or copulation.

Paterson's species notion rests upon prezygotic mechanisms and therefore denies any possible role of reinforcing selection. It is possible under Mayr's definition that breeding between individuals of different species is inhibited by postzygotic mechanisms, such as hybrid embryos that die or hybrid offspring that are sterile. It is therefore possible to reason that would-be parents engaging in such ill-fated matches are wasting valuable gametes, and hence such mating attempts would be selected against. Such selection would promote refinement of mate recognition, and it is specifically this possibility that Paterson argues against.

It is not a purpose of this essay to compare the two foregoing views of sexually reproducing species or to answer the question as to whether reinforcing selection for mate recognition occurs. I have argued elsewhere against reinforcing selection in a more general context (Hailman 1982). Instead, the present task is first to point out that neither species concept is operationally defined (for the same reason) and then to see if an operational approach is feasible. In fact, from the viewpoint as to where the concepts founder, there is no fundamental distinction between Mayr's and Paterson's sexually reproducing species; they differ only in ways that are not the concern of this essay, so will be treated for present purposes as variants of the same concept.

Operationalism in Evolutionary Biology

Operationalism as a method for assuring communicability of scientific concepts grew naturally out of physics early in the twentieth century (Bridgman 1927, 1938, 1945). Physicists could not see and handle entities such as electrons and so had to define them in terms of measurements made by instruments. Furthermore, physicists quickly recognized that even the measured value of a variable had no precise meaning unless the operations by which it was measured were made explicit. For example, the speed of an airplane as measured by an instrument on board that senses how fast air rushes by the plane delivers one value whereas the distance between departure and arrival points divided by the time taken to make the flight may give a quite different answer. In order to communicate a variable such as "speed" one must stipulate the operations by which it is measured. Physicists had to define entities such as "electron" by criterion values of measured variables. And causal relationships were defined as logical functions relating measured variables. These three things—variables, criterion values, and functions—are the stuff of which science is made, and they will be communicable and hence "objective" only if based on explicit procedures of measurement.

There is a philosophical concern connected with operationalism that is not at issue here. Logical positivists—some principal figures being Bridgman, Alfred North Whitehead, and Bertrand Russell—tended to consider the "real"

world as nothing more than our perception of it: things exist only if we can verify them empirically. I am not concerned here with philosophical issues of reality, but only with communicability among scientists. I take the view that our models of the external world are communicable, and therefore "objective," only if they are based in principle on measurable variables.

Biologists, being able to see and handle many of their plants and animals, were slower than were physicists to build their component sciences on operational principles. After all, it was (in most cases) disarmingly obvious what a biological entity such as an individual animal was, so why waste time trying to define it in some way based on measurements? Troublesome cases were decided more or less by fiat. For example, every introductory biology textbook until recent times simply announced to students that siphonophores such as the Portuguese man-of-war (*P. physalia*) were colonies rather than individual organisms—without making explicit how this counter-intuitive judgment was reached. In point of fact, many different operational definitions of an individual are possible, and by some a man-of-war is a colony and by others it is an individual organism. Just as an airplane can travel at two different speeds simultaneously, so is a Portuguese man-of-war simultaneously an individual and a colony—depending upon the definitions used.

Explicit operationalism is being increasingly adopted in biology today, although evolutionary studies have been slow to adopt. The tardiness may be due to the complexity of evolutionary concepts and lack of recognition of the power of operational thinking. Still, many attempts to make evolutionary biology operational are in evidence, as in algorithms for determining phylogenetic trees; concepts such as homology, analogy, and their kin (Hailman 1976); and the notion of adaptation (Hailman 1988). Whenever it is vague as to how one should determine whether a given case meets a stipulated criterion, then the criterion is likely to be improved by more explicit operationalism. The criterion of "interbreeding" or "mate recognition" in species definitions for sexually reproducing organisms is a case in point.

Problems with "Interbreeding" and "Mate Recognition"

The problem with "interbreeding" or "mate recognition" criteria is remarkably easy to state, yet I have never encountered such a statement in the literature. Put as a query, one may ask how to judge whether or not two groups of natural populations are interbreeding (or potentially interbreeding). Or, how is one to judge whether the individuals of a naturally occurring group share a mate recognition system?

Pursuing these questions perhaps a bit further than necessary, it is obvious that all members of one population could not possibly interbreed with all members of another. This is one of the reasons that Mayr's definition contains

the phrase "potentially interbreeding." Even that caveat simply compounds the problem because the definition does not reveal how to assess potentiality. Furthermore, except in hermaphroditic organisms and those (like some wrasses and parrotfishes) that may change sex, sexually reproducing organisms cannot even interbreed with all members of their own population. This latter problem could be circumvented by adding the stipulation that interbreeding connotes "with the opposite sex," a point that is more clearly implied by Paterson's "mate recognition" criterion. Both formations of species, however, suffer from the same vagueness: as not every male could possibly interbreed with or recognize as a potential mate every female in a population (unless it were quite small), and similarly not every female could mate with or recognize as a potential mate every male, the criteria of interbreeding and recognition are simply undefined.

If stipulated criteria of a definition are unspecified, then there is no assurance that two equally competent persons will arrive at the same end point when attempting to apply the definition. Suppose there exists a population of, say, a hundred small flycatchers equally divided between the sexes, males of which sing a distinctive song. If one person adopts the criterion "flying toward a playback speaker broadcasting a recording of the song" as indicating potential interbreeding or mate recognition on the part of females, some percentage of females will qualify. Another person might decide to inject all the females with estrogen and then see if they respond to the playback. Suppose, then, these two procedures identify different collections of females, which have some but not all individuals in common (a likely result of such procedures). Which collection is the species? If both procedures are deemed reasonable interpretations of "potentially interbreeding" or "mate recognition," then both collections define different and overlapping species. That conclusion violates the notion of reproductive isolation and the implication (of all species concepts) that every individual in nature belongs to one and only one species.

Definitions do not necessarily have to be explicit about measuring operations in order to be considered operational, so long as those operations are clearly implied. However, in the case of definitions of species in sexually reproducing organisms, no operations for assessing "interbreeding" or "mate recognition" are implied. As the critical criterion is ambiguous in both cases, no definitions logically exist. The road out of this tangle is toward operationalism, and it forks immediately into two paths.

Operational Approaches to a Species Concept

The alternative paths toward operationality are to abandon notions such as interbreeding and mate recognition on the one hand, or to make them operational on the other. As an example of pursuing the first path, one might consid-

er defining a sexually reproducing species as the smallest group of organisms that was consistently distinct in morphology from all other groups (Cronquist 1978:15). This definition, if taken seriously, would elevate males and females of sexually dimorphic forms to species status as well as create other ludicrous conundrums. Apologists for cladistic analyses of phylogeny get into similar problems when defining species "objectively," and Mayr (1988:326–328) has laid out some telling objections.

To return to any morphologically based, similarity/difference approach to species, even if based explicitly on measurable variables, would be throwing the baby out with the bath. There *is* something special about sexually reproducing organisms, which Mayr and Paterson have attempted to finger. In order to preserve that something special, one needs to try to define it in some more operationally oriented manner. Notions of "interbreeding" or "mate recognition" seem to imply that members of the same species are connected with one another in some way that involves the reproductive process. It is the nature of this connection that we seek to clarify and assess, and there are various types of candidate connections.

For example, many species have apparently species-specific pathogens or parasites. Those already existing are of no help, for they merely constitute an ordinary taxonomic character like some part of the anatomy. However, one could in principle create genetically new pathogens and parasites, introduce these to an individual, and chart their spread. The collection of organisms infected at asymptotic spread would then define the species. Some problems with this approach are obvious: some individuals may be sufficiently resistant that the infecting agent cannot be detected in them, and in many cases pathogens spread across what we consider to be species boundaries (e.g. flu viruses of man come from birds as well as other mammals).

As a more relevant attempt to assess reproductive networks, it might be possible to introduce a new and beneficial gene into one individual and chart its spread to new individuals of succeeding generations. Not many years ago this suggestion would have been dismissed as fantasy, but with modern genetic engineering it is today merely futuristic rather than unthinkable. The spread of the beneficial gene in succeeding generations would sooner or later halt, and all those individuals possessing it could be defined as conspecific. Some drawbacks of this approach are immediately obvious: one does not want to muck around with the gene pools of wild species (we have already altered their environments immensely), and the time required to reach asymptote in the geographic spread of the beneficial gene might render the method impractical for all but very small populations. Worse yet is the high probability, due to genetic factors such as random mutation and laws of Mendelian inheritance, that the beneficial gene never would reach all members of what we consider to be the same species. Of course, if the beneficial gene endowed the possessors

with such selective superiority that all those lacking it would eventually disappear from the species, the method might work. But the wait for the results of selection would be even longer than the wait for genetic spreading, so the whole notion must be abandoned as manifestly impractical.

It would appear that if reproductive connectivity is to be made operational, the only feasible route involves assessment of actual breeding history. Even in highly polygynous and the few polyandrous species, no individual mates with more than a relatively few individuals of the opposite sex. Although sib-sib matings can occur, brothers and sisters are connected reproductively by virtue of the reproductive processes of their parents.

Suppose, then, one attempted to define species in terms of genealogical connectivity. If I had a brother (which I do not), and he married into the Smith family while I married a Brown girl, the Hailmans, Smiths, and Browns could all be connected through the offspring of my brother and me, and our common parents. Could one not pursue such connectivity to create a network that would define the species? Disregarding temporarily the obvious impracticality of working out genealogical relationships for most animal populations, the connectivity approach presents other problems. How far back must records go to create the genealogical network? The answer clearly depends on the degree of outbreeding within local areas of a species' range, and for widely distributed species the number of generations required might be enormous. Nonetheless, this approach may not present unsurmountable problems. Those of us who are genealogical buffs frequently find common ancestors within fifteen or so generations back: thus I discovered quite fortuitously that I am related to one of my former doctoral students and to the former wife of a colleague in my department.

A more troublesome problem relates to the required multigenerational data. Consider two species of chickadees (*Parus*) that are believed to be closely related (and in fact occasionally hybridize in certain areas of contact): the Carolina (*P. carolinensis*) and black-capped (*P. atricapillus*) chickadees. The latter, in particular, has such a large geographic range and such a low dispersal distance that it is conceivable that one might have to go back genealogically past the point of their separation from a common ancestor in order to connect all the individuals within one of the two species. We might therefore end up concluding that all members of both species were in fact members of the same species. The connectivity approach might succeed only if connectivity is such as to "network" currently living individuals without going far enough back in genealogical history to the last speciation event.

Indeed, the universality of the genetic code of base-pair triplets determining amino acids suggests that all life sprang from a common source, so that all individuals of every species show connectivity if one goes back enough generations. So, for the connectivity approach to succeed logically it requires that all

individuals of a species be connected by links occurring since the last speciation event. It might be that this required property exists universally in biological organisms—there are in fact ancillary reasons to believe that it does—but insofar as I can tell there is no proof. Furthermore, it is necessary to identify when in the genealogical history the last speciation event occurred, for one has to have a criterion for deciding when to stop making the retrograde links.

An Example: Florida Scrub Jay Connectivity

With the kind permission of Glen E. Woolfenden and John W. Fitzpatrick, I have analyzed their genealogical records on the Florida scrub jay (*Aphelocoma c. coerulescens*) to assess the feasibility of a connectivity approach to defining a sexually reproducing species. The goal of the analysis was to see how connectivity among individuals increases as a function of increasingly distant connections.

Biology of the Florida Scrub Jay

The Florida scrub jay is a relatively large passerine bird that is restricted to oak scrub habitat of the Florida peninsula. In western United States and Mexico scrub jays classified in various other subspecies live in similar, but more diverse, habitats—separated from the Florida peninsula by about 1500 miles in which no similar habitat and no scrub jays occur. Apparently, a once-continuous range was bifurcated by Pleistocene glaciations in mid-continent. The timing of the last speciation event is unknown, but the only extant sympatric congener is the gray-breasted, formerly Mexican, jay (*A. ultramarina*) of Mexico, which occurs as far north as southern Arizona, where its range overlaps that of the scrub jay, and apparently no hybrids have ever been reported. A third member of the genus, the unicolored jay (*A. unicolor*) occurs in humid montane forests and oak-pine habitat of Central America.

The Florida scrub jay is basically a nonmigratory, permanently territorial, permanently paired, permanently monogamous resident of the Florida oak scrub, which is completely saturated by conterminous jay territories (Woolfenden and Fitzpatrick 1984). Unlike western scrub jays, where young birds survive in peripheral habitats that apparently will not support successful nesting, Florida scrub jays stay on their natal territories or become adopted by breeding pairs other than their genetic parents. Those few young Florida scrub jays that attempt to establish territories or home ranges outside of the scrub soon disappear, apparently mainly being taken by hawks. It thus appears that Florida does not have suitable peripheral habitat for survival, so nonbreeding jays must remain as "helpers" on the territory of a breeding pair until they can become breeders by pairing with a widow or widower on a nearby territory (or by a few other means). Dispersal is low, with males often becoming breeders in a territory adjacent to their natal territory and females averaging only one territory removed. There are cases, however, of banded individuals moving as far as about 15 km. Prebreeding mortality is high, as in almost all animals, but once a Florida scrub jay becomes a breeding bird it may survive for a decade or longer, and lifetime reproductive output of a few individuals can thus be impressively high.

A few more empirical findings about reproduction are necessary background. As stated above, Florida scrub jays are "basically" monogamous and permanently paired; rare exceptions do occur. There are known to me two documented cases of bigamy, one (not on the study tract) that has persisted for several years. There are also very rare cases of divorce and repairing. A breeding bird commonly, however, loses a mate (presumably to predation) and always attempts to re-pair, remating being apparently more successful among males than females. Therefore, a given bird may have several mates over its lifetime. Finally, there is strong incest avoidance among the jays: fathers never pair with their daughters nor mothers with their sons. Brother and sister never pair if growing up together on their parents' territory. If, however, one sibling leaves the territory to become a breeder before the other hatches, and the first subsequently loses its mate, it could pair with the younger sibling. Such pairings have happened a few times in the nearly quarter century of the population study but were not encountered in my analysis.

Operations of the Connectivity Analysis

The heart of my methodology was to connect individual jays by "links." In the present analysis there is only one type of link: parent-offspring. Thus the two parents of an individual are not linked because they paired, but rather because they are each linked to the offspring. The connectivity of parents is thus two units, that of parent and offspring one unit. Graphically, linkage may be represented by an arrow connecting parent and offspring, with the arrowhead at the offspring end. (This is merely one type of diagram used commonly in genealogic and genetic studies, the explanation a bit labored here to make clear the operations behind my analysis.) In short, linkage requires successful reproduction; even pairs that built a nest, laid eggs, and had hatchlings were not considered to be linked in my analysis—unless at least one of the hatchlings subsequently fledged and lived long enough to acquire its full complement of color bands from Woolfenden (about three months of age). My linkage criterion was therefore stringent.

The question naturally arises as to whether the reputed parents are actually the genetic parents of offspring that come from eggs in their nest. At least two potentially confounding factors could exist: the female may have received

extra-pair copulation(s) with a male or males other than her mate, or eggs in the nest might have been laid by some other female. Neither factor appears to be of concern in the Florida scrub jay. Woolfenden and coworkers (pers. comm.) have begun DNA fingerprinting studies of the jays and, to the surprise of no jay researcher, have found so far no evidence of any young being of parentage other than the breeding pair. Although a final statement on this issue must await more extensive samples and analysis, it appears now that if extra-pair copulations do occur in Florida scrub jays they are so rare as to be of no consequence for connectivity studies.

The other possibility—eggs being laid by a female other than the breeding female—seems similarly remote. Egg dumping is known for a few species of birds (mainly nonpasserines), where it constitutes a sort of intraspecific nest parasitism, but not even the suspicion of this phenomenon has been raised with Florida scrub jays. Clutch sizes show a symmetrical, unimodal distribution, with no indication of supernumerary eggs. Furthermore, territorial intrusions are immediately challenged, with no individuals other than the breeding pair and their helpers allowed to remain once detected. Helper females are driven away from the nest by the breeding female during nest-building, egg-laying, and incubation, being allowed at the nest only after the eggs have hatched (at which point helpers commonly bring food to the nestlings). And male breeders actively interfere with any courtship display, manipulation of nesting material, or other signs of breeding in helpers on their territory (pers. obs.). The one type of exception to all this evidence is the very rare occurrence of polygyny (only bigamy) where two females act as if they were breeders and both might contribute eggs to the clutch. There are no such cases of this in the sample I analyzed, and the sole, well-documented case (R.L. Mumme, pers. comm.) is not in jays of the main study tract of Woolfenden and Fitzpatrick. DNA fingerprinting would be as sensitive to eggs from other than the breeding female as it is to extra-pair copulations, and as noted above, results to date show no evidence of any complicating factors.

Assuming, then, that the breeding pair of a given territory are the parents of the offspring in the nest of that territory, connectivity based on census data is genetic connectivity. There are many possible starting points and rules for developing connectivity, the following being those I used for this analysis. The geographic area of study was defined as that area of Archbold Biological Station (Highlands County, Florida) censused monthly by Woolfenden, Fitzpatrick, and their co-workers. This has since become known as the "demography tract" to distinguish it from other areas on the large station, where Florida scrub jays are also under study by a variety of workers. I took one point in time (January 1989, when I began work on this chapter) and listed all birds on the tract, as shown by the census for that month, as the starting point.

It turned out that this choice of study birds from the beginning of 1989

represented a kind of worst-case scenario because of dispersal into the study tract of birds whose ancestry is completely unknown. In retrospect, perhaps I should have chosen birds from about 1980, thus providing a decade of ancestry and a decade of descent. My analysis is thus restricted to a pedigree network connecting ancestors and is thereby robbed of some portion of its power to connect birds. In order to alleviate (but unfortunately not eliminate) the dispersal problem, I discarded from analysis 28 first- or second-year birds that had dispersed into the study tract from elsewhere and were too young to have bred. The remaining 109 individuals thus became the study population.

The 109 birds were designated by their color-band combinations and written down (in computer graphics). Parent-offspring arrows were then drawn among appropriate birds from past census data. (That statement makes it seem easier than it actually was. There existed only hardcopy monthly census sheets for about twenty years. From these, as needed during the progression of the analysis, I created a database of genealogical relationships in Hypercard for the Apple Macintosh computer. The task proved to be an undertaking of stagger-

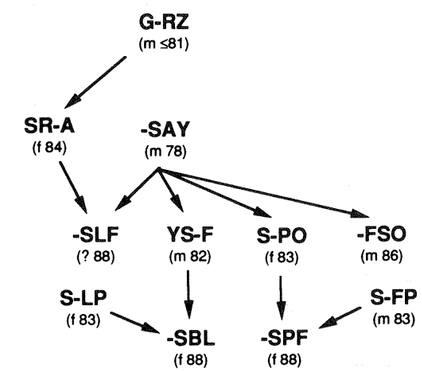

Fig. 6.1. An example of a connectivity "group" of eleven Florida scrub jays defined by one unit of parent-offspring links (arrow from parent to offspring). Color-band combinations always contain three letters and one hyphen (the "dash"), one of the letters being S or Z (silver and zilber, respectively, the U.S. Fish and Wildlife Service–numbered band). Other colors are: A, azure; B, blue; F, flesh; G, green; L, lime; O, orange; P, purple; R, red; Y, yellow; and W (not shown), white. Below each band combination is the sex and year of hatching of the bird; the designation ≤81 (G-RZ at top) means hatched in 1981 or an earlier year. Some sexes of young birds were not known when the analysis commenced in 1989. This is a particularly large group defined by first-order connectivity, primarily due to -SAY, a male that was 11 years old at the starting date and is still alive (as of 1993).

ing proportions, considering the repeated manual searches required in hundreds of raw census sheets. The Hypercard stack has more than 1600 cards, each representing an individual jay, with a summary of its territorial home by month, its parents, its breeding status each year, its mate each year, and the offspring produced each year. Search time to locate a particular card can exceed ten minutes.) Each set of birds that was connected by arrows formed a "group" as exemplified by Figure 6.1.

Note that the methodology is not purely one of common ancestry. In the figure, S-FP (lower right) is connected with all the other birds because he is the father of -SPF, whose mother (S-PO) provides the critical link to other birds through her father (-SAY). It might be, for example, that S-FP shares an ancestor with G-RZ (top of the diagram), but no evidence in the records attests to this possibility.

I then began tracing every parent and every offspring of the 109 birds, a process that began linking previously separate groups through birds that had died before the starting date for the study. (In order to do this I had to create a second database for each group membership so that included birds could be searched for by computer.) Figure 6.2 shows how an intermediary bird (WLS-)

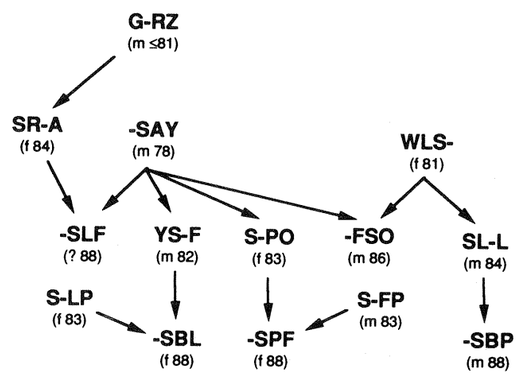

Fig. 6.2. An example of enlarging a group by finding a link (in this case, a common ancestor) in genealogical searches. The birds SL-L and -SBP are added because WLS- was the mother of both -FSO and SL-L. The original group shown in Fig. 6.1 was actually enlarged by many such second-order connections (not shown), so as to encompass 26 of the 109 birds alive in 1989 (the largest such group resulting from second-order linkages). Full connectivity diagrams are far more complicated because of the number of nonstudy birds that are ancestors providing linkages and because two birds can be connected by more than one path of arrows.

connected two previously separate groups, this bird being the mother of both SL-L (hatched in 1984) and -FSO (hatched in 1986).

The process of searching and connecting continued until no further connections could be made. One limitation encountered was that the study tract increased in area over the two decades of data, so as one moved backward in time the genealogical connections became increasingly sparse. Woolfenden began study of the jays in 1969, banding adults of unknown age and parentage, but because the jays are long lived, it was well into the 1980s before the entire population consisted of birds hatched on the study tract (parentage and age known) or young birds dispersing into it (age only known, sometimes not precisely). Again, in retrospect these problems would be less serious if one analyzed, say, birds from 1980 instead of 1989, and worked forward as well as backward in developing connectivity.

Results of the Analysis

The results can be summarized graphically by plotting the number of groups created by parent-offspring linkages as a function of the number of links required to form the groups, as shown in Figure 6.3. Because of the operations I used to find linkages—essentially stopping a line of pursuit when a linkage between two individuals was found—the results have no assurance of parsimony. I also did not attempt to devise an algorithm for path analysis to find the minimum path among those graphed. Therefore, Figure 6.3 really represents the maximum number of groups: the real number of groups is the value plotted or some smaller number.

Figure 6.3 shows that as the number of links increases, the number of groups decreases to a minimum, which in this case was ten groups, reached after seven linkage units. Nearly two-thirds of the birds (68/109 = 62.4 percent) formed the largest group, with the next largest being 14 birds, and the remaining eight groups having 5 or fewer birds each (Table 6.1). At a linkage of just three units, nearly half (50/109 = 45.9 percent) of the birds formed a single group.

The results provide a satisfactory but qualified answer to the posed question: How far back in time does one need to go in order to show connectivity of birds alive at a given point in time? The oldest bird required for asymptotic linkage (which was within the largest group) was one banded as an adult when Woolfenden began the study in 1969. All of the small groups remain unlinked to the large one because pedigree analysis stops with an immigrant from outside the study tract. No small group depends for its internal linkage upon birds banded more than about a decade ago, and most have internal linkages of only a few years back.

Therefore, despite the multiple limitations encountered in the analysis, about two previous decades of reproductive connectivity is sufficient to link all

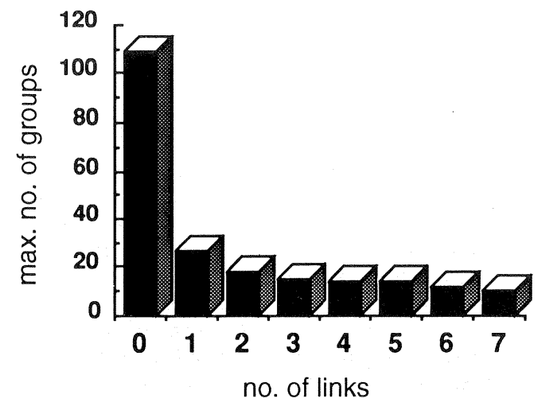

Fig. 6.3. The number of groups defined by increasing numbers of links. The function falls to a minimum of ten groups at seventh-order linkage, where genealogical data were exhausted. The largest group at seventh-order linkage contains two-thirds of the individuals (Table 6.1). As discussed in the text, the number of groups at any linkage between 1 and 6, inclusive, could be smaller than that shown because no formal algorithm was used to find the most efficient paths of linkages; hence the vertical axis is labeled as the "maximum" number of groups.

Table 6.1. Distributions of group sizes as linkage increases

Group size	Number of links							
	0	1	2	3	4	5	6	7
1	109	6	5	4	3	3	2	2
2		3						
3		7	4	4	4	4	4	4
4		4	3	2	2	2	2	2
5		3	2	2	2	2	2	1
7		2						
10			1					
11				1	1	1		
14			1	1	1	1	1	1
15		1						
16		1						
20			1					
26			1					
50				1				
51					1	1		
63							1	
68								1

individuals whose pedigree does not terminate with immigrant dispersers. Because the study tract has arbitrary geographic boundaries, there is no reason to posit any fundamental difference between birds that disperse within the study tract (known ancestry) and those that disperse into it from outside (unknown ancestry). Therefore, two decades is a reasonable general figure for the time required to connect, by pedigree network, all the Florida scrub jays alive at a given point in time and space. If this figure were misestimated by an order of magnitude, 200 years would still fall well before the last speciation event. Indeed, even 2000 years would provide sufficient assurance that Florida scrub jays can be connected reproductively without nearly approaching the timing of the last speciation event.

Conclusions

By way of concluding this essay, it is useful to point out that details of the connectivity operations could be changed and to comment on some things that an operational species definition does not accomplish. Then a summary formulation of the species definition is offered.

Connectivity Operations

Details of the operations used to measure connectivity in the Florida scrub jay example are not the only possible ones, and there is no guarantee the choice was optimal. For example, one could use different criteria for linkages. The one used required the production of independent young that lived at least approximately three months, but one could easily set a looser criterion at the production of eggs or a tighter one at offspring survival to a year of age.

The analysis made is basically that of a pedigree network, but variants and alternatives are possible. A pedigree *sensu stricto* is the ancestry of a given individual, but the connectivity method used is not based solely upon common ancestry. Parents, for example, are connected by two links through their common offspring, even when no common ancestor of the two parents was found by the analysis (e.g. Fig. 6.2). The known pedigree of each focal bird was traced, but these pedigrees were connected with one another by collateral relatives as well as common ancestors. Hence the method may be called that of a "pedigree network."

Furthermore, there might be merit in working forward in time in addition to the pedigree-network approach used. Working forward is what genealogists refer to as family-history analysis: beginning with an individual (or couple) and listing all their descendants. A "family-history network" would be conceptually parallel with the pedigree network, in which each focal individual's descendants are traced and those lineages are interrelated by links to collateral

relatives. In order to assess quickly the potential of this family-history approach, I looked at raw census data for the breeding season of 1989 (the one immediately following the January 1989 census from which the 109 study birds were taken). The 1989 breedings connect at least one of the smaller final groups of Figure 6.3 with the large group. The breedings also connect some of the 28 young immigrants excluded from analysis with existing groups, and make links among other of the immigrants. Thus, as might be expected, a single forward year improves connectivity quickly and reinforces the rationale for doing such analyses on birds that were alive about a decade ago so that links could be forged forward in time—either instead of, or in conjunction with, pedigree-network analysis.

Finally, the example of the Florida scrub jay connectivity suggests the possibility of using different criterion values for accepting the generality that the individuals investigated are all connected by breeding. Perhaps it would rarely or never happen that every focal animal could be connected to every other focal animal because of a variety of practical problems such as those encountered in the jay example. Therefore, one could develop criteria which, if met, justify the conclusion that all focal animals are of the same species—and if not met, leave that conclusion unsupported. The parallel with hypothesis testing in statistics is obvious, where there is general agreement on an arbitrary criterion of $\leq .05$ for a probability value to be considered "significant." For example, Figure 6.3 shows that a linkage of one unit makes a dramatic effect upon creating groups. In that case the first link reduces the number of groups (i.e., the number of individuals at the outset) to about a quarter of the total (27/109 = 24.8 percent to be precise). One could establish a rule of thumb by which first-order analysis had to collapse the number of unconnected groups to some criterion value, such as 25 percent or less.

Table 6.1 suggests at least two other approaches to judging the completeness of connectivity. A criterion could be established requiring that a certain percentage of the individuals analyzed fall into one interconnected group. In the case of the scrub jays, nearly two-thirds of the birds (actually 68/109 = 62.4 percent) were in a single group when the analysis reached the limits of available data at seventh-order linkage. Another approach would be to require that a certain large percentage of the individuals be connected with at least one other individual. Here, the usual statistical alpha level might be a convenient value of choice. If one asked of the jay data that 95 percent of the birds be connected with at least one other bird of the focal animals, this criterion requires that fewer than $0.05 \times 109 = 5.45$ birds be in group sizes of one. Table 6.1 shows that this criterion is met by second-order linkage.

What Connectivity Cannot Accomplish

The connectivity approach is intended to rescue the definition of the sexually reproducing species from its inherent ambiguity of stipulations such as "potentially interbreeding" and "mate recognition." In order to understand that it is intended as no more than this, consider some specific tasks that connectivity does not accomplish.

First, connectivity is not proposed as a practical tool of taxonomy. Decisions as to how many species should be recognized and how individual organisms should be assigned to each always have been and will remain fundamentally based on similar/different criteria. This situation will not be changed regardless of whether classical morphological traits are used or these are augmented by characters derived from behavioral data, nucleotide sequences, or other kinds of studies. If for no other reason, the millions and millions of species of living organisms present a task so great that no alternative to similarity/difference is conceivable. What purveyors of the species concept for sexually reproducing organisms can hope to accomplish is a taxonomic emphasis on traits that reflect breeding connectivity.

Second, the reasonableness of connectivity as an operational statement of what is really intended by vague terms such as *interbreeding* and *mate recognition* cannot be assessed in just any species. The Florida scrub jay was chosen for analysis because relevant data were available. Such a test of the connectivity approach would not be feasible in most sexually reproducing species for a whole host of reasons. Consider two other well-studied avian species. Even though the black-capped chickadee (*Parus atricapillus*), like the Florida scrub jay, is nonmigratory, banding studies suggest that the young typically disperse about 5 km in a random direction as soon as they are weaned. In our study population of color-banded birds in Madison, Wisconsin, we have located subsequently only a few individuals that were hatched in the study area. Furthermore, chickadees are not nearly as long lived as scrub jays, making linkages difficult. Migratory animals present further problems in determining linkages. Some young birds return to the vicinity of their natal territories, but others seem not to do this. The snow goose (*Chen hyperborea*) in North America pairs on the wintering grounds in areas bordering the Gulf of Mexico, and the pair tends to return to the natal colony of the female in subarctic Canada. Therefore, connectivity analysis is practical only through matrilineal links. Oceanic animals, including many coral-reef and pelagic fishes as well as various invertebrates, have planktonic young. Even if the use of genetic markers were feasible, finding offspring of specific parents would clearly be impossible.

Third, connectivity cannot solve the problem of allopatric populations. The "potentially" part of the interbreeding notion in the species definition for sexually reproducing organisms is a double-edged sword. This essay has ad-

dressed the edge concerning what the notion of interbreeding (or mate recognition) really means in a population where no animal could possibly mate with or even court all members of the opposite sex. The other aspect of "potentially interbreeding" refers to individuals that, due to their geographic separation, will never meet and hence physically could not possibly pair, much less produce offspring. Whether or not to consider allopatric forms as the same species because (in the judgment of researchers) they would/will interbreed if/when coming into contact is an old problem that has been dealt with in many ways. Perhaps the most sensible solution, in terms of practical taxonomy, is to recognize a category of allospecies—closely related and highly similar, but geographically separate, populations (see Mayr [1980] for a discussion concerning avian allospecies). It seems unlikely that connectivity or any possible alternative operational approach to defining "potentially interbreeding" or "mate recognition" could solve the problem as to whether similar but allopatric populations are of one or more species.

Last, connectivity would not seem to portend any fundamental changes to the way in which hybridization is treated. Matings between individuals considered to be of different species ordinarily fall into two general categories. There may be occasional matings anywhere within a broad sympatric area of two species, or the matings may occur principally in contact areas between two largely allopatric species. In either case the decision as to whether one or two species are really involved is made arbitrarily according to the frequency of hybridization. Connectivity networks might provide new ways of viewing the degree of hybridization and its potential effect on the gene pools involved, but is unlikely to affect the way in which hybridization rates are actually assessed in the field or the taxonomic decisions based upon such information.

The Species of Sexually Reproducing Organisms

This essay has sought to eliminate the inherent ambiguity in the definition of the sexually reproducing species embedded in such undefined notions as "interbreeding" and "mate recognition." Several operational alternatives were considered, and from them "breeding connectivity" was chosen as the most promising and most attune with the underlying views of Mayr and Paterson. Therefore, it is possible to propose that a species of sexually reproducing organisms may be considered a *naturally occurring group of individuals that are linked by a breeding connectivity network*. "Breeding connectivity network" is operational in that it implies a specific family of measurement procedures based on genealogical data. The uncovered linkages *result from* individuals of the opposite sex, or their gametes, within a network being preferentially attracted to one another (mate recognition). The linkages also *result in* networks that are discontinuous with one another (interbreeding and reproductive isolation).

Summary

Definitions of the species in sexually reproducing organisms focus on "potential interbreeding" (Mayr) or "mate recognition" (Paterson). As not every individual of one sex could possibly even attempt to mate with every individual of the other sex, no clear meaning can be attached to the "interbreeding" or "recognition" stipulation. Nevertheless, the notions underlying such terms seem to imply an important property that would be discarded by reverting to any procedure that relies solely upon similar/different criteria for defining species in sexually reproducing organisms. Several candidate approaches to operationalizing "interbreeding" and "recognition" concepts founder either in failing to capture the essence of the concepts or in being so impractical that empirical verification would be impossible. Breeding connectivity based on genealogical information provides the most promising approach, which was evaluated for the monogamous Florida scrub jay (*Aphelocoma c. coerulescens*) from data gathered by Woolfenden and Fitzpatrick over twenty years. Analysis revealed numerous practical constraints that render such data sets less than ideal, but connectivity based on pedigree did link most of the birds living on the study tract at one specific point in time (January 1989). Suggestions for improving connectivity analyses were offered, and tasks not accomplished by operationalizing the species concept were made explicit. In conclusion, one might offer for consideration the definition of a species in sexually reproducing organisms as a "naturally occurring group of individuals that are linked by a breeding connectivity network."

Acknowledgments

I am grateful above all to Hugh Paterson, who in 1979 convinced me (not without considerable effort) that many of my ideas concerning evolutionary biology were strikingly convergent on his own. I want also to mention that Ernst Mayr first interested me (as an undergraduate) in species concepts. Glen Woolfenden and John Fitzpatrick kindly provided the data on which my analysis of connectivity was based, and my wife, Liz, spent many evenings and weekends helping me create the database and do the genealogical searches underlying the analysis. For their accommodating patience through two years of my reluctant involvement in academic administration, I also thank editors Lambert and Spencer. Comments on the first draft of the manuscript were provided by T. Garland, M. Lambrechts, E. Mayr, A.G. Rodrigo, and G.E. Woolfenden; I hope to have met their helpful criticisms satisfactorily.

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7

Fitness and the Sexual Environment

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DARWINIAN FITNESS is a property of the sexually produced individual organism, such as a single human person, *Drosophila* fly, or plant. The concept expresses the capacity of that individual, relative to his or her fellow members of a local population, to make a genetic contribution to the ensuing generation. As so defined, fitness is a fundamental tenet of population genetics and evolution. This property relates to *genetic* components rather than direct effects of the environment on the soma of the individual. In most cases, fitness clearly has a polygenic basis. In gathering empirical data on the genetic basis of fitness, the population geneticist has relied mostly on measurements of survival, fertility, or fecundity, properties of an individual that are relatively easy to measure.

More important, however, and more difficult to measure, are crucial physiological attributes such as sexual behavior and sexual activity that are directly proximal to the sexual union prior to reproduction. These acquire exaggerated importance for the individual during the brief time in its life that attempts are made to engage in sexual reproduction. Although the term *fitness* has generally been used as an all-inclusive term, I choose to emphasize the strong influence of components proximate to the sex act by invoking the concept of the *sexual environment* as contrasted with the *ambient environment.* Data on the intrademic genetic variability of such attributes are needed. Here I discuss this subject in the light of some of Hugh Paterson's ideas.

Mate Recognition

In 1976, Hugh Paterson first advanced some provocative ideas on the complex syndrome of characters manifested by potential mates in animal populations. These considerations arose largely from his view that efficient sexual