Is Mating Different in Monogamous Species?
The Midas Cichlid Fish as a Case Study[1]

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SYNOPSIS. Monogamous species are typically sexually isomorphic, pair well before spawning is imminent, take much time to pair, are discerning about pairing, and appear to weigh multiple sources of information about species, sex, and quality of mate. The monogamous and polychromatic Midas cichlid (*Cichlasoma citrinellum*) distinguished between its own and a highly similar heterospecific behind a one-way mirror only when visual and chemical cues matched. Likewise, recognition of sex was hindered when interaction was precluded, even in the presence of chemical cues. Female choice of mate was most strongly influenced by the "normal," primitive, color and to a lesser degree by color of parents and siblings, making it difficult to account for positive color-assortative mating in the field. Females also selected the largest and the most aggressive males; size predicted a good defender of territory, and aggressiveness foretold effective protection of the young. Males, however, were not choosy. Pair formation features much aggression between the large male and smaller female, and gold-colored morphs (G) dominate normal (N) ones. That made it difficult for an N female to pair with a G male; using an N female the same size as the G male, however, resulted in the usual proportion of successful pairings. I propose three testable models of pair compatibility: complementarity, parity, and maximum male aggressiveness.

INTRODUCTION

The resurgence of interest in sexual selection during the last two decades moved theory to questions of mate choice (*e.g.,* Bateson, 1983; Bradbury and Andersson, 1987). That theory has been derived mainly from the concept of anisogamy and its corollary, the conflict between the sexes (Trivers, 1972; Williams, 1975). Even among monogamous birds the spotlight remains on asymmetries between mates and the degree of departure from monogamy (*e.g.,* Gowaty, 1985; Westneat *et al.,* 1990). Further, theory has emphasized outcomes as opposed to processes, resulting in an incomplete understanding of mating behavior.

The process of mating is a hierarchical series of decisions. Individuals are first sorted into types, progressing through species, population and sex. Having winnowed out potential mates, which among them is ready to mate? Then, which is the best with regard to genetics or willingness to invest in parental care, as judged by behavior and appearance? If a resource is essential, such as a breeding site, which available potential mate holds the resource of the highest value?

The monogamous Midas cichlid (*Cichlasoma citrinellum*), of Nicaragua, illustrates the complexities of mating as a series of decisions. This species is unusually fidelis. We have not succeeded in tempting them into polygyny (Rogers, 1987), although single mothers have been seen in the field (Barlow, 1976).

Monogamous species are typically isomorphic (Darwin, 1871), as is the Midas cichlid: males and females are indistinguishable. The male of a pair, however, is always bigger than the female, even though larger and smaller fish of both sexes are available (Barlow, 1976; McKaye, 1986). Each sex, moreover, performs the same displays; they differ only in the temporal dynamics of displaying when interacting (Baylis, 1976*a, b*).

Mating in monogamous species differs in a number of respects from mating in polygynous species. The most obvious divergence is the duration of the interaction (Baylis, 1976*b*). Polygynous species come together briefly, on the order of seconds to minutes (Barlow, 1962; McKaye, 1983; Rowland, 1988). Pairs of monogamous cichlids, in contrast, remain together some weeks (Barlow, 1991).

91

Multichannel "dimorphism" in polygynous species facilitates quick recognition of species and sex. In isomorphic monogamous species, more time is needed just to distinguish species and sex, so monogamous species probably attend to more subtle differences (Burley, 1981; Dewsbury, 1988).

The degree of sexual readiness, when the male and female first encounter one another, may also differ in monogamous species compared with polygynous species. In territorial polygynous species, the male typically holds a breeding site where the receptive female approaches him when spawning is imminent. In biparentally monogamous fishes, spawning is well separated in time from pair formation, so the proceptive female is not ready to spawn when the pair forms. Spawning readiness of the female should therefore not be an essential feature of male receptivity or choice of mate, though it could influence choice.

Anisogamy predicts that females will be choosy, males not (Searcy, 1982; Trivers, 1972). But in monogamous species, males and females ought to be equally choosy when male care is indispensable for the survival of the offspring. The pair completes a reproductive cycle together; thus the fitness of the male and female is identical.

RECOGNITION OF SPECIES AND SEX IN THE MIDAS CICHLID

Sympatric species of cichlids in Central America are usually easily told apart by their color patterns, suggesting that such patterns are important in species recognition. However, three species in Nicaragua, *C. citrinellum, C. labiatum* and *C. zaliosum,* are colored alike and are hard to distinguish (Barlow and Munsey, 1976). But can the species tell one another apart, and if so, how? They do not hybridize in captivity when given a choice between hetero- and conspecific mates (Baylis, 1976a). However, given no choice, fertile hybrids resulted.

How cichlids recognize species is almost unknown. Midas cichlids failed to distinguish between their own species and *C. labiatum* when viewing them through one-way mirrors (Holder, 1991). When chemical cues were provided, the Midas cichlids responded differentially to their own species. That indicated that species recognition is based on a simple sensory mechanism involving olfaction. If so, they should have responded to the "wrong" species as their own when visual and odor cues were mismatched.

Mismatching, however, resulted in no choice (Holder, 1991) suggesting the possibility of a "keying out" of species, first chemical then visual. Alternatively, the fish may have been responding to remarkably subtle cues and were confused by the conflict between modalities. Species recognition is obviously complex and may require information of different types (Holder, 1991). This is consistent with Baylis' (1976a) finding that freely-interacting heterospecific pairs sometimes started but did not persist.

The ability to recognize sex was greatly diminished when the choice was through a one-way mirror, which precluded interactive feedback (Holder, 1991). We suspect the female needs to engage the other fish to establish how it reacts in the context of aggression and courtship. In the experiment, female subjects performed more courtship displays to males then to females only when the male exhibited more aggression than did the female. Adding chemical cues did not improve discrimination.

From his studies of courtship in the Midas cichlid and the arrow cichlid, Baylis (1976b) suggested that both species and sex are distinguished through the interactive dynamics of courtship (see also Clarke et al., 1984), especially during pair formation. This remains the most viable hypothesis; Baylis, however, did not try to falsify it (nor did Clarke et al., 1984).

Cichlids obviously recognize the sex of other conspecific fish. Nonetheless, mating proceeded to spawning in isosexual pairs of female orange chromides, *Etroplus maculatus* (Barlow, 1970) and Midas cichlids (Barlow, unpublished). Thus the mechanism underlying sex recognition can be overridden when the need is great. Male orange chromides and Midas cichlids in isosexual groups, however, never formed pairs; a few male orange chromides courted one another, but then lapsed into fighting.

POLYMORPHISM AND THE QUESTION OF SPECIATION

Two of the three species, the Midas cichlid and the *C. labiatum,* are polychromatic. Instead of the typical pattern of grayish green with black bars or spots, called the normal morph (hereafter N), the oligomelanic morphs lack melanin in their skin; that reveals the underlying colorful xanthophores (Dickman *et al.,* 1988). The oligomelanic morphs used in experiments were various shades of orange and are called gold (hereafter G).

Midas cichlids mate assortatively by color in nature, though some mixed-color pairs are seen (McKaye and Barlow, 1976). Because of this, McKaye (1980) and Meyer (1989, 1990a) suggested the Midas cichlid might be undergoing incipient sympatric speciation. A possible complication in this scenario is that Midas cichlids commonly kidnap or adopt abandoned young from other pairs in nature (McKaye and McKaye, 1977). If sexual imprinting were to occur, the adopted offspring of one morph could imprint on the color of the other morph and thereby maintain gene flow between the morphs.

MATE CHOICE BY COLOR

Assortative mating, resulting from active choice of mate by color, is a crucial issue in speciation among cichlid fishes in general (Dominey, 1984), but this subject has been little researched. One of the first questions I asked was whether one color of mate is preferred over another. Because of the protracted parental care in the Midas cichlid, the question was framed in the context of sexual imprinting.

Sexual imprinting was first claimed for a cichlid by Seitz (1940). Kop and Heuts (1973) found in another cichlid only a brief tendency to affiliate with the heterospecific cichlid with whom the subjects had been reared. In other experiments, dominance effects obscured mate choice (Crapon de Caprona, 1982; Fernö and Sjölander, 1976; Siepen and Crapon de Caprona, 1986; Sjölander and Fernö, 1973). Weber and Weber (1976) documented the confounding effect of dominance in mate-choice experiments

on convict cichlids, *Cichlasoma nigrofasciatum,* and Driscoll and Welanko (1981) did the same for another Neotropical cichlid, *Herotilapia multispinosa.*

We (Barlow and Rogers, 1978) tested whether female Midas cichlids spawn next to N or G males in relation to early experience with parents, siblings and self. To rule out dominance effects, the four males, called treatment fish, were confined to large-mesh cages. N females, whose parents were an N male and an N female, spawned overwhelmingly before N males. G females from G parents selected G males to the same degree.

These results seemed to rule out one best color for males; they also excluded early imprinting on sibs because all the fry and juveniles had been N. (All Midas cichlids start life as N. If the parents were G, individuals of a cohort change from N to G at various ages.) However, the results did not distinguish between choice based on own as opposed to parents' color. Thus we still had no evidence for imprinting in a cichlid fish.

The G females used in the preceding experiment had N siblings. If the N sisters of the G females chose G males, that would argue for imprinting on parents because the parents had been G. But if the N sisters chose N males, that would be evidence for the effect of own color. Despite an unusually large number of subjects tested, the results refuted neither hypothesis. The N females chose equally among N and G males. The experiments also ruled out effects of recent association (Barlow and Rogers, 1978). The only obvious conclusion is that N females differed depending on whether they had G or N parents, and both G and N, or just N, siblings. The different results, however, might have been due to the male treatment fish responding differently to the females, depending on the males' color and prior experiences.

We needed to rule out differential responsiveness of the treatment animals, here the males. To eliminate choice by the males, they were presented behind one-way mirrors, preventing them from seeing and responding to the female. Further, the design allowed us to test for effects of color of par-

ents, companions and self (Barlow et al., 1990).

The clearest effect was a significant bias toward N males, irrespective of previous experience. The influence of color of parents was also significant, but it was neither robust nor consistent across groups. Sib color was significant, too, but also inconsistent. Color of self played no role. (Pilot experiments on male mate choice failed to detect any influence of early experience.) Thus the effect of early experience on mate choice among adult females is real but weak. It is outweighed by more evocative individual differences among the treatment fish (see next section).

The findings, nevertheless, are important for four reasons. First, without these experiments on the influence of early experience, further studies on mating would be open to the criticism that the potentially potent effects of early experience had not been assessed (note, too, that sexual imprinting is invoked in one theory of sympatric speciation among African cichlids [Sage et al., 1984]). Second, the absence of sexual imprinting among adopted or kidnapped young Midas cichlids weakens one argument against possible incipient speciation in that species. Third, assortative mating in the field cannot be based on active choice of color alone. Fourth, finally confirming the absence of bird-like sexual imprinting in a monogamous cichlid makes its occurrence among birds a less general phenomenon.

INDIVIDUAL ASSESSMENT—
PREDICTING GOOD FATHERS

We asked three questions about mate assessment in the Midas cichlid, using only N morphs. (1) On what basis do they choose? (2) Do females and males select similarly, as theory predicts (Trivers, 1972)? (3) Do the chosen attributes predict a good parent?

To analyze choice, size and aggressiveness were tested through one-way mirrors; only one variable was altered in each experiment (Rogers and Barlow, 1991). Females were selective, responding most to large, aggressive treatment males. Contrary to predictions, and to our surprise, males did not discriminate on the basis of either trait.

The direct benefit of female choice was

confirmed (Rogers, 1987). Large males proved better defenders of territories. In a separate experiment, aggressive males, irrespective of size, were better at protecting offspring from predators.

Thus assessment by females of individual differences among potential male mates was based on two traits. One, body size, might be accounted for by a simple sensory mechanism. The other trait, aggressiveness, must be processed at higher neural levels.

POLYCHROMATISM AND AGGRESSION

Aggression is central to the biology of the Midas cichlid. Nonbreeding fish in Nicaraguan lakes are not territorial but they do fight over patches of food and over small caves used as refuges (Barlow, 1976). During the five to six-week breeding cycle, territory-holding pairs constantly engage in aggressive behavior toward neighbor pairs and potential usurpers (McKaye and Barlow, 1976). Even if the residents prevail, the young may be lost to predators who the parents ignore while fighting (McKaye and McKaye, 1977). One spawning cave was successively taken over by six different pairs within three months (a breeding cycle requires about 1.5 months [Barlow, 1976]). Only 3% of the holders of breeding territories in Lake Jiloá in 1973 were able to complete a reproductive cycle because of predation on the young and, in some cases, eviction (McKaye and McKaye, 1977; McKaye, 1984).

Competition for breeding sites is thus intense and underscores the strong selection for highly aggressive fish, whether the pair forms on the territory or prior to acquiring it. The male is more active in territorial defense than is the female, but both participate (Barlow, 1976; McKaye and Barlow, 1976; Rogers, 1987).

Color of morph is crucial in the aggressive interactions. A number of experiments have shown that G dominates N when neither is territorial (Barlow, 1973; Barlow and Ballin, 1976; Barlow et al., 1975; McKaye and Barlow, 1976). Dominance results not from G being more aggressive than N but rather from the effect of the gold color on the opponent (Barlow and Wallach, 1976; McKaye and Barlow, 1976). The advantage to G is

equivalent to being 15% heavier than the N opponent (Barlow, 1983*b*). All else equal, a weight difference of 2% is sufficient to determine the outcome of a combat (Barlow *et al.*, 1986).

EFFECT OF GOLD
COLORATION ON MATING

The objective here was to explore compatibility in relation to the effect of gold color on aggressiveness (Barlow *et al.*, 1977). Males and females were taken indiscriminately, but with the females 15% smaller by weight (a normal size difference), and placed together as pairs in aquaria. This "blind date" experiment was a severe test of compatibility (see also Bluhm, 1985) because the smaller female was not free to leave. Free-living females can move away from overly aggressive males, and incompatibility among individuals would be scarcely detectable. Only through manipulation does one learn that many pairs cannot form because of interfering aggressive behavior (Barlow *et al.*, 1977).

For three of the four combinations of two colors and two sexes, about 50% of the fish paired, which is a typical outcome in this laboratory situation. But for G male × N female, only 14% paired; most of those males mauled the hesitant females. Apparently the G males overly inhibited aggressiveness in the N females.

To test this, the experiment was repeated, but now using a female the same size as the male (recall that G is equivalent to a weight advantage of 15%). The rationale was that size would compensate for the female's disadvantage in aggressiveness. Now successful pairings rose to 57%. Thus color and weight, through their effects on aggressiveness, may substitute for one another in a pair situation. That suggested that pairing is facilitated by some appropriate relationship between the prowess of the male and that of the female.

This conclusion is bolstered by two other observations. First, *C. zaliosum* shows more aggression during pair formation than does the Midas cichlid; hybrid pairs succeeded only when the Midas cichlid was unusually large relative to the arrow cichlid of either sex (Baylis, 1976*b*). Second, the few mixed-color pairs of Midas cichlids seen in nature were all G male × N female, the opposite of what one predicts from the laboratory findings. I asked McKaye to check the sizes of those females, predicting they would be much larger than normal. The females in the mixed-color pairs were larger than normal (McKaye, 1986), which is a nice confirmation of a behavioral mechanism found in the lab extending to the field.

MONOGAMOUS PAIRING AS A
MUTUAL-DEFENSE TREATY

Mating in the monogamous Midas cichlid is more multifaceted than in polygynous cichlids because of the inherent conflict between aggressiveness and cooperation in each mate; this conclusion may well generalize to biparentally monogamous species. Mates in such species must share resources, such as breeding sites. Any intruder the size of a potential mate is apt to be a competitor for the resource. Each sex is selected to be aggressive to repel territorial usurpers. Yet biparental mates need to cooperate peacefully over long periods. Forming a pair is thus equivalent to agreeing to mutually defend the resource and offspring, and to not attack one another (Lorenz, 1966).

When the sexes are virtually indistinguishable, each stimulates its potential mate to attack as well as to cooperate (Tinbergen, 1959, 1960). Once pairs have formed, the males are often noticeably larger than their mates and present a genuine risk to their females (Tinbergen, 1959). Bonds may break even after pairing (Baerends, 1986; Barlow *et al.*, 1977; Lamprecht, 1973), with the attendant loss of parental investment. Individuals must therefore choose mates to minimize the risk of injury and of aborting a breeding cycle.

Behavioral mechanisms underlying defense of territory and young may conflict with mechanisms that enhance mating, even in polygynous species (Rowland, 1988; Ward and FitzGerald, 1987). In monogamous species, this conflict may be especially acute at the time of pair formation, which commonly coincides with the time of establishing a territory.

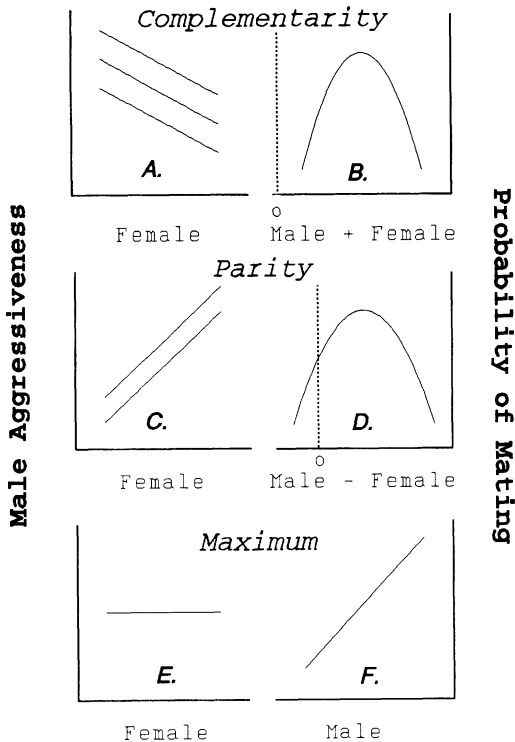Selection for defense, therefore, produces

FIG. 1.　Graphic representation of the three model for mating. The right-hand column derives from the one on the left. The slopes of the rectilinear expressions have no special significance. The lines in panel A show three of the many possible relationships between male and female aggressiveness; one line orthogonal to them produced the inverted U in panel B meant to represent the best solution. The lower line in panel C represents equally aggressive males and females. Further explanation is in the main text.

high readiness to attack. However, this aggressiveness can work against forming and sustaining pair bonds. Behavioral mechanisms may constrain selection in both directions, producing either a compromise, or high inter-individual variability in readiness to attack, or both. Our findings have shown that individuals vary greatly in aggressiveness (Barlow et al., 1986).

RESOLVING DIFFERENCES IN
AGGRESSIVENESS IN
ORDER TO MATE

Exploring how monogamous species reach a mutual-defense treaty when pairing raises alternative hypotheses about the proximate mechanisms of pair formation. The modest models that follow are only a starting point;

but even simple models serve to clarify the level of analysis and to define the assumptions made (Maynard Smith, 1989).

In his oft-cited overview of mate choice, Halliday (1983) referred to behavioral complementarity without delimiting the term or giving examples. He seemed, however, to infer a parallel with genetic complementarity. Here, I define *complementarity* to mean that one part of the system makes up the deficiency in the other to produce a whole. Thus if one bird of a pair is reluctant to incubate, the other must make up for the deficiency (Coulson, 1972). Complementarity in the present model means that as one mate of either sex becomes more aggressive the other becomes more submissive; it has that connotation for humans (Duck and Miell, 1983).

Formally, complementarity for a monogamous cichlid means that mating is most probable at some sum of aggressiveness of the male and female (Fig. 1A). Thus the male could be highly aggressive, the female not, or vice versa, or both could be equally aggressive at some intermediate level. One line, encompassing the range of aggression giving the same sum, should express the maximum probability of forming a pair (Fig. 1B). In a test situation, probability of mating is inferred from the highest level of courtship but can be tested directly.

In the *parity* model, the more aggressive the male, the more aggressive the female must be in order to form a pair. Because the male of a pair is usually more aggressive than his mate, the linear representation of this relationship should find its y-intercept above the origin (Fig. 1C). The inverted-U function, summarizing the family of parallel curves, intercepts the y axis when male and female aggressiveness is equal, and thus crosses over into negative values of x when female aggressiveness exceeds that of the male (Fig. 1D).

Experiments using one-way mirrors (Rogers and Barlow, 1991) indicated that females generally prefer the *maximally aggressive male* when the female is safe from the male's aggression (Fig. 1E, F). Though unlikely, pairs with highly aggressive males might be the most compatible, irrespective of female aggressiveness. This is the only

model that incorporates absolute, but unknown, levels of aggression.

Evidence for complementarity is hard to find; some comes from Baylis' (1976a) study of hybrid pairs. Comparing the closely related Midas cichlid and C. zaliosum, he found that both sexes of the C. zaliosum were more aggressive than were those of the Midas cichlid: Males of both species attached more than did their females, and females avoided more than did males. But female C. zaliosum avoided relatively more often than did female Midas cichlids, suggesting they could be following the complementarity model.

The same study (Baylis, 1976a) also produced evidence supporting parity because size compensated for aggression. In hybrid pairs, the more aggressive C. zaliosum, whether male or female, was relatively small compared to a naturally formed conspecific pair.

Other evidence indicates parity might be important. In an aquarium, the dominant male cichlid of a group establishes a territory and the dominant female mates with him. The next-ranking female mates with the next-ranking male, and so on (Siepen and Crapon de Caprona, 1986; Weber and Weber, 1976; personal observation). However, one cannot distinguish here between favorable levels of aggressiveness between mates as opposed to dominant females progressively excluding the next lower-ranking female (Driscoll and Welanko, 1981), creating a no-choice situation.

The model of maximum male aggressiveness provides the best opportunity to observe the possible conflict of behavioral mechanisms. We know that females prefer the most aggressive males (Rogers and Barlow, 1991). But a timid female might not be able to mate with an aggressive male when the barrier is removed. If so, female choice would be constrained by her inability to cope with an aggressive male.

CONCLUSIONS

Earlier steps in the hierarchical process of mating seem more biased toward simple stimulus filtering. Later steps seem more under the control of higher integrative areas.

But these speculations serve only to focus the search for behavioral mechanisms.

Surprises are inevitable. In the Midas cichlid the anticipation was that both species and sex would be recognized through simple chemical cues. Though chemical information is used, the situation is more complex. Sex and readiness to mate may be better communicated through complex exchanges of visual displays between the male and female. Another surprise was that males are not choosy (but see Burley, 1981). Although tightly monogamous, males behave as though they are polygynous. However, males may need to interact with a female to make a choice, and that has not been tested.

The duration and complexity of pair formation, with its outbursts of aggression, set mating in monogamous species apart from mating in polygynous species, though aggression during mating also occurs in polygynous species (Rowland, 1988; Ward and FitzGerald, 1987). This drawn-out ritual may be the result of counter-acting selection for high aggression against intruders and for peaceful exchanges between mates.

This seems the most likely path to explaining color-assortative mating in the Midas cichlid in the field in the face of pervasive but weak preference by all females for normally colored males. Experiments manipulating color and aggressiveness of potential mates, and permitting aggressive exchange, should illuminate the process of pairing in the Midas cichlid. And that should be informative not only in the context of incipient speciation but also to mating in isomorphic, monogamous animals of diverse types.

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