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Evolutionarily Significant Units among Cichlid Fishes: The Role of Behavioral Studies

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Abstract.—Cichlid fishes represent an outstanding case of explosive evolution and offer extraordinary opportunities to investigate the evolutionary processes that have led to such diversity. Throughout the world, however, these fishes are threatened by overfishing, introduction of exotics, habitat destruction, and pollution of the environment. Determination of the specific status of local taxonomic units is critical for the development of programs both to conserve and to utilize these fishes for food, tourism, disease control, and scientific investigations. Rapid speciation within these fishes, however, has resulted in a paucity of characters for discriminating among species. Our experiences in Africa and Central America demonstrate that in situ behavioral studies, integrated with morphological and genetic analysis of taxonomic units, are vital to determining the specific status and relationships among evolutionarily significant units (ESUs). The critical element in determining whether a taxon is an ESU is knowledge of its reproductive biology; therefore, it is imperative that we develop a multidisciplinary emphasis in biodiversity studies.

The phrase evolutionarily significant unit (ESU) implies that (1) a heritable difference exists among populations; (2) an important statistical difference exists in a group of characters among units; and (3) a classification system is being used. From a pure conservation point of view, any such ESU must be protected. We are not suggesting that the term ESU replace our concept of a species or other formally recognized taxonomic category but that it be used to recognize unique entities that need protection. For example, Waples (1991) suggested that a population should be considered an ESU if it is reproductively isolated from other conspecific populations and if it represents an important component in the evolutionary trajectory of the species. Evolutionarily significant units may also be defined geographically, in that they may be a particular community or ecosystem that harbors a highly diverse fauna or flora or is a site of high endemism. Portions of a widespread population that has a disjunct distribution may be designated as an ESU. For example, the longnose sucker *Catostomus catostomus* (Forster) is panmictic; however, there exists a small disjunct population in the Monongahela River system in West Virginia, Maryland, and Pennsylvania (Stauffer et al. 1995). If this disjunct population were designated as an ESU, then perhaps a vehicle would be in place to protect this unique population of a widely dispersed species.

Minimally, an ESU may be a population that exhibits a distinctive behavior. The importance of behavior in distinguishing among fish taxa was pioneered by Trewavas (1983), who used behavioral characters when delimiting three genera of tilapiine fishes. In many cases, behavioral studies are instrumental in recognizing novel entities, assigning populations to taxa (Brooks and McLennan 1991), and estimating phylogenetic relationships among taxa (Wenzel 1992; deQueiroz and Wimberger 1993).

Nowhere is the designation and protection of ESUs needed more than in tropical ecosystems. It is estimated that as many as half of the extant species inhabit the approximately 6% of the earth covered with tropical rain forests (Myers 1988). With respect to fishes, there are 66 families endemic to tropical freshwaters, whereas only 18 are endemic to temperate freshwaters (Berra 1981); moreover, greater than 70% of the described species of fishes inhabit the tropics (Moyle and Cech 1988). One of the most speciose families of freshwater fishes is the

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Cichlidae, thus many of the examples that follow will be from this family.

Species Concepts

In part, the concept of the ESU involves grouping individuals or populations into distinct taxa, which, in turn, depends on the definition of species or some lower hierarchical taxon. Subsequent to the evolutionary synthesis (Mayr 1982a; Eldridge 1985) there has been much debate concerning species concepts (e.g., Simpson 1961; Wiley 1981; Donoghue 1985; Paterson 1985; Templeton 1989; Mayr 1992; van Devender et al. 1992). This debate can be attributed to a certain degree to some biologists treating species as epiphenomena, whereas others regard species as participants in the evolutionary process (Mayr and Ashlock 1991). We would agree with Mayr (1992) that a nondimensional (nonhistorical) concept of the species is the one with which most biologists are concerned and which is probably the most applicable to conservation and protection programs. We argue, however, that it is difficult to develop an unambiguous species definition given the mixture of conspecific populations, incipient species, and good species that predominate in allopatric populations of freshwater fishes, such as the cichlids. Hence, the ESU provides an effective concept upon which to base conservation practices when dealing with rapidly evolving groups, such as the cichlids.

Speciation

The concept of speciation involves the origin of a unique gene pool. The processes responsible for the ecological separation and reproductive isolation of populations have long been debated. Intralacustrine allopatric speciation has been widely purported to account for the rapid and extensive speciation by cichlid fishes in the African Great Lakes (Fryer 1959; Fryer and Iles 1972; Mayr 1982b). The first stage in allopatric speciation is geographical segregation of a single population into two or more subpopulations. Speciation culminates with the development of reproductive isolating mechanisms that prevent interbreeding even if the geographical barriers are removed and the populations experience secondary contact (Mayr 1942). Both pre- and postmating isolating mechanisms influence reproductive isolation among heterospecific populations. Postmating isolating mechanisms include gametic mortality, zygotic mortality, hybrid inviability, and hybrid sterility; premating isolating mechanisms include incompatible reproductive anatomy, ecological separation, ethological isolation, and allochronic mating. The development of many premating barriers are the direct consequence of changes in behavioral characters.

Several investigators have suggested that speciation of cichlids may have occurred sympatrically as well as allopatrically (Fryer and Iles 1972; McKaye et al. 1990). In sympatric speciation models, reproductive isolating mechanisms originate within the dispersal area of the offspring produced by a single deme (Hartl and Clark 1989) and premating isolation develops before populations inhabit distinct niches (Bush 1975). Controversy over the mechanisms of sympatric speciation center around the question of how reproductive isolation can arise prior to a barrier to gene flow (Mayr 1982b). Kosswig (1963) suggests that populations can be isolated ecologically without overt geographical barriers, due to differences in habitat preference in a varied environment. Factors that may contribute to ecological isolation of populations include competitive isolation (McKaye 1980), seasonal isolation (Lowe-McConnell 1959), mate selection isolation (Trewavas et al. 1972; Barlow and Munsey 1976), and runaway sexual selection (Dominey 1984; McKaye 1991; McKaye et al. 1993). In addition, intrapopulational variation in the expression of a given genotype due to environmental conditions permits the maximum use of a heterogenous habitat (Liem and Kaufman 1984; Via and Lande 1985). Within the cichlids, alternative adaptations (polymorphisms) may also have contributed to the extensive adaptive radiation and sympatric coexistence of closely related forms (West-Eberhard 1983).

Cichlid fishes throughout the tropics and specifically in the Great Lakes of Africa are generally recognized as one of the most dramatic examples of extensive trophic radiation and explosive speciation. Discrimination among species of Cichlidae can be difficult because differences among species may be very small and intraspecific variation may be relatively large (Fryer and Iles 1972; Ribbink et al. 1983). The acquisition of reproductive isolation without significant morphological change makes it difficult to distinguish African haplochromine cichlids (Lewis 1982). Attempts to use starch gel electrophoresis have been inconclusive for delimiting species (Kornfield 1974, 1978). McKaye et al. (1982) electrophoretically examined three color morphs of *Petrotilapia tridentiger* Trewavas (a cichlid endemic to Lake Malawi) that could not be distinguished morphometrically. They found no fixed alleles at any of the 25 loci studied, although allele frequencies were heterogeneous among taxa, suggesting that the color morphs represented isolated gene pools or incipient species. Marsh (1983) subsequently described these morphs as distinct species.

Mitochondrial DNA (mtDNA) has been widely recognized as an important tool for resolving relationships among closely related species. Mitochondrial DNA has also been used to delimit higher taxonomic categories. Meyer et al. (1990) used mtDNA sequence divergence to demonstrate the monophyly of the Lake Victoria cichlid species flock, and Meyer et al.'s data suggest the possible monophyly of the Lake Malaŵi flock. Monophyly of the Lake Malaŵi flock has been implied by morphological studies (Stiassny 1981) and supported by additional mtDNA analyses (Kocher et al. 1993). Moran et al. (1994) conducted studies of phylogenetic relationships among African cichlids by means of restriction fragment length polymorphism (RFLP) analysis of mtDNA. Recent work based on DNA sequencing indicates that mtDNA may be adequate for discriminating among Lake Malaŵi cichlids in some lineages (Bowers et al. 1994). Moran and Kornfield (1993) caution, however, that the rapid speciation of Malaŵian cichlids may have prevented sorting of mitochondrial lineages, allowing distantly related species of Lake Malaŵi cichlids to share mtDNA polymorphisms derived from a common ancestor. These results suggest that mtDNA data alone cannot delimit certain Lake Malaŵi taxa.

Detailed behavioral studies, however, have consistently proven useful in distinguishing among species. Many morphologically and genetically similar species can be separated based on breeding coloration and behavioral characteristics (Ribbink et al. 1983; Witte 1984; McKaye and Stauffer 1986; Stauffer 1988; Stauffer and McKaye 1988; Stauffer and Bolts 1989; Stauffer et al. 1993). Holzberg (1978) and Schröder (1980) first used behavioral observations to conclude that the blue-black color form of *Pseudotropheus zebra* (Boulenger) was reproductively isolated from the blue color morph *Pseudotropheus callainos* Stauffer and Hert (*Pseudotropheus* abbreviated as *P.* hereinafter). That many cichlid species, when artificially crossed under laboratory conditions, can produce viable hybrid offspring forces the taxonomist to rely solely on the study of premating isolating mechanisms when delimiting species. Thus, behavior plays a significant role in defining sympatric species and is essential in inferring whether or not allopatric species would potentially exhibit reproductive isolation.

Sexual Selection

Both natural and sexual selection have contributed to speciation within Cichlidae. The frequently conflicting forces of natural and sexual selection were first noticed by Darwin (1871). Natural selection arises from differential viability and fertility, whereas sexual selection results from differential mate acquisition. In effect, a particular male trait can be a handicap in terms of survival but result in more fertilizations (Trivers 1972; Nur and Hasson 1984). Sexual selection pressures can shift mean male character values far from their equilibria attained under natural selection alone (Kirkpatrick and Ryan 1991). Although sexual dimorphism can arise from other causes (Lande 1980; Hedrick and Temeles 1989), it is often a useful indicator of the magnitude of sexual selection acting on a character. Commonly observed dimorphisms in body size, plumage, coloration, or weaponry can often be ascribed to this force.

In a recent review, Kirkpatrick and Ryan (1991) classified models of female-choice selection according to whether selection on preferences was direct or indirect. They concluded that in many species preferences evolve in response to direct selection on female fitness. For example, female convict cichlids, *Cichlosoma nigrofasciatum* (Günther) consistently prefer larger males when given a choice between two mates (Noonan 1983; Keenleyside et al. 1985). This preference may be interpreted as direct selection for reproductive success because larger males provide better defense and resources for the young. Female preferences for males with larger nuptial gifts (Thornhill and Alcock 1983) or for those carrying a lower load of a communicable disease (Borgia and Collis 1990) have a direct positive effect on female fitness.

Several models can be classified as invoking indirect sexual selection on male and female preferences. In the "good genes" models, female preference is derived from the improved fitness of a female's progeny because of genes acquired from the male. One such model postulates that females prefer males carrying genes that make those males resistant to parasites (Hamilton and Zuk 1982).

Conversely, "nonadaptive" models have been postulated in which female preference is not related to the forces of natural selection acting on the population. Hert (1989) demonstrated that the egg spots of male *Astatotilapia elegans* Trewavas could stimulate spawning and that female *P. aurora* Burgess spawned more frequently with males possessing higher numbers of egg spots (Hert 1991). Fisher

(1930) was the first to propose a "runaway" process, which has since been extensively modeled (O'Donald 1980; Lande 1981; Kirkpatrick 1982) and discussed (Arnold 1983; Kirkpatrick 1987). One feature in the nonadaptive models is that the runaway process can be initiated by arbitrary female preferences, and several recent studies have shown that female preference for particular male characters can evolve long before the characters themselves. Basolo (1990, 1991) demonstrated a preexisting preference for caudal swords in swordless species of the poeciliid *Xiphophorus*. Meyer et al. (1994), however, provided genetic evidence suggesting that the ancestor of this genus possessed a sword. Preferences may frequently arise from sensory biases (Ryan and Keddy-Hector 1992) and may be an inherent property of sensory systems (Enquist and Arak 1993). Kirkpatrick and Ryan (1991) interpret this to mean that direct selection was responsible for the evolution of female preferences. Ryan and Rand (1993) have stressed the importance of recognizing that sexual selection and species recognition are elements of a single process: the matching of male signal traits to female preference function.

The existence of speciose flocks of animals restricted to isolated habitats may best be explained by sexual selection in many cases. The large number of *Drosophila* species endemic to Hawaii led Ringo (1977) to elaborate on the hypothesis of Spieth (1974) that sexual selection can accelerate the divergence of populations. Carson (1978) suggested that sexual selection could create coevolutionary races between particular male characters and female preferences, leading to the evolution of increasingly complex courtship behaviors. Possible interaction of founder effects and sexual selection during speciation was suggested by Kaneshiro (1989) as an explanation for the *Drosophila* species flock. Dominey (1984) generalized these hypotheses to account for rapid speciation in African cichlids and recognized that the cichlids share many characteristics with the Hawaiian *Drosophila*, including sexual dimorphism, lek-based breeding systems invoking a high degree of female choice, and isolated local populations.

We propose that the variations observed in male coloration, bower size (breeding platform), and courtship behavior among closely related cichlid species are the result of intraspecific sexual selection (McKaye 1991). In many instances, morphologically similar populations may in fact be subspecies, sibling species, or incipient species at various stages of speciation (Mayr 1963). Divergence in female preference for male secondary sexual traits may lead to assortative mating of populations prior to a sympatric speciation event or during secondary contact following allopatric speciation; thus, one or several sexually selected traits may become differentiated with each speciation event. Strong sexual selection may cause differentiation of breeding behaviors even in the face of considerable gene flow and among diverging populations in secondary sympatry. Natural selection may act to differentiate morphological and behavioral traits further. Therefore, it is our contention that the use of both morphological and behavioral data to delimit closely related species, such as the Lake Malaŵi cichlids, is essential. Below we discuss the use of color, bower shape, courtship behavior, and feeding behaviors to discriminate among cichlid species. We consider color form and bower shape to be manifestations of behavioral characteristics via female choice. In many cases, behavioral studies may first identify novelties that indicate which specific forms might be valid species.

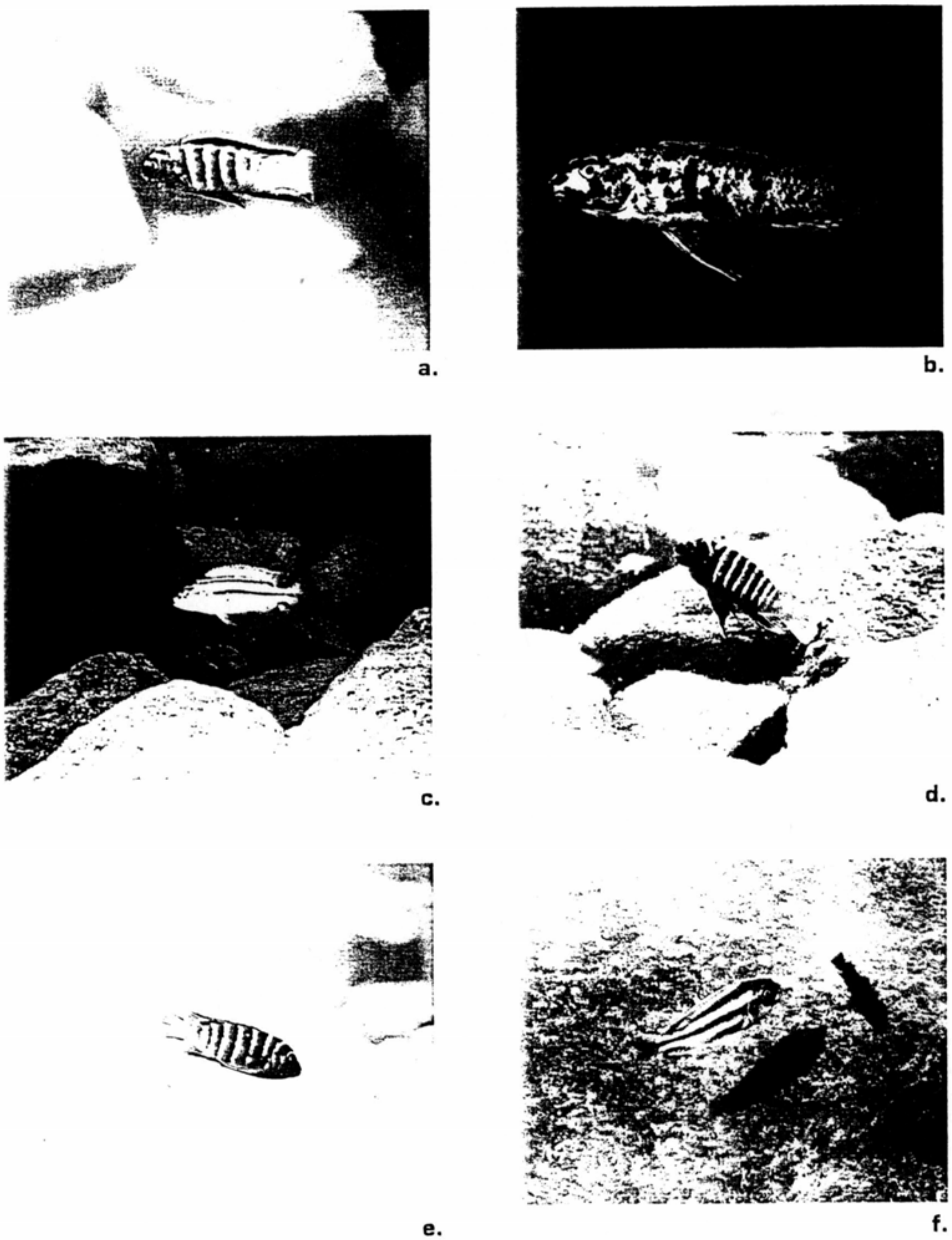
Case Histories Demonstrating the Value of Behavioral Studies

Role of Color in Delimiting Species

The incredible variety of color patterns within the haplochromine cichlids of the African Rift lakes is well known (see Figures 1a–f; Fryer and Iles 1972; Greenwood 1981; Ribbink et al. 1983; McKaye and Stauffer 1986), and we consider it to be essential in female mate selection. The existence of unique color patterns is recognized to be suitable for delimiting species (Barlow 1974; Barel et al. 1977; Greenwood 1981; Hoogerhoud and Witte 1981; McKaye et al. 1982, 1984), and in many cases new species have been recognized solely on the basis of male color pattern (McElroy et al. 1991). Although color is certainly a morphological character, we regard it as a manifestation of female preference, which is a behavioral trait.

The following rock-dwelling (mbuna) taxa were first hypothesized to be valid species based on male breeding color and later substantiated based on morphometrics and meristic data: *P. aurora* (Burgess 1976), *P. barlowi* (McKaye and Stauffer 1986), *P. flavus* (see Figure 1a), *P. ater*, *P. cyanus* (Stauffer 1988), *P. xanstomachus* (Stauffer and Boltz 1989), and *P. callainos* (Stauffer and Hert 1992), among others.

Holzberg (1978) and Schröder (1980) demonstrated that color patterns of females may also be useful in delimiting species, such as within the *P. zebra* species complex. Male *P. callainos* are pale



[illegible] Representative examples of the diverse color patterns exhibited by Lake Malaŵi cichlids: (a) *Pseudotro-* [illegible] from Chinyankwazi Island; (b) orange blotch (OB) morph of *Labeotropheus trewavasae* from Thumbi West [illegible] *Melanochromis* [illegible] from Chinyankwazi Island; (d) blue-black (BB) color form of *P. zebra* from [illegible] West Island; (e) [illegible] from Thumbi West Island; and (f) *Chilotilapia* c.f. *rhodesii* from Kanjedza

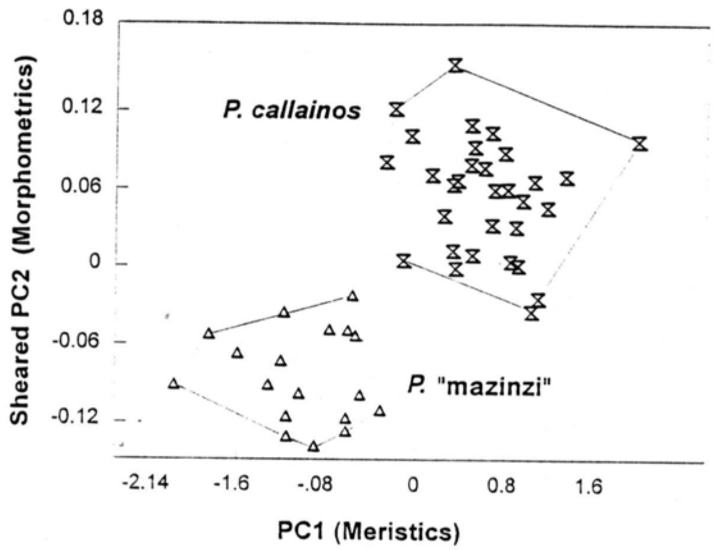


FIGURE 2.—A plot of the second principal component (PC2: morphometrics) and the first principal component (PC1: meristics) based on data from *P. callainos* and *P.* c.f. *zebra* "mazinzi."

blue (Stauffer and Hert 1992) and closely resemble an undescribed *P.* c.f. *zebra* from Mazinzi Reef, Lake Malaŵi. Many female *P. callainos* are white, whereas white females of *P.* c.f. *zebra* from Mazinzi Reef have never been collected. This observed difference in female color pattern prompted us to complete a more detailed morphological study of these two forms. Based on sheared principal component analysis of morphometric data and principal component analysis of meristic data (see Stauffer 1993 for an explanation of the methods employed), the two taxa were shown to be heterospecific (Figure 2).

The importance of color pattern is not limited to the haplochromine fishes in the Great Lakes of Africa. Our work over the past 3 years throughout the Great Lakes basin in Nicaragua has impressed upon us, as it has earlier workers (Meek 1907; Barlow and Munsey 1976), the great variation among cichlids in coloration and body form in isolated water bodies (see Figures 3a–c). For example, in the midas cichlid *Cichlasoma citrinellum* group, several species have been described. With respect to this commercially important group of cichlids, Meek (1907:122) stated, "Of all the species of fishes in these lakes, this one is by far the most variable. I made many repeated efforts to divide this material . . . in from two to a half-dozen or more species, but in all cases I was unable to find any tangible constant characters to define them. To regard them as more than one species meant only to limit the number of material at hand, and so I have lumped them all in one." Three species of this group are presently recognized by Barlow and Munsey (1976), although Villa (1982) only recognized two. Our behavioral work, however, confirms that the three species recognized by Barlow and Munsey (1976) are, in fact, valid. Furthermore, our direct underwater observations that these forms assortatively mate by color and that their habitat preferences and nest forms differ suggest that at least three additional undescribed species are also present. Preliminary morphological analyses of two of these forms (Figure 4) confirm that they are distinct from the type specimens housed in the Natural History Museum (London).

Similarity in color patterns, however, may be misleading. For example, many authors (e.g., Fryer and Iles 1972; Ribbink et al. 1983) regard the two populations of the Lake Malaŵi blue-black (BB; Figure 1d) color form of *P. zebra* at Nkhata Bay and Thumbi West Island to be conspecific. McKaye et al. (1984) found differences in allele frequencies between northern and southern populations of BB *P.* c.f. *zebra* although there were no fixed allelic differences. Examination of the morphological data (Figure 5) suggests that these two populations are actually heterospecific. Another example includes

FIGURE 3.—Representatives of the species complex of the midas cichlid *Cichlasoma citrinellum* Günther. (a) *Cichlasoma* c.f. *citrinellum* "Xiloa" from Laguna de Xiloa, Nicaragua; (b) *Cichlasoma* c.f. *citrinellum* "amarillo" from Laguna de Xiloa, Nicaragua; and (c) *Cichlasoma* c.f. *citrinellum* "chancho" from Laguna de Apoyo, Nicaragua.

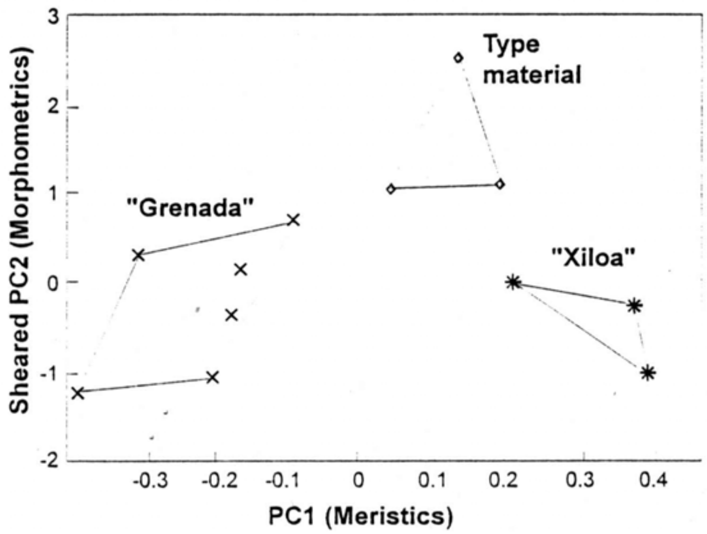


FIGURE 4.—A plot of the sheared second principal component (PC2; morphometrics) and the first principal component (PC1; meristics) based on data from three members of the *Cichlasoma citrinellum* species group: *Cichlasoma citrinellum* type material from the British Museum (Natural History), *Cichlasoma* c.f. *citrinellum* "grenada" from Lake Nicaragua, and *Cichlasoma* c.f. *citrinellum* "Xiloa" from Laguna de Xiloa.

the orange blotch (OB) morphs of many Lake Malaŵi cichlids (e.g. *P. zebra*, *Labeotropheus trewavasae* Fryer [see Figure 1b], and *P. tropheops* Regan). Color differences would initially suggest that these forms are heterospecific with the similarly shaped, normally colored individuals; however, closer examination shows that all OB morphs are female, suggesting that these color forms are not valid species.

Color differences in allopatric populations may also be misleading. For example, two populations of a *Melanochromis* species occur at Chinyamwezi and Chinyankwazi Islands in Lake Malaŵi. Because male coloration differed between the two populations, Ribbink et al. (1983) regarded these taxa to be heterospecific. Examination of the morphometrics and meristics of 13 populations of this form from other locations within Lake Malaŵi revealed slight clinal variation in shape pattern (Bowers and Stauffer 1993), suggesting that these populations are conspecific. This conclusion was supported by allozyme analysis, which showed very low variation at 3 polymorphic loci out of 24 loci that were assayed. Because the morphological evidence indicated no differences in shape among the populations, and variation in male coloration tended to be greater within than among populations, Bowers and Stauffer (1993) described this form as a single species, *Melanochromis heterochromis* Bowers and Stauffer (Figure 1c).

Color pattern may also provide insight into the phylogeny of certain groups, although care should be taken when interpreting the results. For example, the prevalence of the BB color morph in most of the rock-dwelling cichlid genera (see Figure 1d–e) and some sand-dwelling forms (Figure 1f) throughout Lake Malaŵi suggests that this color pattern is primitive, whether one uses the commonality principle or outgroup comparisons (Smith and Koehn 1971; Watrous and Wheeler 1981). Conversely, the presence of the red dorsal fin within *P.* c.f. *zebra* "red dorsal," *P.* c.f. *zebra* "cobalt mbenji," and *Labeotropheus trewavasae* implies that this character state is a product of convergent or parallel evolution.

In their recent monograph of non-mbuna haplochromines endemic to Lake Malaŵi, Eccles and Trewavas (1989) suggested that similarity of color patterns among species may reflect phyletic relationships. For example, the "polystigma" pattern, which consists of three longitudinally arranged features of either stripes or a series of spots or blotches, is restricted to the genus *Nimbochromis* (Figure 6d). Conversely, the following melanin pat-

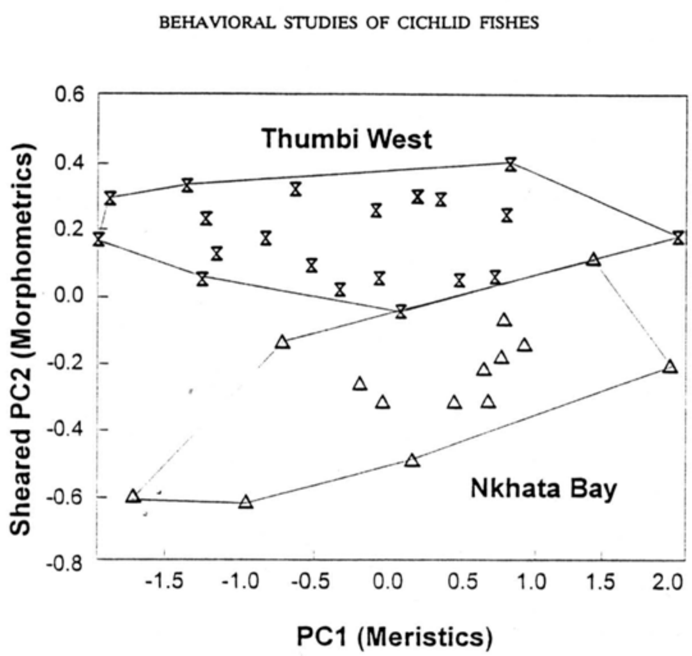


FIGURE 5.—A plot of the sheared second principal component (PC2: morphometrics) and the first principal component (PC1; meristics) based on data from two populations of the blue-black color form of zebra mbuna *P. zebra* from Nkhata Bay (northern population) and Thumbi West Island (southern population), Lake Malaŵi, Malaŵi.

terns are found in more than one genus: "kirkii" pattern (Figure 6a), which emphasizes the horizontal elements of the very common and hence perhaps pleisiomorphic color pattern, is represented by *Nyassachromis breviceps* (Regan), *Lethrinops lethrinus* Günther, and *Protomelas kirkii* (Günther); transverse bars (Figure 6b), is represented by *Placidochromis johnstoni* (Günther), *Lethrinops gossei* Burgess and Axelrod, and *Alticorpus peterdaviesi* (Burgess and Axelrod); "dimidiatus" pattern (Figure 6c), which is a simple, straight, midlateral band, is represented by *Dimidiachromis dimidiatus* (Günther) and *Taeniochromis holotaenia* (Regan); oblique band (Figure 6e), which consists of an oblique band or series of spots from nape to middle of the caudal base, is represented by *Docimodus evelynae* Eccles and Lewis, *Mylochromis anaphyrmus* (Burgess and Axelrod), and *Taeniolethrinops praeorbitalis* (Regan); three-spot patterns (Figure 6f), which consists of a series of spots that appear along the position of the midlateral component of the horizontal element of the plesiomorphic pattern, is represented by *Otopharynx ovatus* (Trewavas) and *Copadichromis quadrimaculatus* (Regan), which have the spots below the upper lateral line, and *Cyrtocara moori* Boulenger and *Ctenopharynx pictus* (Trewavas), which have the spots above or on the upper lateral line; and "rostratus" pattern (Figure 6g), which consists of three series of large spots approximately in the position of the stripes or rows that constitute the kirkii pattern, is represented by *Fossochromis rostratus* (Regan) and *Eclectochromis festivus* (Trewavas). Consequently, Eccles and Trewavas (1989) considered the rostratus color pattern a result of parallelism and thus uninformative.

Role of Bower Shape in Delimiting Species

Research on the breeding behavior of several Lake Malaŵi sand-dwelling fishes has demonstrated that the process by which females choose mates is complex. McKaye et al. (1990) found a preference for males with larger bowers in female *Copadichromis conophorus* Stauffer, LoVullo, and McKaye. Males of this species form huge leks that may have more than 50,000 males at the height of the breeding season (McKaye 1983, 1984). In comparisons between paired bowers, males on larger bowers received a two- to threefold increase in female attention (bower entry and circling behavior) over males on smaller bowers. In a smaller lek occupied by 20 to 50 *Otopharynx argyrosoma* (Regan) males, the males occupying bowers closest to the center of

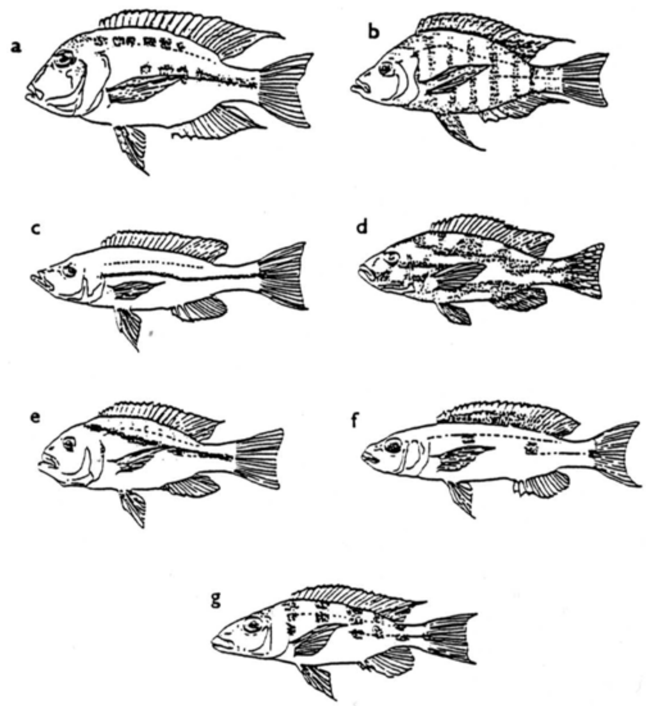


FIGURE 6.—Examples of the color patterns recognized by Eccles and Trewavas (1989) as being phylogenetically informative for Lake Malaŵi cichlids: (**a**) kirkii pattern, (**b**) transverse bars, (**c**) dimidiatus pattern, (**d**) polystigma pattern, (**e**) oblique band, (**f**) three-spot pattern, and (**g**) rostratus pattern.

the lek received approximately three times as many matings as did the males around the periphery (McKaye 1991). In order to separate the effect of bower size and bower location, we substituted artificial bowers in the lek of *Lethrinops* c.f. *parvidens* (Trewavas). Several tagged males located on the periphery of the lek had not been observed to fertilize any eggs during a 3-week period during which approximately 1,800 eggs were laid in other areas of the lek. The same tagged males were observed fertilizing between 15 and 30 eggs per day when large (approximately 22 cm in height) bowers were placed on top of the tagged males existing ones. In another arena, female *Lethrinops auritus* (Regan) preferred to mate with males whose bowers contained more peripheral bumps. In general, these data suggest that within several species, a specific character, bower size, can influence the mate preference of females and that males will evolve behaviors that increase the size, shape, or position of their bower in order to attract more females.

In Lake Malaŵi, 10 major bower forms, which vary in size from small depressions in the sand to elaborate castles, have been identified (McKaye 1991). Within each class of bower shape, significant quantitative variation in bower dimensions occurs. Among bowers within a lek, height varies depending on the age of the bower and the activities of the male. Some dimensions of the bower remain constant, despite variation in height, strongly suggesting a genetic basis to bower form. The diameter of the breeding platform of the bowers of *Copadichromis conophorus* appears to be species specific (Stauffer et al. 1993). We demonstrated that three closely related species in the *Copadichromis eucinostomus* group had differently shaped bowers, and we used these data to aid in the differentiation of these species. Similarly, McKaye et al. (1993) studied five leks of *Tramitichromis* near Nankumba Peninsula in Lake Malaŵi and demonstrated significant differences in bower shape among these leks. These data are discussed in more detail in the section

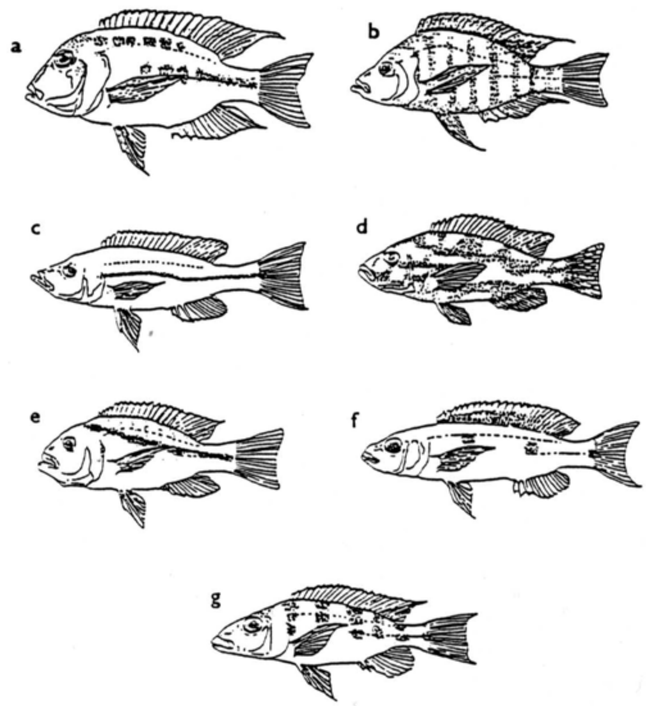


FIGURE 6.—Examples of the color patterns recognized by Eccles and Trewavas (1989) as being phylogenetically informative for Lake Malaŵi cichlids: (**a**) kirkii pattern, (**b**) transverse bars, (**c**) dimidiatus pattern, (**d**) polystigma pattern, (**e**) oblique band, (**f**) three-spot pattern, and (**g**) rostratus pattern.

the lek received approximately three times as many matings as did the males around the periphery (McKaye 1991). In order to separate the effect of bower size and bower location, we substituted artificial bowers in the lek of *Lethrinops* c.f. *parvidens* (Trewavas). Several tagged males located on the periphery of the lek had not been observed to fertilize any eggs during a 3-week period during which approximately 1,800 eggs were laid in other areas of the lek. The same tagged males were observed fertilizing between 15 and 30 eggs per day when large (approximately 22 cm in height) bowers were placed on top of the tagged males existing ones. In another arena, female *Lethrinops auritus* (Regan) preferred to mate with males whose bowers contained more peripheral bumps. In general, these data suggest that within several species, a specific character, bower size, can influence the mate preference of females and that males will evolve behaviors that increase the size, shape, or position of their bower in order to attract more females.

In Lake Malaŵi, 10 major bower forms, which vary in size from small depressions in the sand to elaborate castles, have been identified (McKaye 1991). Within each class of bower shape, significant quantitative variation in bower dimensions occurs. Among bowers within a lek, height varies depending on the age of the bower and the activities of the male. Some dimensions of the bower remain constant, despite variation in height, strongly suggesting a genetic basis to bower form. The diameter of the breeding platform of the bowers of *Copadichromis conophorus* appears to be species specific (Stauffer et al. 1993). We demonstrated that three closely related species in the *Copadichromis eucinostomus* group had differently shaped bowers, and we used these data to aid in the differentiation of these species. Similarly, McKaye et al. (1993) studied five leks of *Tramitichromis* near Nankumba Peninsula in Lake Malaŵi and demonstrated significant differences in bower shape among these leks. These data are discussed in more detail in the section

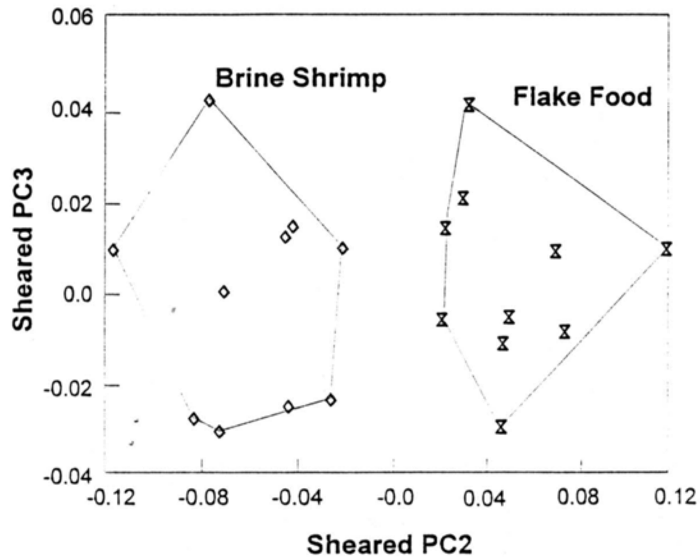


FIGURE 7.—A plot of the second and third sheared principal components based on eight head measures collected from a split brood of *P.* c.f. *zebra* "red-top" fed two different diets.

the effects of diet on the phenotype of two New World cichlids: a mouthbrooder, the redhump eartheater *Geophagus steindachneri* (Eigenmann and Hildebrand), and a substrate spawner, the pearl eartheater *Geophagus braziliensis* (Quoy and Gaimand). The experimental design was similar to that of Meyer's (1987) and both species exhibited the expected trend. Based on this study it would appear that mouthbrooding may not greatly alter the phenotypic plasticity induced by diet in substrate-spawning cichlids.

Similar studies have not been conducted on Old World cichlids, but there have been some important observations. Witte (1984) reported that wild-caught (Lake Victoria) and domesticated *Haplochromis squamipinnis* Trewavas had differently shaped premaxillaries. The difference was attributed to the fact that those individuals kept in aquaria dug in the sand with their mouths, thus increasing the power of their bite over that of the wild-caught ones, which did not exhibit this digging behavior. In addition, Witte (1984) noted that the change in premaxillary shape was not limited to young fish, indicating that it was not strictly controlled by some ontogenetic factor. A second important observation was reported by Greenwood (1965) for *Astatoreochromis alluadi* Pellegrin. Individuals feeding on thick-shell snails had stronger pharyngeal bones and larger molariform teeth than did those individuals that ate snails with thinner shells. In preliminary experiments conducted in our laboratory, we used F_1 siblings derived from wild-caught *P.* c.f. *zebra* "red top" and randomly divided them into two dietary treatments: (1) brine shrimp nauplii and *Daphnia magna* and (2) commercial flake food and tubifex worms. After 18 weeks the fish were sacrificed and morphometric measurements were recorded. A sheared principal components analysis, in which cheek depth, head depth, and snout length accounted for most of the variability, resulted in complete separation of the two groups (Figure 7).

Clearly, approaches integrating morphological, genetic, ecological, and ethological data are required for species-level description of these fishes. In a study of five putative populations of *Tramitichromis* species in the vicinity of Nankumba Peninsula in Lake Malaŵi, McKaye et al. (1993) examined protein electromorphs of 24 enzyme loci and compared these data with bower shape of each of the five populations. No fixed differences were found for any of the alleles. Frequency differences indicated that the two populations found at Cape Maclear were distinct from the populations from Kanjedza Island, Mpandi Island, and Nkudzi Point. The population inhabiting Nkudzi Bay, which is located between Kanjedza Island and Mpandi Island was intermediate between these islands and the populations at Cape Maclear. Shape analysis of bower forms produced two major groupings, which showed that the bowers from populations located at Cape Maclear were distinct from those found at the other three localities. A critical examination of the lower pharyngeal bone and the gill rakers located on the ceratobranchial showed that populations from Nkudzi Bay, Mpandi Island, and Kanjedza Island were *Lethrinops* c.f. *parvidens*, whereas those located at Cape Maclear were *Tramitichromis* c.f. *lituris*. Hence, the results suggested by the morphological, genetic, and behavioral data were congruent.

Another example of congruence among genetic, morphological, and behavioral data is found in the three species *Copadichromis conophoros*, *C. cyclicos*, and *C. thinos*, which were recently described by Stauffer et al. (1993). For over a decade, extensive research on the ecology and behavior of these sand-dwelling fishes indicated that at least three populations, which fit the original description of *Copadichromis eucinostomus*, constructed bowers with three different population-specific shapes. The clusters formed by plotting the principal component analysis scores (see Humphries et al. 1981 and Bookstein et al. 1985 for a discussion of shape analysis) of the morphometric and meristic data for *Copadichromis conophorus* and *C. cyclicos* did not overlap. *Copadichromis thinos*, although intermediate, was significantly different ($P < 0.05$) from the other two species. Shape analysis also confirmed that bower shapes for the three species were significantly different ($P < 0.05$), although data from the bowers of *Copadichromis conophorus* were intermediate. Subsequent to the description of these taxa, mtDNA haplotype frequencies in *Copadichromis conophorus*, *C. cyclicos*, *C. thinos*, and an undescribed species of *Copadichromis* from Thumbi West Island were examined (Table 1). Haplotype frequencies were significantly different ($P < 0.05$) among populations. Males on the small lek at Thumbi East Island are nearly fixed for a single mtDNA haplotype. These data confirm the genetic uniqueness of *Copadichromis conophorus*, *C. thinos*, and *C. cyclicos*, which had been inferred from morphological evidence.

Conclusions

In sympatric situations behavior can provide direct evidence for reproductive isolation or cohesion. In both allopatric and sympatric circumstances, detectable behavioral differences may have initiated the speciation process through assortative mating, which may, in turn, lead to runaway sexual selection. Thus, behavioral data are extremely valuable and, at least with some groups such as cichlids, are essential and can (1) initially identify distinct taxa or identify novelties which prompt further investigation; (2) confirm or support genetic and morphological data needed to delimit taxa; and (3) provide needed information to speculate on phylogenies.

It is our contention that if ESUs are recognized at the population level, the population designated should possess some heritable atypical trait, such as an unusual behavior pattern. Perhaps an ESU can be designated on a temporary basis because of an unresolved taxonomic status. We are not proposing that the ESU replace existing taxonomic categories but that these units be given standard nomenclatural status when possible, so that they are formally recognized by the scientific community. Such distinction provides the necessary framework to initiate and foster debate on the significance and reality of such discrimination. We realize that species definitions and concepts are difficult and sometimes burdensome, but we urge investigators not to regard these varied concepts as mutually exclusive. We also conclude that behavioral data are essential to delimit species.

We further propose that the ESU be defined in geographical terms, so that areas of high diversity or endemism can be designated as ESUs. Such a unit may consist of crater lakes in Nicaragua or particular islands or shorelines in Lake Malaŵi. For example, in the southeast arm of Lake Malaŵi more than one-third and one-half of the species native to the Maleri Islands and to Chinyankwazi and Chinyamwezi Islands, respectively, are endemic (Figure 8). Such a geographical approach to conservation must permit the continued use of the lake by Malaŵians, who derive about 70% of the animal protein consumed from fish, and must also preserve those areas that harbor high concentrations of ge-

TABLE 1.—Distribution of mitochondrial DNA haplotypes among four populations of *Copadichromis* once suspected to be conspecific. All populations are from southern Lake Malaŵi.

Population	Mitochondrial DNA haplotypes								
	A	B	C	D	E	F	G	H	I
Thumbi West Island	16	3	0	0	0	0	0	0	0
Cape Maclear	1	11	0	4	2	1	0	0	0
Kanchedza Island	0	0	14	1	0	0	2	0	0
Mazinzi Reef	2	3	0	2	1	0	0	1	3

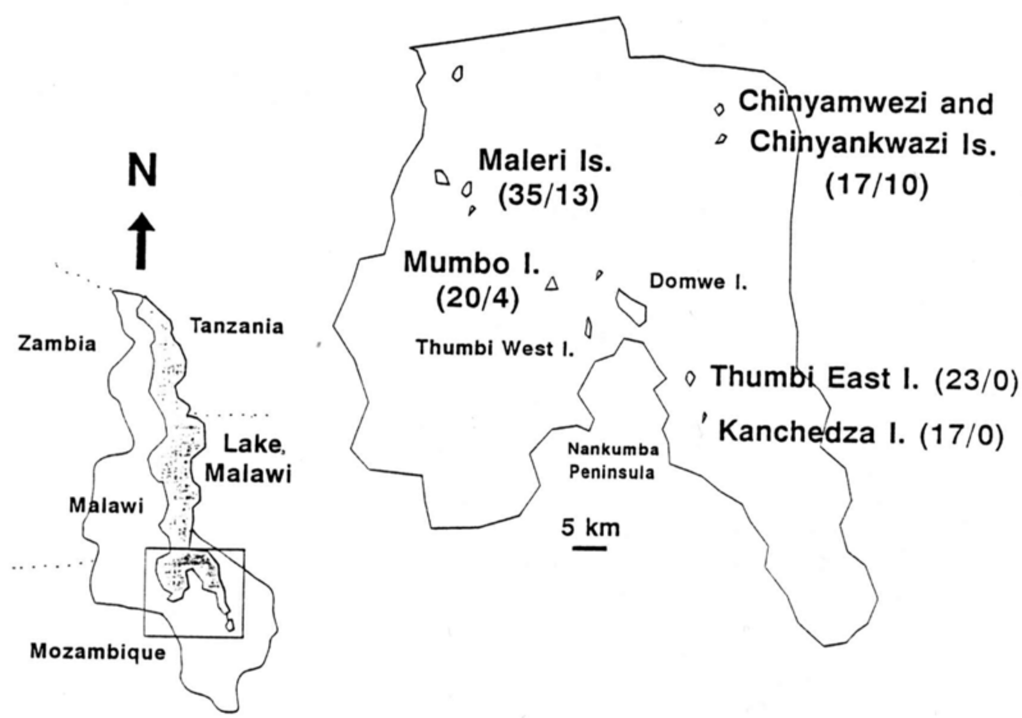


FIGURE 8.—A map of the southern region of Lake Malawi showing the total number of species of mbuna at a given location and the number of those species that are endemic to the location.

netic diversity. As stated by Orville Freeman (former U.S. Secretary of Agriculture), "We make a potentially dangerous mistake when we assume that we must choose between serving humanity or serving the environment. It must be a priority to bring these goals into harmony. They need not and they must not be mutually exclusive."

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