THE SOCIAL EVOLUTION OF THE BUTTERFLYFISH,
Chaetodon multicolor:
MONOGAMY, SEXUAL SELECTION, JUVENILE BEHAVIOR,
AND TERRITORIAL AGGRESSION

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ABSTRACT

Monogamy has many meanings. The term has variously been used to describe exclusive mating (genetic monogamy), two organisms living together (social monogamy), and the nature of the relationship between those two organisms (pairbonding). These various aspects of monogamy can be thought of in terms of shared genes, shared space, and shared time respectively. The butterflyfish, *Chaetodon multicinctus*, breeds exclusively with its mate though sneakers are occasionally present (genetically monogamous), defends a male-female territory (socially monogamous), and pairmates spend most of their time in very close proximity. Social monogamy is proximately the result of mate guarding by both sexes. Females defend males’ territorial defense abilities whereas males defend females for spawning access. Pairbonding is evolutionarily favorable because both sexes feed at higher rates when with their pairmate. Males, but not females, show a preference for larger mates in tank studies. This may be the result of a female preference for a male’s territory quality or some characteristic other than size or be a case of sex role reversal. Males and females pair assortatively by size; this is likely due to intra-cohort pairing rather than sexually selected means, though it may be reinforced by intrasexual competition among females. Juvenile *C. multicinctus* settle near adult territories. Most do not survive. Pairing behavior occurs shortly after settlement and seems to co-occur with territorial behavior. Adult populations appear to be saturated; juveniles recruit to the adult population either by pairing up when small and successfully defending a larger and larger territory or they become a floater. All ages of *C. multicinctus* feed primarily on coral, but the percentage of non-coral items in the diet decreases with age. Adults show seemingly more intense displays toward juvenile intruders. The more intense display may be the result of a greater threat to the territory posed by juveniles, avoidance of injury in fights with other adults, or a lack of pairmate recognition behavior toward juveniles.
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CHAPTER I
GENERAL INTRODUCTION

This dissertation describes the social behavior of the multibanded or pebbled butterflyfish, *Chaetodon multicinctus* Garrett, 1863. Butterflyfishes are colorful inhabitants of coral reefs, and many species are well known for living in pairs. Living in pairs is noteworthy because male and females have different methods for increasing their reproductive success. In general, the reproductive success of females is limited by the number of eggs they can produce, and so females typically invest more in the production of eggs and their care. In contrast, male reproductive success is limited by access to females, thus males typically invest more in traits that promote multiple mates (Bateman 1948, Williams 1966, Trivers 1972). These differences produce a fundamental conflict of interests between the sexes, and therefore, due to these differing interests, monogamy is an uncommon social system, and its evolution is of interest.

The main purpose of this dissertation is to explore the evolution of monogamy in *C. multicinctus*. In order to understand the evolution of monogamy, a critical definition of monogamy is necessary. In this introduction, I review definitions of monogamy and present an alternative method of defining monogamy that helps to clarify the many confusing questions about its evolution. I then present a brief review of the natural history of *C. multicinctus*. In Chapter II, I review the existing hypotheses on the evolution of monogamy in general and others that have been advanced in particular to
explain the evolution of monogamy in butterflyfishes. I test these hypotheses in *C. multicinctus* and describe the various selection pressures that have led to social monogamy and pairbonding. In Chapter III, I test several hypotheses regarding mate choice in a monogamous species and examine sexual selection and assortative mating and their relationship to monogamy. In Chapter IV, I examine the settlement of *C. multicinctus* and how they recruit into adult populations as well as describe the shift in feeding behavior as new settlers get larger. In Chapter V, I describe some agonistic behavior of resident pairs towards adult and juvenile intruders. Chapter VI is a conclusion and has suggestions for future work.

**WHAT IS MONOGAMY?**

To say that a given organism is monogamous conveys certain information (there is some sort of relationship between two animals), but does nothing to describe the nature of that relationship. Two animals may or may not mate exclusively, may or may not live together, and may or may not coordinate their behavior or associate strongly. As Barlow (1984) noted, monogamy may seem a simple concept, but it is notoriously difficult to define.

Many authors have written on the subject of monogamy, and there are as many different definitions of monogamy as there are authors (see Table 1.1 for a summary). Darwin (1871) referred to monogamous relationships as marriage, and in cases of polygamy, the primary female was referred to as the wife. Attempts to specifically define
Table 1.1. Summary of historical definitions of monogamy

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<th>Definition</th>
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<td>Animal marriage</td>
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<tr>
<td>Wilson (1975)</td>
<td>Two animals involved in biparental care</td>
</tr>
<tr>
<td>Kleiman (1977)</td>
<td>Monogamy is either facultative (Type I – based on the inability to sequester multiple mates) or obligate (Type II - based on the need for parental care)</td>
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<td>Rothe (1975)</td>
<td>An emotional bond between two animals</td>
</tr>
<tr>
<td>Wittenberger and Tilson (1980)</td>
<td>Relative exclusivity of mating and also a prolonged association between those two animals</td>
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<td>Wickler and Seibt (1981, 1983)</td>
<td>Monogamy as a social system – an association between two animals</td>
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<td></td>
<td>Monogamy as a mating system – exclusive mating between two animals</td>
</tr>
<tr>
<td>Barlow (1984, 1986)</td>
<td>Two animals remaining together after fertilization to raise offspring or Relatively exclusive mating between two animals</td>
</tr>
<tr>
<td>Gowaty (1985)</td>
<td>Equal contribution of gametes by males and females</td>
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</table>

Monogamy go back as far as 1894. Wundt (1894, cited from Dewsbury 1988) defined monogamy as animal marriage when a mating relationship becomes a permanent social bond. With the advent of sociobiology, monogamy began to be explored in a new theoretical framework. Wilson (1975) defined monogamy as two animals involved in biparental care. Kleiman (1977) defined two types of monogamy in mammals based on
whether individuals were seen as part of a family unit. Rothe (1975) stated that exclusivity of mating is not sufficient to define monogamy and that there must be an emotional bond between two animals. Wittenberger and Tilson (1980) defined monogamy as relative exclusivity of mating and also a prolonged association between those animals. Wickler and Seibt (1981, 1983) began to bring some clarity to confused discussions of monogamy by drawing attention to the varying definitions of monogamy being used. They distinguished between monogamy as a social system (two animals associating in some way) and monogamy as a mating system (exclusive mating between two animals or genetic monogamy). Barlow (1984, 1986) gave two different definitions depending on whether or not there was parental care, but both involved relative exclusivity of mating. Because of the difficulty in confirming exclusive mating, he used a sociographic definition of monogamy (two animals associating in some way) as an approximation for exclusive mating when observations of mating were not possible. He felt that socially monogamous animals that show some sort of coordinated behavior would likely mate exclusively, but also that some solitary animals may come together at times to mate exclusively. He did not discuss socially monogamous animals that do not mate exclusively. Gowaty (1985) advocated a gametic definition of monogamy in which a mating system is defined by gametic contribution ratios. When males and females each contribute an equal number of gametes to reproduction, then monogamy is the result. An equal contribution of gametes, however, can be achieved by polygynandry and total promiscuity as well, so this definition fails to distinguish between those three mating systems. Most recent authors (e.g., Freed 1987, Dewsbury 1988, Mock and Fujioka 1990, Gowaty 1996, Reichard 2003, Whiteman and Cote 2004) have recognized the need
to distinguish between social and genetic monogamy and to consider them separately, however, it is worth emphasizing that different selective forces may be acting to shape social as opposed to genetic monogamy.

The lack of a unifying definition of monogamy has been furthered by the understandable tendency of many reviewers to focus within their taxon of expertise (e.g., Kleiman 1977, Barlow 1984, 1986, Gowaty 1996, Whiteman and Cote 2004). Clearly the inventor of the term “extra-pair copulation” (EPC) did not study fish or we would be referring to “extra-pair spawnings.” This is not meant as a criticism of any of these excellent reviews for it surely is a monumental undertaking to review all the instances of monogamy even within just one taxon. However, a lack of knowledge of taxa outside the expertise of the authors has at times hampered our understanding of the underlying issues in monogamy. For instance, Wittenberger and Tilson (1980) claimed that broadcast spawning fish could not be genetically monogamous, and those authors who discuss monogamy in terms of parental care (see above) are ignoring the many cases in which there is no parental care.

The fact that even today, over 100 years after Wundt (1894) and 30 years after Wilson (1975), authors on monogamy must still devote space to describing how they are using various definitions of monogamy (e.g., Reichard 2003, Whiteman and Cote 2004) indicates the complexity and enormity of the problems faced when studying monogamy. The challenge now is to come up with a better way of describing monogamy that will account for the variety of social organizations within monogamy and will be general enough so that researchers from diverse fields will still find it useful. Without being
precise in our language, we cannot be clear about our understanding of the selective pressures that shape the evolution of monogamy.

**Genetic vs. Social Monogamy**

Barlow (1984) and Gowaty (1985) held that exclusive mating (or monogamy as a mating system) was the important criterion for defining monogamy due to its evolutionary consequences in terms of population genetics and sexual selection. The genetic consequences of monogamy are indeed important, but it is also important to understand the behavioral mechanisms that lead to genetic monogamy as well as any social behaviors that are associated with genetic monogamy. Exclusive mating would seem to limit the opportunity for intrasexual variation in reproductive success. However, many authors (Gowaty 1985, Mock and Fujioka 1990, Andersson 1994) including Darwin (1871) have described how sexual selection can take place in monogamous species. Intrasexual variation in reproductive success in monogamous species can arise from the exclusion of certain individuals from breeding either through dominance interactions or through territoriality, from variation in the timing of breeding, and from opportunities for extra-pair copulations. Knowledge of the causal behavior associated with genetic monogamy, therefore, is important to our understanding of the genetic consequences of monogamous mating systems. These behaviors can also give us information on variation in the degree of genetic monogamy, whether it is a mating system that is mutually beneficial or constrained in some way, and help us to understand the conditions under which it evolves. Knowledge of the related social behavior is therefore complementary to our understanding of genetic monogamy in the same way
that knowledge of the proximate causation of behavior is complementary to its ultimate causation.

Social Monogamy vs. Pairbonding

Though the difference between genetic and social monogamy is firmly established today among researchers of monogamy, another aspect remains ill defined. This relates to the difference between why there are only two animals in a relationship and the nature of the relationship between those two animals. Though the terms social monogamy and pairbonding are often used synonymously or interchangeably, they refer to quite different aspects of monogamy and are shaped by natural selection independently of each other. The ineffectiveness of the term social monogamy as a descriptor by itself can be illustrated by a few examples of species that have all been described as socially monogamous:

- The Japanese serow and the klipspringer are two species of antelope in which a male and female occupy the same home range. In the serow, the male and female rarely associate (Kishimoto and Kawamichi 1996), whereas in the klipspringer, the male and female show highly coordinated behavior and stay close to one another (Dunbar and Dunbar 1980).

- Driscoll and Driscoll (1988) studied three species of butterflyfishes in which a male and female share a home range. One species spent over 75% of their time together, another spent 35%, and a third spent less than 20% of the time together.
• In the Mongolian gerbil, males and females spend most of their time together except when the female comes into oestrus, at which point she spends significantly more time away from the male (Agren 1984).

• Hannon and Dobush (1997) described polygynous pairbonds in willow ptarmigan with males forming pairbonds with more than one female.

• In noisy miners, a cooperatively breeding bird in Australia, Poldmaa and Holder (1997) described strong exclusive associations between pairmates in one population, whereas in another population, Dow and Whitmore (1990) described highly promiscuous copulations. Both populations show genetic monogamy (Poldmaa et al. 1995).

• Gray wolves live in packs of more than two animals, but show partner preferences within the pack with respect to mating (Derix and VanHoooff 1995).

• King penguins form multiple pairbonds and switch mates before mating (Olsson et al. 2001).

• Seahorses live on solitary territories except for a few minutes each morning when pairmates greet each other and spawn repeatedly and faithfully (Vincent and Sadler 1995, Jones et al. 1998).

• Fat-tailed dwarf lemurs (like many bird species) live essentially solitary lives on the same home range, but return to a nest site to alternate parental care (Fietz 1999).

The complexity of relationships and the lack of a clear distinction between social monogamy and pairbonding are evident in the definition used in a recent review. Reichard (2003, p. 4) defined social monogamy as "a male and female's social living
arrangement (e.g., shared use of a territory, behaviour indicative of a social pair, and/or proximity between a male and female).” This definition lumps together disparate aspects of social monogamy related to space use (e.g., shared use of a territory) and the interactions between two animals (e.g., proximity between a male and female). Because social monogamy as defined by Reichard (2003) consists of very broad categories, vastly different social organizations emerge depending on which aspects are chosen to describe a species as socially monogamous. Each of the characteristics used by Reichard (2003) to define social monogamy, plus other characteristics not listed, is shaped by unique selective pressures. Obviously, seahorses and klipspringers have evolved so-called social monogamy through different mechanisms and by different pathways. By using a single term to describe such varied social organizations, we gloss over our ability to understand their evolution.

**Toward a Better Definition**

Though the important distinction between the genetic and social aspects of monogamy has served the field well and has rightly become deeply engrained in our thought, over the last 20 years, relatively little attention has been paid to disentangling the various aspects of social monogamy. By attempting to constrain social monogamy to one category of social behavior, we end up using such a broad, vague, and imprecise definition that we end up lumping very different and often unrelated behaviors together. We are then unable to tease apart the varying selection pressures that affect social behavior.
The many characteristics that have been used to classify an organism as socially monogamous can be divided into two broad categories – those dealing with space use and those dealing with the interaction between pair members. By dividing social monogamy into these two categories, we can now begin discussing the separate questions of 1) why there are two organisms in an association and how did that pairing evolve and 2) what is the nature of the association and why did that type of association evolve. Therefore, rather than dividing our discussions of monogamy into two categories as has been done for the last 20 years, they should now be divided into three – genetic monogamy, social monogamy, and pairbonding (Figure 1.1). Genetic monogamy, as above, refers to the degree of mating exclusivity between a male and female. Social monogamy now refers strictly to a male and female living together more or less exclusively on a home range or territory, whereas pairbonding now refers to the type and degree of association between a male and female. Another way of viewing this classification scheme is to describe monogamy based on the amount of shared genes (genetic monogamy), shared space (social monogamy), and shared time (pairbonding). An important aspect of this new division of monogamy in the broad sense is that genetic monogamy, social monogamy, and pairbonding are three separate and independent measures of a relationship between two animals. Genetic monogamy could be measured by the percent of shared parentage, social monogamy could be measured as the degree of home range overlap between male and female pairmates, and pairbonding might be measured as the amount of time pairmates spend together. The species under study and the methods being used would determine the exact measurements used to describe that species.
This is not to say that the different categories do not interact. For instance, selection for a strong pairbond may result in social monogamy even in the absence of selection for social monogamy. Similarly, genetic monogamy might result from selection for social monogamy even if an individual may have higher reproductive success via genetic polygamy. As can be seen in Figure 1.1, none of these measurements of a monogamous relationship necessarily co-occur with any other (see Table 1.2 for examples). Rather than trying to define monogamy as requiring just one or two or all three of these categories, instead, whenever there is some sort of relationship between two animals, we should define that relationship by describing which of these categories are applicable and how they apply. Put another way, rather than worry about trying to define a relationship as monogamous or not, we should worry about describing the monogamous relationship. We then ask the following questions about that relationship:

1. Does the pair mate exclusively? How exclusively? Why?

2. Does the pair live together? Are they solitary? Are they group living? Why? Do they live together in a defended territory, in a loose home range, or only at a nest site? What is the extent of territory or home range overlap?

3. Does the pair interact? What is the nature of the association within the pair? How strongly are they associated? Why did that particular association evolve?
Figure 1.1. Diagram of the interaction of different aspects of monogamy. Roman numerals refer to Table 1.2.
Table 1.2. Descriptions of the different social organizations that occur with different aspects of monogamy from Figure 1.1.

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<th>Description</th>
<th>Example</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>A pair of animals that live together in the same home range, but do not mate exclusively and do not associate strongly</td>
<td><strong>Japanese Serows</strong> – males and females have overlapping territories and do not associate with each other. Some bigamous males are present, so no strict mating exclusivity.</td>
<td>Kishimoto and Kawamichi 1996</td>
</tr>
<tr>
<td>II</td>
<td>A pair of animals that mate exclusively, but do not live as a pair together in the same home range or associate strongly</td>
<td><strong>Seahorses</strong> – greet in the morning and mate exclusively, but are otherwise solitary with separate home ranges. <strong>Meerkats</strong> – live in cooperative groups with the dominant male and female responsible for the great majority of breeding.</td>
<td>Vincent and Sadler 1995, Jones <em>et al.</em> 1998, Griffin <em>et al.</em> 2003</td>
</tr>
<tr>
<td>III</td>
<td>A pair of animals that associate strongly, but do not mate exclusively or live together as a pair on a home range</td>
<td>Many <strong>colonially breeding birds</strong> that nest in large groups and have frequent EPC’s <strong>Gray Wolves</strong> – pack living animals in which pairs within the pack show mutual partner preferences. Mating is often with the preferred partner, but not completely.</td>
<td>Møller and Birkhead 1993, Derix and VanHooff 1995</td>
</tr>
<tr>
<td>IV</td>
<td>A pair of animals that live together in the same home range and mate exclusively, but do not associate strongly</td>
<td><strong>Ornate Butterflyfish</strong> – share a territory but don’t associate strongly and are presumed to be genetically monogamous like most other corallivorous butterflyfish <strong>Elephant Shrews</strong> – males and females share a territory, move about solitarily, sleep separately, and rarely attempt EPC’s</td>
<td>Driscoll and Driscoll 1988, FitzGibbon 1997</td>
</tr>
</tbody>
</table>
Table 1.2. (Continued) Descriptions of the different social organizations that occur with different aspects of monogamy from Figure 1.1.

<table>
<thead>
<tr>
<th>Type</th>
<th>Description</th>
<th>Example</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>V</td>
<td>A pair of animals that live together in the same home range and associate strongly, but do not mate exclusively</td>
<td>Many bird species</td>
<td>Birkhead and Møller 1992, Petrie and Kempenaers 1998, Griffith et al. 2002</td>
</tr>
<tr>
<td>VI</td>
<td>A pair of animals that associate strongly and mate exclusively, but do not live together as a pair on a home range</td>
<td>Noisy Miners – cooperatively breeding honeyeaters which show strong associations and mating exclusivity between pairmates within a larger social group</td>
<td>Poldmaa and Holder 1997</td>
</tr>
<tr>
<td>VII</td>
<td>A pair of animals that live together in the same home range, mate exclusively, and associate strongly</td>
<td>Klipspringers – antelope that jointly patrol a territory and mate exclusively</td>
<td>Dunbar and Dunbar 1980</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Jackals – a male and female mate exclusively and cooperate in territorial defense and parental care</td>
<td>Moehlman 1987</td>
</tr>
</tbody>
</table>

It is also important to note that these three characteristics of monogamy (genetic, social, and pairbonding) are not categorical variables and may not fall neatly into any particular classification. Many of the examples from Figure 1.1 and Table 1.2 could easily fall into different classifications depending on how strict an interpretation one takes of each of the categories. Rather than ask if a species is monogamous or how many
extra-pair copulations or fertilizations can an organism have before it is no longer considered genetically monogamous, we should ask what is the degree of shared parentage. Rather than ask if a species is socially monogamous or how much home range overlap is allowed in socially monogamous organisms, we should ask if the male and female share a home range and why. Rather than ask if a species is pairbonded or how much time do pairmates have to spend together for them to be considered pairbonded, we should ask what is the nature of the association and why did that particular association evolve. The important questions pertain not to how an organism fits into our artificial classification scheme, but to how and why it has evolved the traits it has. Only by separating the questions can we understand the selective pressures affecting the social behavior.

Of these three categories of monogamy, pairbonding is probably the most ambiguous. The use of the word bond in the term pairbond almost implies that there is some sort of emotional connection between the two pairmates. It needs to be clear that in this usage though, pairbonding is used synonymously with association and is simply a descriptor for the type of interactions shown by a pair. Despite its potential confusing implications, the use of the term is retained because of its ubiquitous use in the literature. Pairbonds can be very weak to non-existent as in solitary animals, or may be quite strong. Kleiman (1981) points out that most authors appropriately steer clear of trying to define pairbond strength because variations from species to species in the nature of the relationship between the two animals mean that measurements of the strength of the pairbond will vary from species to species. A pairbond may be defined by the amount of time a male and female spend together, by coming together at a nest to raise offspring, by
an emotional bond, by coordinated behavior, by mate guarding, etc. The important part, however, is not to find a universal method for defining pairbond strength, but to understand why a particular type of association between two animals has evolved.

Another variable of note in these characteristics of monogamy is time. In this case, time is a factor in our descriptions of genetic monogamy, of social monogamy, and of pairbonding. Some pairs exist for life, some pairs exist for a breeding season, and some pairs only exist for the duration of parental care. How long do two organisms have to mate exclusively for it to be considered genetic monogamy? How long does a pair have to live together for it to be considered social monogamy? How long does a pair have to associate for them to be considered pairbonded? Again, we should not concern ourselves with the duration of an association as a criterion for assigning an organism to a certain place in a classification scheme. We should instead ask ourselves why does the association last as long as it does, and what are the selective pressures that produce that behavior.

Further Issues

Several other issues often related to monogamy, but not essential to its definition, deserve mention at this point. The first is parental care. Parental care has historically been so intertwined with theory on monogamy that it is difficult to separate. It could easily be laid over the classification scheme from Figure 1 as a fourth factor. However, because so many monogamous species do not show parental care, and because so many polygamous species do, it is hardly a necessary aspect of the relationship between two organisms. Rather than being a part of the definition of monogamy, parental care is part
of the answer to many of our questions about monogamy. The need for paternal care may explain why many females rebuff EPC attempts by males. The need for bi-parental care may explain why a male and female show a strong pairbond if they have precocial offspring. A male and female may only occasionally associate at a nest site because they have to take turns providing parental care. This also affects space use by the pair; a male and female may share a nest site exclusively, but have solitary, monogamous, or group territories away from the nest. For all of these reasons, parental care should be left out of our descriptions of monogamy, but often is absolutely vital to our discussions of causality.

A second issue is whether we apply our descriptions of monogamy to an individual, a pair, a population, or a species. This classification scheme can easily be applied to any of the above, and whichever one we choose is simply a matter of what questions we’re interested in. However, as per Barlow (1984), applying it on an individual level, for instance describing an individual as monogamous while its mate is polygamous, does little to advance our understanding of the evolution of monogamy. Social systems can vary within and between populations. To apply this classification to levels of organization greater than the pair, we simply ask how many pairs within a population show monogamy, or how many populations within the species show predominantly monogamy. Again, defining a population or species as monogamous or not is not the relevant question. Asking why certain pairs within a population or certain populations within a species vary in the expression of monogamy is the important question. This allows us to understand the evolution of social behavior at a higher level of organization than the individual.
A final issue when discussing why monogamous associations evolve is to distinguish between proximate and ultimate causation. Proximate causation of monogamy involves the mechanistic behavior that leads to monogamy. Ultimate causation involves the reproductive success and possible evolutionary benefits of monogamy. These two modes of causation can be complementary or work in opposition. For example, selection that favors strong mate guarding behavior by one mate may constrain the other mate from gaining multiple matings even when multiple matings may increase that individual’s reproductive success. By examining issues of proximate and ultimate causation, we can gain an understanding of the cases where monogamy is mutually beneficial or whether it is constrained.
Butterflyfishes (Family: Chaetodontidae) have a worldwide distribution on tropical coral reefs (Burgess 1978). The multibanded butterflyfish or pebbled butterflyfish, *Chaetodon multicinctus*, is endemic to the Hawaiian Islands and Johnston atoll and grows up to 10 cm SL (Gosline 1955, Randall 1985).

Chaetodontids have a variety of social systems that correlate with feeding guilds (Reese 1975, 1991, Hourigan 1989). Coral-feeding butterflyfishes are almost always found in pairs; planktivorous butterflyfishes tend to be schooling; omnivorous butterflyfishes have a variety of social organizations including solitary, paired, large groups, and harems. *C. multicinctus* belongs to the guild of coral-feeding butterflyfishes. They are obligate, generalist corallivores, and feed by picking individual polyps from coral heads (Tricas 1985, Motta 1988, Hourigan 1991), with pairs often feeding together from the same coral head.

*C. multicinctus* is strongly territorial with large (approximately 50-200 m²), contiguous, temporally and spatially stable, feeding territories. Territory size is inversely related to coral abundance (Tricas 1989a, Kosaki 1999). They defend the territories against conspecific and other corallivores. Like most territorial butterflyfish species, overall aggression levels are low, and they are able to maintain their territories with relatively low intensity agonistic displays of erected fins and occasional chases (Reese 1975, Ehrlich *et al.* 1977, Roberts and Ormond 1992). Intraspecific aggression is primarily directed against same sex individuals (Hourigan 1987, 1989).
They are socially monogamous with male-female pairs living together exclusively on a territory (Reese 1975, 1991; Tricas 1985; Hourigan 1989; Roberts and Ormond 1992). They are also likely to be mainly genetically monogamous. *C. multicinctus* spawns at dusk, and the spawnings that have been observed have been between pairmates. Though sneakers are occasionally present and may at times be successful at fertilizing some eggs, on the whole, they appear to have only limited success (Hourigan 1987, Lobel 1989). They are broadcast spawners, and there is no parental care. In addition, they are strongly pairbonded (Reese 1975, Hourigan 1987). Driscoll and Driscoll (1988) found that pairs spent over 75% of their time together. The amount of time they spend together, however, is variable. Tricas (unpublished data) found that pairs stayed together about 57% of the time, and Hourigan (1987) found that they stayed together about 74% of the time. *C. multicinctus* is long-lived, and pairs have been observed together for several years but probably stay together even longer (Hourigan 1989). According to the classification scheme in Figure 1.1 and Table 1.2, *C. multicinctus* would be considered Type VII.

*C. multicinctus* is site-attached and acclimates readily to the presence of divers which makes them easy to find and easy to observe at close range. Individuals are recognizable by natural variation in their markings. This allows for repeated and very detailed behavioral observations of known individuals. The sexes are monomorphic which allows for unbiased data collection by not knowing the sex of the observed fish beforehand.
CHAPTER II
SOCIAL MONOGAMY, PAIRBONDING, AND MATE GUARDING

INTRODUCTION

Monogamy is expected to be a rare social system because males and females have different methods of increasing their reproductive success. In general, the reproductive success of females is limited by the number of eggs they can produce, and so females typically invest more in the production of eggs and their care. In contrast, male reproductive success is limited by access to females, thus males typically invest more in traits that promote multiple mates whether through female choice or male-male competition (Bateman 1948, Williams 1966, Trivers 1972). This fundamental conflict between the sexes makes the evolution of monogamy rather rare, as males typically behave polygynously. Therefore, it is important to understand the circumstances in which monogamy does evolve because it provides us with a better understanding of social behavior, mating systems, and reproductive behavior.

Three models have traditionally been used to explain social monogamy. 1) When biparental care is required to successfully rear any offspring, monogamy often occurs (Wittenberger and Tilson 1980, Mock and Fujioka 1990). 2) When the polygyny threshold (Orians 1969) is not met, then environmental conditions are such that no male has a territory of sufficiently high quality to attract multiple females. In this situation, females will prefer to pair with an unmated male and monogamy results. 3) When
females are limiting, male efforts to sequester more than one female will be unsuccessful, so male fitness will improve by assisting existing mate. This will result in monogamy (Emlen and Oring 1977). This can occur when females are territorial, when they are found in low densities, or when they mate synchronously. None of these explanations, however, are adequate to explain the social system of the butterflyfish, *Chaetodon multicinctus* (see Discussion, Table 2.1).

### Table 2.1. Traditional models for the evolution of monogamy

<table>
<thead>
<tr>
<th>Model</th>
<th>Monogamy results when:</th>
<th>Problem</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biparental care</td>
<td>The reproductive success of the parents is increased by both parents caring for the offspring.</td>
<td>No parental care in butterflyfishes</td>
</tr>
<tr>
<td><em>(Wittenberger and Tilson 1980, Mock and Fujioka 1990)</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Polygyny Threshold Model</td>
<td>No male is able to hold a large enough or high enough quality territory to attract multiple females.</td>
<td>Threefold range in territory size and quality, but not in number of females.</td>
</tr>
<tr>
<td><em>(Orians 1969)</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low female availability</td>
<td>Females are territoriality.</td>
<td>Females do not show territorial defense.</td>
</tr>
<tr>
<td><em>(Emlen and Oring 1977)</em></td>
<td>Females are found in low densities.</td>
<td><em>C. multicinctus</em> is abundant.</td>
</tr>
<tr>
<td></td>
<td>There is synchronized spawning.</td>
<td>No synchrony among nearby pairs, and other butterflyfishes spawn at dusk.</td>
</tr>
</tbody>
</table>
One of the difficulties in the study of monogamy has been a lack of clear definitions. In order to understand the evolution of monogamy, it is necessary to distinguish among questions of genetic monogamy, social monogamy, and pairbonding (Chapter I). Though they may interact, selection pressures act on each of these aspects of a social system independently.

*C. multicinctus* is socially monogamous and strongly pairbonded (Reese 1975, 1991; Tricas 1985; Hourigan 1987, 1989; Driscoll and Driscoll 1988; Roberts and Ormond 1992) and is likely to be mainly genetically monogamous as well (Hourigan 1987, Lobel 1989). This species is notable because the usual explanations for monogamy do not explain the presence of social monogamy in *C. multicinctus*, nor do they explain the presence of the strong pairbonds seen in this species. Also, since much of the work on monogamy has been conducted on terrestrial species (mostly birds and mammals), marine fishes may provide new models for our understanding of monogamy.

Several authors have suggested other hypotheses for the evolution of monogamy that may be applicable to *C. multicinctus* and other monogamous coral-feeding butterflyfishes (Table 2.2). 1) Improved territorial defense – if pairs can defend a territory more efficiently than a solitary individual by each individual defending half as much territory as it would have if solitary, social monogamy may be the result (Barlow 1984, Roberts and Ormond 1992). In order to gain this benefit, individuals of a pair must patrol the territory independently of each other. Also, if the necessity of co-defense of a territory were the selective pressure driving social monogamy, then we would expect that solitary individuals would be unable to hold a territory or that they would be less successful at doing so. 2) Improved territorial signal – Fricke (1986) suggested that the
Table 2.2. Hypotheses, assumptions, and predictions for causation of monogamy in butterflyfishes

<table>
<thead>
<tr>
<th>Hypotheses:</th>
<th>Assumptions:</th>
<th>Predictions:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Improved territorial defense by two fish (Barlow 1984, Roberts and Ormond 1992)</td>
<td>Each fish in a pair only needs to patrol half the territory boundary, both sexes are equally competent at territorial defense, and solitary fish are as good as pairs at territorial defense.</td>
<td>Pairmates move within their territory independently of each other. Both sexes will show territorial behavior, and solitary fish cannot defend a territory.</td>
</tr>
<tr>
<td>Improved territorial ownership signal (Fricke 1986)</td>
<td>Two fish together can more effectively repel or deter an intrusion.</td>
<td>Pairs show tightly coordinated behavior. Intrusion rates are lower against pairs than solitary individuals. Solitary fish cannot defend a territory.</td>
</tr>
<tr>
<td>Feeding advantage (modified from Hourigan 1989)</td>
<td>Female reproductive success is limited by food intake.</td>
<td>Females feed more and show less aggression when the male is present. Males feed less and show more aggression.</td>
</tr>
<tr>
<td>Mutual mate guarding (Fricke 1986)</td>
<td>Both sexes provide a resource which the opposite sex defends.</td>
<td>Individuals show more aggression when their mate is present, and aggression is restricted to same sex individuals. The pairbond is mutually maintained by individuals making more movements toward the mate than away from the mate. Small individuals should show more movements toward their mate than larger individuals.</td>
</tr>
</tbody>
</table>
presence of a pair together on the territory allows for more efficient territorial defense by
an improved signal of territory ownership. This hypothesis presumes that a pair of fish
can more effectively repel an intruder or deter an intrusion than a solitary fish. If so, we
would expect pairs to be tightly coordinated in their behavior and that intrusions would
be less likely when the pair is together. Like the previous hypothesis, if pair formation is
necessary for territorial defense and is the force driving social monogamy, then solitary
individuals would likely not be able to defend a territory or would be less successful at it.
3) Feeding advantage – if pairing allows for a division of labor such that males assume a
larger role in territorial defense while females feed more, this allows the female to
produce more eggs which the male then fertilizes and thus increases the reproductive
success of both pairmates (Barlow 1984; Hourigan 1987, 1989). Though there is some
evidence for this hypothesis in *C. multicinctus* (Hourigan 1989), it is unclear whether this
is a hypothesis for social monogamy or for pairbonding. If the formation of a tight
pairbond were what actually provides the feeding advantage, then we would expect
females to feed at higher rates when in the presence of the male and that her aggression
rates would be lower when the male is present. Males would be expected to have lower
overall feeding rates and higher rates of aggression, though this does not necessarily vary
with the presence of the female. 4) Mate guarding – mutual mate guarding might limit
each sex to social monogamy by defending the mate from other individuals of the same
sex (Fricke 1986). If *C. multicinctus* mate guards, we would expect higher aggression
rates when the mate is present, that aggression would be restricted to same sex
individuals, and that both sexes would maintain the pairbond by making more
movements toward the mate than away from the mate. Also, if larger individuals
represent a more valuable resource whether through better territorial defense or increased egg production, we would expect that relatively small fish would show a higher rate of movement toward their mate.

I examined these four hypotheses using data from this study as well as other published data. Three things should be noted about these hypotheses. First, the improved territorial defense hypothesis deals with the benefits of social monogamy but not pairbonding, while the improved territorial signal hypothesis deals with the benefits to pairbonding but not social monogamy. The feeding advantage hypothesis, as I have adapted it, deals with the benefits to pairbonding, though social monogamy may result by default from selection for pairbonding, and the mate guarding hypothesis could address either social monogamy or pairbonding or both, but does not address the benefits to either. Second, the first three of these hypotheses are based on ultimate benefits, while mate guarding is a proximate mechanism by which monogamy is maintained and does not say anything about what the ultimate benefits to pairing are. Lastly, all of these hypotheses are not necessarily mutually exclusive.

The goals of this study, then, were to understand the selective pressures that favor both the evolution of social monogamy as well as the tight pairbonds seen in *C. multicinctus*. In addition, understanding the nature of the pairbond and how it is maintained and whether or not the social system is mutually beneficial or if one sex is constrained to it in some manner were also goals.
METHODS

Behavioral Observations

I conducted this study in the summer and fall of 1999 at two sites in Hawai‘i. With several field assistants, I observed 11 pairs of *C. multicinctus* at Kahe Pt. (21°21' N, 158°7' W) on the island of Oahu and nine pairs at Puako (19°57' N, 155°54' W) on the island of Hawai‘i. We collected data on the feeding rates, measured in bites of coral per minute, and on agonistic rates, measured in the number of chases and displays per minute. We collected these data for males and females both while in the presence of their pairmate and while separated from their pairmate but with both still on the territory. A pair was designated as being together when they were within one meter of each other, and the amount of time a pair spent together was also noted. I calculated how much time a pair would spend together if the pairmates were moving independently of each other using a formula developed by Waser (1982, 1984, 1987). The time spent together is given by

\[ T = \frac{\pi^2}{2} \rho r^2 \]  

(1)

where \( T \) is the proportion of time spent in association, \( \rho \) is the density of fish, and \( r \) is the criterion distance that defines association. In this case, \( \rho = \) two fish/territory size, and \( r \) is one meter, thus giving

\[ T = \frac{\pi^2}{t} \]  

(2)

where \( t \) is the size of a pair’s territory measured in square meters. In order to understand which sex or both was primarily responsible for maintaining proximity in the pairbond, I
counted the number of movements made by each sex toward and away from its pairmate. A movement toward the pairmate was defined as any switching or altering of current behavior in order to maintain proximity within the pairbond. This was most often seen as one fish ceasing to feed on a coral head and following the pairmate when it left. A movement away from the pairmate was defined as any switching or altering of current behavior that caused a break in the pairbond. This was most often seen as one fish swimming away from its pairmate. Lastly, we also measured territory size and the amount of coral within that territory for each pair. After the behavioral observations were completed, all fish were collected, and sex was determined by dissection.

**Statistical Analyses**

Comparisons of territory size, percent coral cover, coral area, and the amount of time pairs spent together were made using two-sample t-tests. The comparison of the observed and predicted amounts of time that pairs spent together was made with a paired t-test. The data on feeding rates were analyzed using analysis of variance (ANOVA) with site, sex, and presence of the pairmate as independent variables. One extreme outlier was excluded; this was an observation of a male without its pairmate that was feeding outside its territory. The exclusion of this observation did not affect the overall conclusions. Tukey’s pairwise comparisons were used for comparisons of different categories. The data on agonistic rates did not meet the assumptions for ANOVA, so the data were coded as a categorical variable as either chase or display(s) occurred or did not occur and then analyzed using a binary logistic regression that analyzes the probability of observing agonism given a set of independent variables. Site, sex, and presence of the
pairmate were the independent variables. Movements toward and away from the pairmate were analyzed using ANOVA with site, sex, and direction (toward or away) as the independent variables for the movement data. Tukey’s pairwise comparisons were used for comparisons of different categories. The relationship between size and rate of movement toward the pairmate was conducted by an analysis of covariance. All analyses were performed on Minitab 12.1.

RESULTS

Study Sites

Kahe Pt. consisted of a fringing reef about five to seven meters in depth with *Porites lobata*, *Pocillopora meandrina*, *Montipora patula*, and *M. capitata* being the dominant coral species. The site at Puako was at the base of a drop off in about 10 meters of water with *Porites compressa* and *Porites lobata* dominating. Mean territory sizes (± SE) were larger at Kahe Pt. (140.9 m² ± 14) than at Puako (87.4 m² ± 11; T = 3.12, df = 16, p = 0.007). The overall percent coral cover was lower at Kahe Pt. (37.17% ± 2.5) than at Puako (85.80% ± 1.7; T = -15.98, df = 15, p < 0.00005). The total amount of coral in the territory showed a trend of being lower at Kahe Pt. (52.1 m² ± 6.8) than at (Puako 74.6 m² ± 8.7; T = -2.03, df = 15, p = 0.06). The lack of a statistically significant difference was due to a single particularly large territory at Kahe Pt. that was an extreme outlier. There was an approximately threefold range in the size of the territories and in the amount of coral food within a territory at both sites (Table 2.3). There was never, however, any instances of a social system other than monogamy.
Table 2.3. Range of territory sizes and coral abundances at the two study sites

<table>
<thead>
<tr>
<th>Territory Size (m²)</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Mean</th>
<th>Std. Dev.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kahe Pt.</td>
<td>86.6</td>
<td>225.8</td>
<td>140.9</td>
<td>42.9</td>
</tr>
<tr>
<td>Puako</td>
<td>45.5</td>
<td>143.7</td>
<td>87.4</td>
<td>31.6</td>
</tr>
<tr>
<td>Coral Abundance (m²)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kahe Pt.</td>
<td>34.16</td>
<td>111.28</td>
<td>52.1</td>
<td>21.6</td>
</tr>
<tr>
<td>Puako</td>
<td>43.11</td>
<td>116.02</td>
<td>74.6</td>
<td>26.0</td>
</tr>
</tbody>
</table>

Feeding Rates

Feeding rates were higher at Kahe Pt. (13.6 ± 0.78 bites/min.) than at Puako (11.0 ± 0.61 bites/min.) and were higher for females (13.5 ± 0.77 bites/min.) than for males (11.3 ± 0.68 bites/min.) (Table 2.4). The significant site*sex interaction, however, shows that this relationship is driven by female feeding rates at Kahe Pt. (Figure 2.1). Females at Kahe Pt. fed at 15.8 (± 1.0) bites/min., while feeding rates were similar for males at Kahe Pt. (11.4 ± 0.99 bites/min.), for females at Puako (10.7 ± 0.81 bites/min.), and for males at Puako (11.3 ± 0.93 bites/min.).

Table 2.4. ANOVA results for the effects of site, sex, and presence of the pairmate on feeding rates

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F ratio</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>site</td>
<td>1</td>
<td>138.42</td>
<td>127.24</td>
<td>7.56</td>
<td>0.008</td>
</tr>
<tr>
<td>sex</td>
<td>1</td>
<td>94.23</td>
<td>80.02</td>
<td>4.76</td>
<td>0.033</td>
</tr>
<tr>
<td>pairmate</td>
<td>1</td>
<td>102.94</td>
<td>102.06</td>
<td>6.07</td>
<td>0.016</td>
</tr>
<tr>
<td>site*sex</td>
<td>1</td>
<td>123.96</td>
<td>126.82</td>
<td>7.54</td>
<td>0.008</td>
</tr>
<tr>
<td>site*pairmate</td>
<td>1</td>
<td>7.08</td>
<td>7.63</td>
<td>0.45</td>
<td>0.503</td>
</tr>
<tr>
<td>sex*pairmate</td>
<td>1</td>
<td>23.28</td>
<td>20.03</td>
<td>1.19</td>
<td>0.279</td>
</tr>
<tr>
<td>site<em>sex</em>pairmate</td>
<td>1</td>
<td>14.27</td>
<td>14.27</td>
<td>0.85</td>
<td>0.360</td>
</tr>
<tr>
<td>Error</td>
<td>71</td>
<td>1194.48</td>
<td>16.82</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>78</td>
<td>1698.67</td>
<td></td>
<td></td>
<td>30</td>
</tr>
</tbody>
</table>
Figure 2.1. Mean feeding rates in bites of coral per minute at Kahe Pt. and at Puako for males (solid bars) and females (open bars). Error bars are standard errors. See Table 2.4 for p-values.

Both sexes fed at higher rates when their mate was present (Table 2.4, Figure 2.2). When data from both sites and sexes are pooled, on average, fish with their mate present fed at 13.6 (± 0.58) bites/min., while fish without their mate present fed at 11.3 (± 0.85) bites/min. Though we did not collect quantitative data on all activities of the focal fish at the same time, a few anecdotal impressions suggest that males seem to be involved in territorial defense activities when not with the female. When females were alone, they were occasionally seen to rise off the bottom up to one meter seemingly looking for the male. She often followed him when nearby or resumed feeding when he was not.
Figure 2.2. Mean feeding rates in bites of coral per minute of males and females while with their pairmate (solid bars) and while without their pairmate (open bars). Error bars are standard errors. See Table 2.4 for p-values.

Agonistic Rates

Agonistic behavior by both sexes occurred in the form of both chases and displays. Chases consisted of a rapid swim toward another fish often within the territory. Displays were often seen between two fish along a common territorial border. The display consisted of a sideways turning of the body with erected dorsal, anal, and pelvic fins and often with the head tilted down slightly (see Chapter V).
Males and females were more likely to show a chase or display against an intruder when they were with their pairmate (Figure 2.3, Table 2.5), and they were also more likely to be chased or displayed at by another fish when they were with their pairmate (Figure 2.4, Table 2.6). Aggression rates by a focal fish against intruders were significantly correlated with aggression rates by intruders against the focal fish ($r = 0.618, p = 0.002$). Agonistic encounters often consisted of a pair of neighbors chasing each other back and forth several times over the border of their territories.

Aggression was more likely to be observed both against an intruder (Table 2.5) and by an intruder against the focal fish (Table 2.6) at Puako than at Kahe Pt. Males were much more likely than females to show aggression toward another fish (Table 2.5), but both sexes were equally likely to be aggressed against (Table 2.6). Though most aggression is seen between same sex individuals, males more often chased females than females chased males (Hourigan 1987).

Higher rates of aggression did not lead to larger territories or higher quality territories. The average aggression rates of a pair were not significantly correlated with either territory size (Kahe: $r = -0.047, p = 0.897$; Puako: $r = -0.032, p = 0.934$) or the percentage of coral cover within a territory (Kahe: $r = 0.065, p = 0.858$; Puako: $r = 0.057, p = 0.883$). Likewise, the average aggression rate of the male was not significantly correlated with either territory size (Kahe: $r = -0.146, p = 0.687$; Puako: $r = -0.064, p = 0.870$) or the percentage of coral cover within a territory (Kahe: $r = -0.007, p = 0.984$; Puako: $r = 0.140, p = 0.719$).
Figure 2.3. Probability of the focal fish chasing or displaying at an intruder for males and females while with their pairmate (solid bars) and while without their pairmate (open bars). See Table 2.5 for p-values.

Table 2.5. Results of binary logistic regression for the effects of site, sex, and presence of the pairmate on the probability of a chase or display toward an intruder

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Coefficient</th>
<th>Standard Deviation</th>
<th>Z</th>
<th>P-value</th>
<th>Odds Ratio</th>
<th>95% C.I.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-3.67</td>
<td>0.963</td>
<td>-3.81</td>
<td>&lt; 0.0005</td>
<td>39.05</td>
<td>6.17 - 247.28</td>
</tr>
<tr>
<td>Site</td>
<td>3.66</td>
<td>0.942</td>
<td>3.89</td>
<td>&lt; 0.0005</td>
<td>39.05</td>
<td>6.17 - 247.28</td>
</tr>
<tr>
<td>Sex</td>
<td>1.88</td>
<td>0.767</td>
<td>2.45</td>
<td>0.014</td>
<td>6.56</td>
<td>1.46 - 29.53</td>
</tr>
<tr>
<td>Pairmate</td>
<td>-1.87</td>
<td>0.770</td>
<td>-2.43</td>
<td>0.015</td>
<td>0.15</td>
<td>0.03 - 0.70</td>
</tr>
</tbody>
</table>

Response = “a chase or display by the focal fish occurred” (n = 78; 20 events)
Hosmer-Lemeshow goodness-of-fit test: P = 0.799
Figure 2.4. Probability of the focal fish being chased or displayed at by an intruder for males and females while with their pairmate (solid bars) and while without their pairmate (open bars). See Table 2.6 for p-values.

Table 2.6. Results of binary logistic regression for the effects of site, sex, and presence of the pairmate on the probability of a chase or display by an intruder toward the focal fish

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Coefficient</th>
<th>Standard Deviation</th>
<th>Z</th>
<th>P-value</th>
<th>Odds Ratio</th>
<th>95% C.I.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-2.49</td>
<td>0.807</td>
<td>-3.08</td>
<td>0.002</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td>1.74</td>
<td>0.785</td>
<td>2.22</td>
<td>0.026</td>
<td>5.72</td>
<td>1.23 – 26.68</td>
</tr>
<tr>
<td>Sex</td>
<td>1.09</td>
<td>0.756</td>
<td>1.45</td>
<td>0.148</td>
<td>2.99</td>
<td>0.68 – 13.16</td>
</tr>
<tr>
<td>Pairmate</td>
<td>-2.97</td>
<td>1.115</td>
<td>-2.66</td>
<td>0.008</td>
<td>0.05</td>
<td>0.01 – 0.46</td>
</tr>
</tbody>
</table>

Response = “focal fish was chased or displayed at” (n = 78; 12 events)
Hosmer-Lemeshow goodness-of-fit test: P = 0.994
Pair Behavior

The amount of time pairs spent together on average was similar at the two sites. At Kahe Pt., pairs spent 69.4% (± 3.8) of the time within one meter of each other, while at Puako, pairs spent 61.6% (± 4.8) of the time together (T = 1.28, df = 15, p = 0.22). The behavior of the pairs was tightly coordinated, and they showed a very strong association between pairmates. Pairs spent much more time together than would be expected if they were moving about the territory independently of each other (T = 18.80, df = 18, p < 0.0005; Figure 2.5).

Figure 2.5. The relationship between territory size and the observed proportion of time a pair spent together (solid circles) and the predicted proportion of time a pair would spend together if pairmates moved independently of each other (open circles).
Both sexes actively maintained the pairbond. Males and females made a similar number of movements toward each other ($p = 0.34$; Figure 2.6). Females made many more movements toward the male than away from the male ($p = 0.0015$). Males showed a trend of making more movements away from the female than toward the female, but this difference was not statistically significant ($p = 0.09$). Males made significantly more movements away from the female than females made away from the male ($p = 0.0001$). During these away movements, males were often seen in territorial defense related activities. Thus, though both sexes were actively moving to maintain proximity within

![Figure 2.6. Mean movement rates in number of moves per minute of males and females both toward (solid bars) and away from (open bars) their pairmate. Error bars are standard errors.](image-url)
the pairbond, females appear to do more following than the male. Though females did do more following than the male, they often continued to feed and did not follow the male when he did move away.

The rate of movement toward the pairmate was inversely related to size ($p = 0.032$, Figure 2.7), with smaller fish making more movements toward their mate than larger fish. There was no difference in this relationship for the two sexes ($p = 0.521$).

![Figure 2.7. The relationship between fish size (x) and movement rates (moves/min.) toward the pairmate (y) by males (solid circles) and females (open circles), where $y = 1.78 - 0.016x$. There was no difference in the regression line for males and females.](image-url)
DISCUSSION

Traditional models for the evolution of social monogamy are not able to explain the social system of *C. multicinctus* (Table 2.1). One of the most common explanations for the evolution of monogamy is the need for biparental care in the raising of offspring (Wittenberger and Tilson 1980, Mock and Fujioka 1990). Butterflyfishes, however, are broadcast spawners meaning they release their gametes into the water column and show no parental care whatsoever. Therefore, this is not a possible explanation for the social system of *C. multicinctus*.

Social monogamy may also evolve when there is a high polygyny threshold. The polygyny threshold model (Orians 1969) is based on a system in which males establish territories, and then females choose among those males or their territories. Monogamy results if no male is able to hold a territory of sufficient size or quality to attract multiple females, thus a high polygyny threshold. This model, however, is insufficient for two reasons. First, in *C. multicinctus*, pairing seems to occur before the establishment of adult territories (Chapter IV), and so violates the assumption that female choice of established territorial males is driving the social system. Second, there is an approximately threefold difference in the size of territories and in the amount of food within territories at each of the two sites. If the polygyny threshold model holds for *C. multicinctus*, we would expect that the largest territories could support multiple females, but *C. multicinctus* is never seen in groups larger than two. The polygyny threshold has seemingly been surpassed, but polygyny is not seen. This then, is not a likely explanation for monogamy in *C. multicinctus*. 
A third model for the evolution of monogamy was proposed by Emlen and Oring (1977). This model assumes that the distribution of resources determines the distribution of females. Males then distribute themselves according to the dispersion of females. Their ability to monopolize females determines the social system. Anything that limits the ability of a male to monopolize more than one female leads to monogamy. This can occur for three reasons. 1) When females are territorial, they become spread out over the habitat making it difficult for a male to defend a large enough area for multiple females. However, since nearly all the aggression shown by females was toward other females and only when the male was present, aggression by the female seems to be related to defense of the male rather than defense of the territory. Territorial defense by females then would not be a factor that limits the ability of males to monopolize females. 2) When females are found in absolute low densities, this can limit the ability of a male to monopolize multiple females. C. multicinctus is one of the most common butterflyfishes in Hawai‘i, however, and is certainly very abundant anywhere coral is found. Therefore, the absolute densities of C. multicinctus would not seem to limit this species to monogamy. 3) When spawning is synchronized, this may limit the ability of one sex to find and mate with multiple members of the opposite sex and could limit a species to monogamy (Knowlton 1979, Neudecker and Lobel 1982). Butterflyfishes do spawn at dusk, and this could be a factor that might potentially limit them to monogamy. However, Fricke (1986) and Colin (1989) reported little spawning synchrony among nearby pairs. In addition, other butterflyfish species (as well as many non-butterflyfish species) that spawn at dusk are not precluded from having other social systems. C. trifascialis spawns at dusk and forms harems (Yabuta and Kawashima 1997), and C. fremblii also forms harems but spawning
has not been observed (Hourigan 1989). Therefore, this too is an unlikely explanation for the presence of monogamy and strong pairbonds in *C. multicinctus*.

Because these three traditional models cannot account for the social system of *C. multicinctus*, I tested four other hypotheses that have been offered to explain the social system in monogamous butterflyfishes (Table 2.2). 1) Social monogamy may result if a pair of fish could defend a territory more efficiently than a solitary fish (Barlow 1984, Roberts and Ormond 1992). This only works, however, when both fish patrol the territory independently of each other and assumes that those solitary fish could repel an intruder as well as a pair. *C. multicinctus* is very strongly pairbonded, and they do not move about the territory independently. Furthermore, Hourigan (1987, 1989) found that males were successfully able to defend a territory when the female was removed and that his feeding rates were unaffected and even increased in some instances. The need for two fish to defend a territory would therefore not seem to be a factor in the evolution of social monogamy. 2) Pairbonding may result if two fish make a more effective territorial ownership signal than a solitary individual (Fricke 1986). The strong pairbonds seen in *C. multicinctus* are consistent with this hypothesis. Territorial intrusions, on the other hand, were more likely against a pair of fish than against a solitary fish, which would argue against this hypothesis. However, since chasing often consisted of two fish chasing each other back and forth over a territorial boundary, the increased probability of being chased while paired could be due simply to the correlation between chasing and being chased and the higher chase rates while with the pairmate. The fact that males were able to defend a territory without the mutual signal of a female (Hourigan 1987, 1989) does not support this hypothesis. 3) If the formation of a pairbond allows the female to feed
more, thus producing more eggs, and the male to participate in this increased reproductive output, then social monogamy may arise as the byproduct of selection for pairbonding. When with their pairmate, females did feed more, but were also more likely to be involved in aggression as well. Males showed higher probabilities of aggression, both overall and while with their pairmate. Males had lower overall feeding rates at Kahe Pt. but not Puako, and also fed at higher rates when with their pairmate. Thus, the increased feeding rates of both sexes would argue for the formation of the pairbond, but the data on aggression is more equivocal. Lower female aggression and higher male aggression is consistent with this hypothesis, but increased female aggression when the male is present is not expected. 4) If both sexes guarded their mates, then social monogamy and possibly a strong pairbond would be the result. As expected, both sexes showed higher probabilities of aggression when their mate was present, and both sexes restricted almost all their aggression to same sex individuals (Hourigan 1989). Females made many more movements toward their mate than away from. Males made a similar number of movements toward the female as the female made toward the male. This is consistent with both sexes showing mate guarding behavior. However, males did show a trend toward making more movements away from the female than toward. During many of these movements away from the female, the male was often observed to chase an intruder or patrol the territory. Males then would seem to still be showing mate guarding behavior, as evidenced by males and females having a similar number of movements toward the pairmate, but they are also showing territorial defense, which leads to more away movements. Lastly, smaller individuals did show higher rates of movement toward the mate, which is consistent with the idea that larger fish are a more valuable resource.
and should be defended more vigorously. Furthermore, increased aggression by the pair or by the male was not correlated with larger territory sizes or relatively higher coral cover within the territory. The differences in aggression, then, seem to be related less to territorial defense than to mate defense. Taken together, these data show strong support for mutual mate guarding by *C. multicinctus*.

The evidence supports, at least partially, both the feeding advantage hypothesis and the mate guarding hypothesis. Both sexes gain a feeding advantage while with their pairmate which provides a selective advantage for the socially monogamous pair to form a pairbond. So the feeding advantage hypothesis most likely applies to the formation of a pairbond. Females were involved in more aggression when with the male, which argues against the feeding advantage hypothesis, but for the importance of mate guarding in controlling the social system of *C. multicinctus*. Mutual mate guarding results in a socially monogamous pair. Both sexes acted to maintain proximity in the pairbond, aggression by both sexes was higher when the pairmate was present, and aggression was limited to same sex individuals.

**Social Monogamy and Mate Guarding**

The fact that both sexes attempt to form bigamous social relationships when neighboring individuals are removed (Hourigan 1987, 1989), would seem to indicate that selection pressures are not actively favoring social monogamy. *C. multicinctus* defends large territories relative to its body size and spends most of its daily time budget in feeding activities (Tricas 1989a). This leaves little time for attempting to defend two territories. The mate guarding behavior by both sexes represents the strongest proximate
constraint that limits each sex to social monogamy. The increased aggression shown while with the mate and the fact that increased aggression levels did not lead to larger territories or territories with more coral in them strongly suggests that this aggressive behavior is related to mate guarding. In addition, the fact that nearly all aggression shown by females was only in the presence of her pairmate (only one instance of aggression was observed by a lone female in this study, and only one instance out of 71 was observed by Hourigan (1987)) would argue against female aggression being important in territorial defense. Males, on the other hand, did show high levels of aggression when the female was absent. This indicates that aggression in males is important both for mate guarding and territorial defense purposes.

Fricke (1986) suggested mutual partner guarding in *C. chrysurus* (= *C. paucifasciatus*) as an explanation for monogamy, but he did not state any benefit that either sex may gain by guarding their mate. Hourigan (1987, 1989) found that in two species of coral-feeding butterflyfish (*C. multicinctus* and *C. quadrimaculatus*), when a female pairmate was removed, males were able to retain their territories alone with no decrease in feeding rates. Though these studies were short term, the males never lost a territory while solitary, showed very little alteration in their behavior, and showed no signs that they might eventually lose the territory. When the male pairmate was removed, however, the females suffered drastic drops in feeding rates and eventually lost the territory if they did not re-pair. In addition, the fact that females do not normally show aggression except when with their mate further supports that females are not involved in territorial defense. So it would seem that the female guards the male for access to the territorial resources. The male and his territorial defense, then, are resources that the
female defends. Kokita and Nakazono (2001) found that for the monogamous longnose filefish, female reproductive success was reduced when she mated with the occasional polygynous male. This was due to the lower territorial defense effort per territory by polygynous males. Male *C. multicinctus* are likely guarding females for access to a mate and the increased fecundity that results from the female feeding on the territory with him. The increased feeding rates of each sex when with the pairmate along with female defense of a male’s territorial defense abilities results in the maintenance of this social system throughout the year. Like the tropical house wren (Freed 1987), mate guarding and few opportunities for switching mates are constraints that also maintain social monogamy throughout the year as well as from year to year.

Reavis and Barlow (1998) found a similar social system in a goby with paternal care. Males were primarily responsible for burrow construction and maintenance and all males had a burrow. Both sexes mate guarded which led to social monogamy. Females that were paired with large males fed at higher rates and burrowed less. Burrows were maintained and spawning occurred year round.

Nearly all butterflyfishes that feed on coral are territorial and socially monogamous (Reese 1975, 1991; Tricas 1985; Hourigan 1989; Roberts and Ormond 1992). In addition, many of the territorial omnivorous species are monogamous as well. Roberts and Ormond (1992) argued that because of the tight correlation between the occurrence of territoriality and social monogamy, that monogamy must have evolved for the purposes of improved territorial defense. However, correlation does not prove causation. For *C. multicinctus*, and possibly many other coral-feeding species, social monogamy has evolved by way of mate guarding and not improved territorial defense.
**Pairbonding**

Because social monogamy is not synonymous with pairbonding, there must be some benefit accrued by a socially monogamous pair of fish to put the energy into maintaining proximity. In the case of *C. multicinctus*, we see that they spend much more time very close to each other than would be expected by chance. They are making a rather exceptional effort to maintain their strong pairbond. Both sexes of *C. multicinctus* fed at higher rates when the pairmate was present. This provides a selective advantage for a monogamous pair to then form a strong pairbond. It also provides another advantage for pairs to guard one another. The feeding advantage gained from feeding with the pairmate is similar to the courtship feeding seen in many bird species (e.g., Helfenstein *et al.* 2003). Food that the male brings to the nesting female increases egg production by the female, and thus the reproductive success of both members of the pair. This hypothesis might also be applied to non-territorial species if the male spends more time in other behaviors such as predator vigilance rather than in territorial defense. This has been demonstrated in a lizard in which females showed faster responses to predators when with a male (Bull and Pamula 1998).

Hamilton (1990) suggested that bright coloration in monogamous species serves as a quick advertisement of health when health cannot be assessed more closely and is used to attract distant mates for extra-pair copulations. Staying close together, then, may also be a signal to counter a pairmate’s attempt to attract multiple mates. Since attempts at sneak spawnings have been observed in *C. multicinctus* (Hourigan 1987, Lobel 1989), females may attempt to attract male sneakers at times when she is ready to spawn. Males, on the other hand, may try to attract females throughout the breeding season.
The increased probability of a focal fish being chased by a neighbor while with its mate would seem to argue against the formation of a pairbond. However, there was a correlation between chases by the focal fish and chases against the focal fish as they chased each other back and forth across territorial boundaries. This combined with the fact that aggression rates were higher with the mate present results in the increased probability of a focal fish being chased when with its mate.

The data do not completely rule out that the formation of a pairbond could act as a mutual signal of territorial ownership. Several authors have noted the importance of passive advertisement rather than overt aggression in the maintenance of territories (Reese 1975; Tricas 1985, 1989a). However, given that males in two coral-feeding species were able to defend a territory without a mutual signal (Hourigan 1989) and that females do not seem to be much involved with territorial defense, it does not seem likely that the need for a mutual signal is a key selective pressure driving the formation of a pairbond. The mate guarding behavior and the increased feeding rate while with the pairmate must be stronger factors in the evolution of a pairbond. The pairbond may still act as an improved signal, but this is likely a side effect of the pairbond rather than a cause of its evolution.

Fricke (1986) found that in *C. chrysurus*, both sexes were unable to maintain a territory when the pairmate was removed. Thus, the need for a mutual signal might be more important in this species. *C. chrysurus* is an omnivore, and so the nature of territorial defense is likely to be different from territorial defense in a corallivore, with corals being an evenly distributed, nutritionally poor resource (Tricas 1985, 1989b). Fricke (1986) did acknowledge that his mutual signal hypothesis does not explain why
some polygamous group would not make a more effective signal and thus result in a larger group size. In addition, though it could explain the presence of a pairbond, it does not explain why social monogamy would have evolved in the first place.

**Pairbond Maintenance**

Males and females made a similar number of movements toward their mate showing that both pairmates were actively maintaining the pairbond. This would be expected if both sexes were guarding their mate. Females made many more movements toward the male than away from. She basically followed the male around the territory. Though males made a similar number of movements toward the female as females made toward the male, males did make many more movements away from the female. Frequently, when the male was observed to swim away from the female, he was seen patrolling the territory or chasing an intruder. Thus, these data are consistent with the feeding and aggression data that show that males guard their mates, but in addition, also show territorial defense aggression.

Females showed more following behavior than the male, but they were also frequently seen to continue feeding rather than follow the male when he did move away. This points to the importance of feeding behavior to the female in addition to her mate guarding behavior and is consistent with the feeding advantage hypothesis.

**Is Social Monogamy Mutually Beneficial or Constrained?**

The access to a territory and the higher feeding rates while with the male make pairbonding beneficial to the female. The increased fecundity of a female that feeds on
his territory and his own increased feeding rates while with a female make pairbonding beneficial to the male as well. This mate guarding and pairbonding behavior though, are proximate constraints on the evolution of a social system other than monogamy. The question remains whether social monogamy is selected for and is mutually beneficial to males and females, or whether some other social system may be more favorable to one sex or the other but they are limited by proximate constraints.

The fact that both sexes mate guard, both gain an increased feeding rate while with their pairmate, and both act to maintain the pairbond might suggest that the social system of *C. multicinctus* is mutually beneficial. That one sex or both is constrained to monogamy is supported by the fact that pairing with a new mate occurs very rapidly, often within an hour, after the removal of a pairmate (personal observation) and that when a pairmate is removed, neighbors often attempt to form a bigamous group with the widowed fish, though this is never successful (Hourigan 1987, 1989). Pairbonding, then, might represent a ‘best of a bad situation’ tactic given that an individual is limited to social monogamy. Establishing a pairbond allows each sex to feed more and also increases the female’s fecundity within the constraints of social monogamy.

For males, in order to distinguish between these two situations, we would have to measure the reproductive success of males that have two females on their territory and compare it to the reproductive success of males with one female. Presumably, if the male is bigamous, he is less able to devote as much time to the territorial defense of each female. Growth rates of multiple females may be reduced if the male spends less time with each (Hourigan 1989, Kokita and Nakazono 2001). Therefore, two females might not gain a large feeding advantage, whereas a single large female might. Since natural,
stable bigamous relationships are unknown, we cannot measure reproductive success directly. Tricas (1986), however, generated a size-fecundity relationship for *C. multicinctus*. As can be seen in Figure 2.8, it would take a female that is approximately 6.9% longer to equal the reproductive output of two smaller fish. Therefore, if having only a single female on a male's territory allows her to grow about 7% larger, then social monogamy is beneficial to males. Otherwise, it would seem that males are being

![Figure 2.8](image_url)

**Figure 2.8** – The relationship between female size and fecundity in *Chaetodon multicinctus* for a single fish (solid line) and for two fish of that same size (dotted line). Modified from Tricas (1986).
constrained to social monogamy and pairbonding represents a ‘best of a bad situation’ tactic. Answering this question would take very detailed knowledge of female growth rates and could perhaps only be done in captive studies.

For females, it seems unlikely that polyandry would give a large advantage. However, we could also look at the reproductive success of females that live on two males’ territories compared to the reproductive success of a female with one male. Again, direct measurements are not possible, but we may be able to answer this question with studies on the growth rates of females on different sized territories. Hourigan (1987) found that females from coral-rich territories produced more eggs than females from coral-poor territories. If female growth rates increase significantly with much larger territories, then females may be constrained to social monogamy. If female growth rates are not increased significantly, then social monogamy as well as pairbonding may be beneficial to females.

Conclusions

Males of C. multicinctus are primarily responsible for the defense of a pair’s feeding territory, while females tend to feed more. Females guard the male for access to his territory and possibly because polygyny may decrease her reproductive success. Males guard females to take advantage of their increased fecundity from feeding on their territory. Both sexes have increased feeding rates while with their mate. Thus, both sexes gain a selective advantage for forming a tight pairbond.
Whether social monogamy is evolutionarily advantageous to either sex depends on various aspects of the growth rates of females. It may be that, 1) selection for the mate guarding and pairbonding behavior of *C. multicinctus* outweighs any selective advantage to social bigamy and thus social monogamy results, or 2) if both sexes are constrained to social monogamy, then mate guarding and pairbonding behavior may be a 'best of a bad situation' tactic, or 3) social monogamy and pairbonding may both be beneficial.

Classical models for social systems have focused on the role of female choice of males or of male competition for females as primary determinants of the social system (Orians 1969, Emlen and Oring 1977). Recent work has pointed to the importance of female choice of territories and female territorial defense as factors influencing the social system (Arcese 1989, Davies 1992). This study points to the importance of female defense of males as a primary determinant of the social system in *C. multicinctus*. 
Mate Choice

Sexual selection is a form of natural selection in which competition for mating opportunities, as opposed to survival, can drive evolution (Darwin 1871). It can operate intrasexually, through competition among individuals of one sex for access to the other, or intersexually, through mate choice. Males and females produce different sized gametes, a condition known as anisogamy. Females produce large energetically expensive eggs and tend to increase their reproductive success by investing in the production of more or larger eggs and by providing parental care of those eggs. Males produce many more energetically inexpensive sperm and tend to increase their reproductive success by competing with other males for access to multiple females. Because of the different tactics used by males and females and the different types of investments they make in reproductive success, sexual selection acts on them differently (Williams 1966, Trivers 1972). Females typically make the larger investment in offspring and so are choosier about whom they mate with. Males tend to be less choosy about their mates because they have a lower energetic investment in each mating.
In general, the sex that invests more in reproduction is choosy about its mates, while the other sex is less choosy and competes intrasexually for mating opportunities (Trivers 1972). Though typically, the female invests more and is choosier, in sex-role reversed species, males invest more and are choosier, while females compete for access to males (Berglund and Rosenqvist 2001).

In the case of monogamy, there is less variance in reproductive success for sexual selection to act upon, and therefore might be assumed to be weak or unimportant. However, even Darwin (1871) recognized that sexual selection could still act in monogamous species when there are differences in the timing of breeding, differences in mate quality, or with skewed sex ratios (see Andersson 1994 for a review). Because monogamous species are often physically monomorphic, again sexual selection is presumed to be weaker in monogamous species. Physical monomorphism, though, may be the result of weak sexual selection or of similar levels of sexual selection acting on both sexes. Even when there is weak sexual selection on physical characters, it may still produce large differences in behavior between the sexes (Andersson 1994). Burley (1981) defined sexual indistinguishability as the lack of morphological cues which identify sex. There can be behavioral differences, though, as long as they are not continuously displayed. She suggested that indistinguishability evolve in socially monogamous species to avoid sexual competition from neighbors.

In monogamous species, males and females often have similar levels of investment in offspring and are therefore expected to have similar levels of choosiness (Rogers and Barlow 1991). Choosiness, however, should be correlated with the levels of investment rather than the mating system (Trivers 1972). Male mate choice has been
shown to be both present (Riechert and Singer 1995) and absent in monogamous species (Rogers and Barlow 1991), as well as present in polygynous species (Sargent et al. 1986).

The first goal of this study is to examine both male and female mate choice in relation to size. *Chaetodon multicinctus* is both socially and genetically monogamous, and for these reasons, we might expect to see equal choosiness by both sexes (Table 3.1). In addition, individuals pair assortatively by size with the larger males paired with the larger females and smaller males paired with smaller females. This could indicate an equal preference by both sexes for larger pairmates. Lastly, there is very little size dimorphism in this species, which suggests similar levels of choosiness by both sexes.

Table 3.1. Hypotheses, assumptions, and predictions for mate choice

<table>
<thead>
<tr>
<th>Hypotheses:</th>
<th>Assumptions:</th>
<th>Predictions:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Classical Mate</td>
<td>The reproductive success of females increases with larger mate size</td>
<td>Only females will spend more time with the larger stimulus fish</td>
</tr>
<tr>
<td>Choice</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Monogamous Mate</td>
<td>The reproductive success of both males and females increases with larger mate size</td>
<td>Both sexes will spend more time with the larger stimulus fish</td>
</tr>
<tr>
<td>Choice</td>
<td></td>
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</tbody>
</table>

Several lines of evidence, however, suggest that mate choice and monogamy are not typical in *C. multicinctus*. It appears that *C. multicinctus* begins pairing soon after arriving on the reef and before sexual maturity (Chapter IV, Tricas and Hiramoto 1989). Given the long-term pair bonds in this species, this may limit the ability for mate choice to be expressed. Though they are monogamous, they appear to be constrained to
monogamy by mutual mate guarding (Chapter II). Given the opportunity, both sexes will attempt polygamy, though this situation is never stable for more than a few days (Hourigan 1989). Despite being monogamous, since there is no paternal care, females likely have a larger investment in the offspring due to their higher gametic investment, and so might be expected to be choosier (Table 3.1). Lastly, though they show little size dimorphism, males show higher aggression rates and lower feeding rates than females. This difference could be the result of sexual selection acting through stronger female choosiness.

Assortative Mating

In assortative mating, organisms that share some phenotype such as size, age, or color tend to mate with each other. This can lead to divergence within the population and the creation of polymorphisms or eventually to speciation (e.g., Schliewen et al. 2001). In butterflyfishes, assortative mating can be based on coloration, but some species may still interbreed regardless of color differences (McMillan et al. 1999). In positive size assortative mating, large males mate with large females and small males mate with small females.

Though many selective pressures act to determine animal size, Darwin (1871) first suggested that sexual selection might be important in driving the evolution of size. This can result either through intrasexual competition, with large individuals of one sex preventing access by small individuals to large individuals of the other sex, or through intersexual mate choice, with large individuals showing a preference for large mates (Andersson 1994). Whether by competition or choice, assortative mating may result
from mutual preferences for larger mates or by just one sex if that sex is able to enforce its preference on the sex. Basolo (2004) found that in a poeciliid fish, there was variation between the sexes in the type of preference shown, with females preferring larger males and males preferring females that were similar in size.

The second goal of this study is to describe the assortative mating pattern in *C. multicinctus* and to examine the selective pressures that produce that pattern. However, because we are not actually observing mating, this chapter is actually examining assortative pairing rather than assortative mating. Pairing in this case though, is a good approximation of mating since pairmates spawn with each other (Hourigan 1987, Lobel 1989).

Assortative mating in *C. multicinctus* may be the result of either sexual or non-sexual selection (Table 3.2). If both sexes prefer a larger mate, then an assortative mating pattern will be seen. Males may prefer larger females due to increased fecundity (Tricas 1986), whereas females may prefer larger males due to increased territory quality or genetic benefits. Similarly, if both sexes prefer a mate that is similar in size, then an assortative mating pattern will be seen. Basolo (2004) suggested that a preference for a similar sized mate, as opposed to the largest possible mate, would be favored by avoidance of intrasexual competition. An assortative mating pattern might also be driven by females only, if they could then enforce that preference on males. Females may show intersexual mate choice for larger or similar sized males, or intrasexual competition for those same males. They could then enforce that preference on males by driving away any other females from that male. Because males are site-attached and are primarily responsible for defense of the pair's territory (Chapter II), they probably could not
Table 3.2. Hypotheses, assumptions, and predictions for assortative mating

<table>
<thead>
<tr>
<th>Hypotheses:</th>
<th>Assumptions:</th>
<th>Predictions:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mutual preference for larger mates</td>
<td>The reproductive success of both males and females increases with larger mate size</td>
<td>Both sexes will spend more time with the larger stimulus fish</td>
</tr>
<tr>
<td>Mutual preference for similar sized mates</td>
<td>The reproductive success of both males and females increases with similar mate size</td>
<td>Both sexes will spend more time with the similar sized stimulus fish</td>
</tr>
<tr>
<td>Female only preference for larger or similar sized mates</td>
<td>The reproductive success of females increases with a larger or similar sized mate</td>
<td>Only females will spend more time with the larger or similar sized stimulus fish</td>
</tr>
<tr>
<td></td>
<td>The largest females are able to enforce their preference or get first choice</td>
<td></td>
</tr>
<tr>
<td>Female only competition for larger or similar sized mates</td>
<td>The reproductive success of females increases with a larger or similar sized mate</td>
<td>Only females will spend more time with the larger or similar sized stimulus fish</td>
</tr>
<tr>
<td></td>
<td>The largest females are able to enforce their preference or get first choice</td>
<td>Female-female aggression will be high</td>
</tr>
<tr>
<td>Male only preference for larger or similar sized mates</td>
<td>The reproductive success of males increases with a larger or similar sized mate</td>
<td>Only males will spend more time with the larger or similar sized stimulus fish</td>
</tr>
<tr>
<td></td>
<td>The largest males are able to enforce their preference or get first choice</td>
<td></td>
</tr>
<tr>
<td>Male only competition for larger or similar sized mates</td>
<td>The reproductive success of males increases with a larger or similar sized mate</td>
<td>Only males will spend more time with the larger or similar sized stimulus fish</td>
</tr>
<tr>
<td></td>
<td>The largest males are able to enforce their preference or get first choice</td>
<td>Male-male aggression will be high</td>
</tr>
</tbody>
</table>

58
Table 3.2. (Continued) Hypotheses, assumptions, and predictions for assortative mating

<table>
<thead>
<tr>
<th>Hypotheses:</th>
<th>Assumptions:</th>
<th>Predictions:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-sexual selection</td>
<td>Pairing takes place within cohorts</td>
<td>Large size differences between pairmates will be rare</td>
</tr>
<tr>
<td></td>
<td>Cohorts from different years are different in size</td>
<td>No clear mate preferences will be seen</td>
</tr>
</tbody>
</table>

prevent a smaller male on another territory from pairing with a female or prevent a female from choosing another male. Therefore, it seems unlikely that an assortative mating pattern could be due to a male preference alone since they could not then enforce that preference. Lastly, an assortative mating pattern could be the result of a non-sexually selected mechanism. *C. multicinctus* has distinct recruitment seasons (Walsh 1987). At one year of age, they are approximately 70% of maximum size, and at two years, they are approximately 90% of maximum size (Tricas 1986). Within a few months of arriving on the reef, the juveniles begin pairing up with other juveniles. By the next recruitment season, all the fish from the previous year’s cohort are much larger, but are still distinctly smaller than two-year-old fish. After two years, the differences among cohorts are small, but may still be reflected in the assortative mating pattern.

Alternatively, it might be argued that this could be interpreted as a result of sexual selection if juveniles and first year fish are prevented from pairing with larger fish by competition or choice. Adult *C. multicinctus* are very aggressive toward juveniles, however, both sexes are aggressive towards all juveniles, and so this aggression is likely related to territorial defense rather than being sexually selected aggression.
METHODS

Experimental Design

*C. multicinctus* were collected from the wild as pairs. They were housed with their pairmates in sections (70 cm x 40 cm x 40 cm) of a larger tank (360 cm x 67 cm x 40 cm) and received fresh coral food several times a week. The sections did not allow for visual contact, but water flow between sections may have allowed for chemical contact. Experiments were performed in a separate large tank (360 cm x 67 cm x 40 cm) divided into three sections – a larger middle section (220 cm x 67 cm x 40 cm) and two smaller sections (70 cm x 67 cm x 40 cm) on either end (Figure 3.1). These sections were separated by a large mesh (3 cm x 3 cm) barrier that allowed for maximal contact between fish without allowing them to cross into the other section. The middle of the three sections was further divided into three subdivisions by two vertical lines drawn on the outside of the tank at 50 cm from either end section.

![Figure 3.1. Experimental mate choice tank set up. Tank is drawn to scale, but fish are approximately 2x scale. The centermost section had coral and shelter in the middle for the test fish that did not block its view of either end. Each end section had a small amount of coral and shelter that the stimulus fish could use but would not block viewing by the test fish. The 50 cm sections in front of each end section were bare.](image-url)
An experimental run consisted of placing a test fish in the middle section of the large tank. An artificial cinder block shelter and several coral heads were placed in the center (120 cm) subdivision of this middle section. The test fish was given one hour to acclimate, during which it spent most of the time in the shelter and around the coral heads. A 15-minute pre-trial run was then performed and the time spent in each subdivision was measured.

Following this, two stimulus fish of different sizes and of the opposite sex of the test fish (but not its pairmate) were placed one in each of the two end sections, with the side being determined by coin toss. In the end sections were small shelters and a small coral head, but nothing that might have impeded the view of the stimulus fish by the test fish in the center section. The experimental trial began immediately upon putting the stimulus fish in the end sections, and two 15-minute trials were run. A trial consisted of measuring the amount of time the test fish spent in the two 50 cm subdivisions next to each end section. Also, the number of times the test fish swam from the center subdivision into the 50 cm subdivisions on either end (= visits) was also noted. Data from the two experimental trials were averaged.

Any movement away from shelter and food and across the open area of the tank was considered to be a reaction to the stimulus fish because of the relatively long distance over exposed areas of the tank from the shelter to either end section (75-100 cm) and because with no stimulus fish present, the test fish spent most of its time next to the shelter and the coral. During a trial, all fish were observed for any unusual behavior such as swimming very rapidly from end to end without stopping or inspecting the stimulus fish or any unresponsive behavior such as not leaving the center shelter. If any of the test
or stimulus fish were not being responsive or if the test fish did not make at least one visit to each end, the trial was discarded. In a typical trial, the test fish reacted almost immediately after the stimulus fish were placed in the tank by leaving the shelter or swimming towards one of the stimulus fish. Whenever the test fish approached one of the end sections, it and the stimulus fish in that section often swam back and forth along the mesh barrier.

In order to test the validity of this design, the amount of time the test fish spent in the sheltered center subdivision during the pre-trial was compared with the amount of time it spent in the center subdivision during an experimental trial. Any difference must be due to the presence of the stimulus fish in the tank and the test fish reacting to them. If there is no difference, then the time spent next to either end section could be considered exploratory behavior rather than a preference for that stimulus fish. In addition, several trials \( n = 6; 4 \) females, 2 males) were run that were designed to create the conditions most favorable to an expression of choice. This was done by following the same procedures as above, but using the pairmate of the test fish and a heterospecific butterflyfish, \( C. fremblii \) as the stimulus fish. \( C. fremblii \) is a non-coral feeding species that is not known to interact aggressively with \( C. multicinctus \) in the wild. If the test fish does not spend more time next to its own pairmate, this is likely not a valid design.

For the mate choice analyses, a two-tailed paired t-test was used to compare the amount of time the test fish spent in the two 50 cm subdivisions next to each end section as well as the number of visits to each end section. To test whether a size assortative mating pattern is the result of a preference for similar sized mates, the previous mate choice data were reanalyzed with the stimulus fish categorized as either closer or farther
in size compared to the test fish. If selection is acting on some trait, then the variability in that trait should be reduced. To examine this, I performed an F-test to compare the variance in the time difference spent with the two stimulus fish by males and females. I also performed the F-test for the difference number of visits to either stimulus fish.

The data on size assortative mating came from 69 wild-caught pairs that were collected both for this study and for other studies. Where sex could not be determined by behavior or an abdomen obviously swollen with eggs, sex was determined by dissection. Fish were measured to the nearest 0.5 mm standard length.

RESULTS

Experimental Design Validation

The test fish spent statistically significantly more time (mean ± SE) in the sheltered center subdivision during the pre-trial periods (9.95 min ± 0.75, n = 45) compared to the experimental trial periods (6.73 min ± 0.61, n = 38) (two-sample T = 3.33, p = 0.001, df = 79) indicating a reaction by the test fish to the presence of the stimulus fish. The test fish spent statistically significantly more time in the subdivision next to their pairmate (2.83 min ± 0.58) compared to the subdivision next to C. fremblii (0.63 min ± 0.20) (paired-T = 4.04, p = 0.01, n = 6). All six fish, regardless of sex, spent more time in the subdivision next to their pairmate. The test fish visited the subdivision next to their pairmate (14.0 visits ± 4.19) more often than the subdivision next to C. fremblii (7.0 visits ± 2.62) (paired-T = 2.21, p = 0.078, n = 6), but this difference was not quite statistically significant.
Mate Choice I – Larger vs. Smaller Mates

Males spent statistically significantly more time in the subdivision next to the larger of the two female stimulus fish (Fig. 3.2). There was no statistically significant difference in the number of visits to the two subdivisions by males (Fig. 3.3). Females, on the other hand, did not spend statistically significantly more time in the subdivision next to either of the two male stimulus fish (Fig. 3.4). There was also no statistically significant difference in the number of visits to the two subdivisions (Fig. 3.5). No aggression between any of the fish was observed in any of the mate choice trials.

Males showed significantly less variability in the difference in time spent with the larger stimulus fish versus the smaller stimulus fish than females showed (Male $\sigma = 1.37$, Female $\sigma = 3.86$, $F$-test $= 7.940$, $p < 0.0005$). The difference was not statistically significant for the number of visits (Male $\sigma = 4.26$, Female $\sigma = 2.51$, $F$-test $= 2.880$, $p = 0.074$).

In the male mate choice experiments, the mean size difference between the two female stimulus fish was 4.64 mm ($\pm 0.41$), which represents a 5.37 % ($\pm 0.49$) difference relative to body size. In the female mate choice experiments, the mean size difference between the two male stimulus fish was 6.94 mm ($\pm 0.471$), which represents an 8.44 % ($\pm 0.94$) difference relative to body size. In none of the experiments did the size difference between the stimulus fish or the proportional size difference statistically significantly correlate with time spent in the subdivision next to either stimulus fish ($p > 0.25$ for all analyses) or with the number of visits to either subdivision ($p > 0.10$ for all analyses).
Figure 3.2. Time spent by test male next to the larger or smaller females. Mean (± SE) time difference = 0.872 min (± 0.354), 95% C.I. (0.112, 1.631). Paired-T = 2.46, p = 0.027, n = 15.

Figure 3.3. Number of visits by test male to the larger and smaller females. Mean (± SE) difference = 0.62 visits (± 1.10), 95% C.I. (-1.74, 2.98). Paired-T = 0.56, p = 0.582, n = 15.
Figure 3.4. Time spent by test female next to the larger or smaller males. Mean (± SE) time difference = 0.34 min (± 1.07), 95% C.I. (-1.99, 2.68). Paired- T = 0.32, p = 0.755, n = 13.

Figure 3.5. Number of visits by test female to the larger or smaller males. Mean (± SE) difference = 0.654 visits (± 0.697), 95% C.I. (-0.864, 2.172). Paired-T = 0.94, p = 0.366, n = 13.
Mate Choice II – Closer vs. Farther

Males did not spend statistically significantly more time in the subdivision next to the female that was closer in size to the male (Fig. 3.6). They also did not make statistically significantly more visits to that side (Fig. 3.7). Likewise, females did not spend statistically significantly more time in the subdivision next to the male that was closer in size to the female (Fig. 3.8), though there was a statistically non-significant trend to make more visits to that side (Fig. 3.9). Again, the size difference between the two stimulus fish did not statistically significantly correlate with the time spent in either subdivision (p > 0.10 for all analyses) or with the number of visits to either subdivision (p > 0.55 for all analyses).

Assortative Mating

There was a very strong statistically significant correlation between the size of the male and the size of the female in a pair (Fig. 3.10). The male of the pair was only slightly but statistically significantly larger than the female of the pair (Fig. 3.11). In nine of these pairs, the male was more than five mm longer than the female, and in five of these nine, the male was more than 10 mm longer. Two of these five males were the largest of the 69, and all were among the 12 largest. In only two of the pairs, was the female more than 5 mm larger than the male.
Figure 3.6. Time spent by test male next to the closer or farther in size females. Mean (± SE) time difference = 0.241 min (± 0.363), 95% C.I. (-0.538, 1.021). Paired-T = 0.66, p = 0.517, n = 15.

Figure 3.7. Number of visits by test male to the closer or farther in size females. Mean (± SE) difference = 1.392 visits (± 0.989), 95% C.I. (-0.730, 3.514). Paired-T = 1.41, p = 0.181, n = 15.
Figure 3.8. Time spent by test female next to the closer or farther in size males. Mean (± SE) time difference = -1.06 min (± 1.03), 95% C.I. (-3.31, 1.19). Paired-T = -1.03, p = 0.325, n = 13.

Figure 3.9. Number of visits by test female to the closer or farther in size males. Mean (± SE) difference = -1.19 visits (± 0.634), 95% C.I. (-2.57, 0.19). Paired-T = -1.88, p = 0.085, n = 13.
Figure 3.10. Size of male and female pairmates. Each point represents one pair. Dashed line represents equal sized pairmates.

Figure 3.11. Size of male and female pairmates. Mean size (± SE) difference = 1.40 mm (± 0.56), 95% C.I. (0.286, 2.505). Paired-T = 2.51, p = 0.014, n = 69.
DISCUSSION

Experimental Design and Statistical Power

In trials where fish did not show a preference, it is necessary to confirm that the lack of a preference is real, rather than the result of an inappropriate design or a lack of statistical power (i.e., Type II error). Several lines of evidence support the validity of this experimental design in demonstrating preference behavior. First, when the test fish was in the tank alone, it spent most of its time in or around the shelter. An increase in the amount of time spent next to each end section when stimulus fish were introduced indicates that the test fish can detect the presence of the stimulus fish, and that the time the test fish spent in those sections is not simply exploratory behavior. Furthermore, the fact that test fish spent more time next to their pairmates rather than a heterospecific butterflyfish indicates that they are not reacting simply out of curiosity to the presence of a new fish in the end sections, and also that they respond differently to different fish in the end sections. Thus, this is a valid design for detecting preference behavior in *C. multicinctus*.

If the size difference between the two stimulus fish was not large enough for the test fish to detect, this would not allow for the demonstration of preference behavior by the test fish. The mean size difference between the two female stimulus fish was 4.64 mm and the male test fish showed a preference. For females though, the mean difference between the male stimulus fish was larger (6.94 mm), but they still did not show a preference. Therefore, either females prefer larger males but are not as good as males at discriminating sizes, or they are able to discriminate between the sizes of the stimulus
fish but do not have a preference. The lack of a correlation between the size difference of the stimulus fish and the amount of time spent next to (or visits to) any section, further supports that the degree of size difference between the two stimulus fish was not a factor for either sex. Thus, the fact that they were different in size seems to be the relevant factor, not the magnitude of that size difference.

Following Colegrave and Ruxton (2003) and Nakagawa (2004), I reported the 95% confidence interval for the results of paired-T tests, rather than the statistical power. They argue that post hoc power analyses can be misleading and offer no more information than the p-value. They suggest that looking at the size of the confidence interval is more informative. Though the confidence intervals in experiments with females tended to be larger than with males, this was not always the case. Nor was it the case that the only statistically significant result had the smallest confidence interval. The fact that there was a detectable significant difference in the amount of time males spent next to a large and small female by itself indicates that there was enough statistical power to detect a difference with this experimental design. Only in the trial of female preference for closer and farther sized males did the 95% confidence interval for the difference in the number of visits approach zero. For all other negative results, there was a high p-value and a confidence interval that was not close to including zero.

Mate Choice and Sexual Selection

Males spent more time on the side of the tank next to the large female. Females on the other hand did not show any difference in the amount of time they spent next to large and small males. There were no significant differences in the number of visits to
either side by males or females. Hourigan (1987) described a courtship behavior in *C. multicinctus* and termed it 'leading.' During this behavior, one fish approaches another, and then swims away from it towards the middle of its territory, seemingly trying to induce the other fish to follow. It repeatedly swims towards, then away from the other fish. It may have been possible to use this leading behavior as a measure of preference, but the width of the subdivision next to each end section may have been large enough to contain the behavior within that subdivision. Thus, as the test fish was swimming away from, then back toward the stimulus fish, it never re-entered the subdivision. This would explain why the number of visits to each side did not indicate any preference. With a narrower subdivision next to each end section such that whenever the test fish swims away from the stimulus fish it leaves the subdivision and then re-enters it as it returns to the stimulus fish, it might be possible to use this leading behavior as an indicator of choice.

Female choice of mates is the typical pattern of sexual selection for most species, but in monogamous species, both sexes are predicted to show similar levels of mate choice (Trivers 1972, Rogers and Barlow 1991). In *C. multicinctus*, the data do not support either pattern. Only the males showed signs of mate choice. Tricas (1986) showed a very strong relationship between female size and fecundity in *C. multicinctus*, so it is not surprising that males show a preference for larger females. Males are primarily responsible for the defense of the territory, so if there is only one female on his territory, it would be beneficial for him to have the largest female possible.

Why don’t females show choice? A large male could presumably hold a larger or higher quality territory than a small male. Two explanations might account this pattern.
The first may be that females are in fact choosy, but choose based on some characteristic other than male size. This may be aggression, territory quality, or the winner of contests. Since females appear to guard males for their territorial defense abilities (Chapter II), aggression levels may be an important trait. Rogers and Barlow (1991) found that female cichlids preferred more aggressive males. Aggression was not controlled for in the current experiment, but aggression levels in *C. multicinctus* did not correlate with larger territory size or the amount of coral (Chapter II). There may be, however, some other aspect of territory quality that aggression correlates with. Females may also assess the size or quality of a territory directly, rather than the size of the male on that territory. This could be comparable to female birds assessing a male's quality based on the amount of courtship feeding (Helfenstein et al. 2003). Without a territory in the mate choice experiments, the female may be unable to assess the quality of the males. Hourigan (1987) found that when a female was removed from her territory and a female from another known territory switched into the vacated territory, the vacated territory had higher coral cover than the original territory. However, this was only true for one species of coral that made up a significant portion of their diet. In addition, his sample size was only four, so any conclusions from these data remain tentative. Freed (1991) found that when attempted territory takeovers occurred in tropical house wrens, residents did not defend their mate and accepted whoever was the winner of the contest. In *C. multicinctus*, females may not be concerned with which male is defending a territory, just that a male is defending the territory. If indeed, females do show mate choice based on some other characteristic (perhaps territory quality), then there would be mutual mate choice as is predicted for monogamous species. The different characteristics preferred by
each sex could explain the behavioral dimorphism seen in *C. multicinctus*—higher feeding rates for females and territorial defense by males (Hourigan 1989, Chapter II).

A second explanation for the lack of female choosiness in *C. multicinctus* might be sex role reversal. In the typical sex role pattern, females have a higher investment in each mating and are choosy about their mates, while males have a lower investment per mating, tend not to be choosy, and compete among themselves for access to females. In sex role reversal, males have the higher investment per mating and so are choosy about their mates, while females compete for mates. Several lines of evidence suggest a higher level of investment by males in *C. multicinctus*, which might explain the lack of choice shown by females and the choosiness shown by males. Males show significantly more aggression than females and have significantly lower feeding rates than females (Hourigan 1989, Chapter II). The increased costs of aggression and lowered benefits of feeding must be a significant investment by the male. Furthermore, female *C. multicinctus* are primarily responsible for maintenance of the pairbond. She makes many more movements toward the male than away from him, while there is a trend for males to make more movements away. It appears that females are competing with other females and guarding a male’s territorial defense capabilities as a resource (Chapter II).

If males prefer larger females, why hasn’t sexual selection produced females that are larger than males? It may be that intersexual selection is indeed favoring larger females, but the energetic investment in egg production slows her growth rates. It may also be that intersexual selection is favoring larger males indirectly if females prefer high quality territories and male size is correlated with territory quality; intrasexual selection may also favor large males if male size is correlated with territory quality. Tricas (1989a)
found that in some instances, male size did correlate with territory size, though this relationship does not always hold.

Though sexual selection has produced very little physical dimorphism in this species, behavioral dimorphism is likely the result of different levels and different types of sexual selection acting on each sex. Since both sexes will attempt polygamy (Hourigan 1987, 1989), and since males will attempt sneak spawnings (Hourigan 1987, Lobel 1989) that could potentially be induced by female behavior (Hamilton 1990), sexual competition appears to be high. Monomorphism may have evolved in *C. multicinctus* in an attempt to avoid this competition (Burley 1981).

**Assortative Mating and Sexual Selection**

There was a strong correlation between the sizes of male and female pairmates, indicating a size assortative mating pattern. Though the difference in size between the male and female was quite variable, males on average were 1.4 mm longer than females. This agrees with Hourigan (1987) and Tricas (1989a) who found that males were larger than females on average by 2.0 mm and 1.1 mm respectively.

Size assortative mating may be the result of sexual selection through either intersexual mate choice or intrasexual competition or it may be the result of a non-sexual selection mechanism. Because females did not show a preference for larger or similar sized mates, hypotheses involving mutual mate choice as the mechanisms producing assortative mating are not supported.

Size assortative mating could still be the result of sexual selection acting through one sex if that sex has a preference and the largest individual can enforce that preference
on the opposite sex and smaller individuals of the same sex. Females do not have a size preference, which rules out female only mate choice. Female competition for larger males could produce a size assortative mating pattern, but without a preference for a large male, it would appear that females are not competing for the largest male. The lack of preference for larger males, however, could be interpreted as a choice for both fish if the female is trying to defend both of them (though it doesn’t explain male preferences). A size assortative mating pattern, therefore, might still result from intrasexual competition among females if females compete for the highest quality territory and male size is correlated with territory quality (Tricas 1989a).

Males do show a preference for larger females, though not similar sized females, but it seems unlikely that a site-attached territorial male could prevent a female from pairing with another smaller male. Absent some female behavior, the males would not have a method of enforcing their preference. Similarly, without the ability to enforce their preference, male-male competition could not produce a size assortative mating pattern.

Alternatively, assortative mating could be the result of non-sexual selection processes. Due to distinct recruitment seasons, juveniles, one-year olds, and two-plus year olds have very distinct size distributions (Tricas 1986). Juveniles show pairing behavior soon after arriving on the reef and this associative behavior is primarily limited to other juveniles (Chapter IV). They sometimes try to associate with adults, but this is generally met with intense aggression (Tricas 1985, Chapter V). Interestingly, juveniles of different butterflyfish species sometimes show interspecific pairing behavior at small sizes (personal observation). The lack of many large size differences between pairmates
indicates that most pairing is between members of the same cohort. This would be sufficient to generate a size assortative mating pattern. Because both sexes of adults are very aggressive towards juveniles, and at sizes before they reach sexual maturity, this aggression seems more likely to be related to territorial defense than any sexual selection processes such as intrasexual competition or intersexual mate choice.

Assortative mating in *C. multicinctus* is likely due to non-sexual selection processes, but may also be the result of intrasexual competition among females. Though female competition may help to drive this pattern, it is probably not strong enough by itself to be solely responsible, as there are relatively few opportunities for females to compete over available males or territories.

If pairing occurs within cohorts, then the size assortative mating pattern is also an age assortative mating pattern. To my knowledge, no one has examined the size-age relationship in *C. multicinctus*. Because of low growth rates after the second year (Tricas 1986), and because *C. multicinctus* is long lived (Hourigan 1989), any relationship between size and age is likely to be clearest during the early years of their life. Age and breeding experience can be correlated with reproductive success in some species (reviewd by Pärt 1995), but it is unclear how age or experience may affect reproductive success in a broadcast spawning species with no parental care.
CHAPTER IV
EARLY LIFE HISTORY BEHAVIOR

INTRODUCTION

Though much is known about the social systems and behavior of adult *Chaetodon multicinctus* (Tricas 1985, 1986, 1989a; Hourigan 1987, 1989; Reese 1991), much less study has been devoted to the behavior of juveniles. Adults are paired, territorial, and obligate corallivores. New settlers on a reef, however, are solitary, apparently non-territorial, and have to shift from a planktivorous diet as a larva to coral as an adult (Harmelin-Vivien 1989). The mechanism by which new settlers find a pairmate, gain a territory, and shift their diet is unknown.

An understanding of the behavioral mechanism by which these juveniles make this transition and recruit into the adult population is important for a variety of reasons. First, very little information on this stage of the life history exists for any fishes, much less for butterflyfishes (Roberts and Ormond 1992). Without a complete understanding of the entire life history of a species, we cannot fully understand processes affecting the adults. Second, butterflyfishes do not have parental care, are broadcast spawners (Thresher 1984), and have a long larval life span (Leis 1989). Since new recruits are unlikely to be related to each other (Avise and Shapiro 1986), kin selection is not likely to have a strong effect on the behavior of butterflyfishes (Hourigan and Reese 1987, Reese 1991). Therefore, in species without parental care, the choices made by juveniles...
will have an immediate and significant impact on their survival, and thus their ultimate reproductive success (Stamps 1978). In barnacle geese, which form long-term pairbonds, the early pairing behavior of juveniles has a significant impact on their future reproductive success (Van Der Jeugd and Blaakmeer 2001). Finally, and perhaps most importantly, the behavior of juveniles can have a significant impact on adult population dynamics. The behavior occurring during settlement and early in the life history can affect later adult dominance relationships and habitat use (Stamps and Krishnan 1994a,b), territorial competition between adults (Arcese 1989), or may even be solely responsible for the entire adult population structure (Doherty and Fowler 1994). Because all of these factors (dominance, spatial distributions, habitat use, and density) can have strong effects on the social and mating system, it is important to understand the dynamics of this early stage of the life cycle, specifically, juvenile behavior and the mechanism by which they recruit into adult populations. The tactics that juveniles use has been examined in terrestrial vertebrates (Stutchbury and Robertson 1987, Arcese 1989, Stamps and Krishnan 1994a, b), but has largely been ignored in fishes, though Jones (1987) and Booth (1995) have recognized the importance of this stage in the life cycle.

An understanding of the mechanisms by which juveniles recruit to the adult population is essential to an understanding of adult population structure and dynamics as well as social systems. In *C. multicinctus*, these mechanisms have implications for our understanding of sexual competition amongst adults, mate guarding, and sexual selection. Juvenile behavior has already been shown to be the likely cause of the assortative mating pattern seen in adults (Chapter III). This study has two goals: 1) to observe and document the settlement of juvenile *C. multicinctus*, paying special attention to
movements, pairing behavior, and territorial behavior, and 2) to examine the feeding behavior of juveniles and compare it to the feeding behavior of adults.

METHODS

Settlement

In order to understand how juveniles recruit to the adult population, I intended to follow individuals from the time of settlement until they reached adulthood. During the summer of 1994, I began following the behavior of newly settled *C. multicinctus* off Makaha on the west coast of Oahu. Fifteen new settlers were identified by variations in their natural markings. The presence of these individuals was tracked from early May until early August when ocean conditions prevented further diving. Observations were made using scuba approximately every third or fourth day, and the presence and location of the 15 settlers was noted.

The study site was located several hundred meters from shore. It was a flat coral reef with little vertical relief at approximately 12 m deep with a ledge that descended to about 14-16 m. At the base of the ledge were boulders and coral rubble. This sloped down further into sand flats around 18 m deep.

In addition, anecdotal observations on juvenile behavior were collected opportunistically during other dives. The bulk of these came from a trip to Kaho‘olawe in 1995, from video footage on Maui in 1996, and from frequent dives at Kahe Point in 1997 and 1999.
Feeding

Feeding data were collected for 31 juveniles from Kahe Point Beach Park on the west coast of Oahu in the summer of 1997. These were compared to similar data collected for 28 adults at the same time and location. Feeding data were collected in 10-minute intervals, and the number of bites taken was recorded. The majority of the bites were on coral; bites were identified to species for corals or as non-coral. Juveniles were grouped into three size categories – small (<30 mm), medium (30-40 mm), and large (>40 mm).

Habitat descriptions for Kahe Pt. were made by combining data from adult territories. Territories were marked with flagged nails and then a transect line was laid out on the long axis of the territory. Along this transect, another line was extended to the border of the territory every meter. On this second line, the identity of the bottom cover was noted every 0.5 m. Juvenile territories were not marked and so coral cover data for specific juvenile territories is lacking.

RESULTS

Settlement

The first settler of 1994 was seen in early May, but the next juvenile to arrive at the study site did not show up until June 20th. The bulk of settlement occurred in the latter half of June and first half of July (Figure 4.1). Adult territories were primarily located on the flat area of the study site in about 12 m of water. Juvenile settlement occurred mostly at the base of the ledge in areas with good shelter. To a lesser extent,
Figure 4.1. Graph of the dates of settlement of *Chaetodon multicinctus* showing numbers per day plus cumulative proportion.

juveniles settled in the interstices between adult territories or within adult territories. In these cases, however, the juveniles settled in locations where they had especially good shelter with holes that the adults could not enter. Juveniles that settled amongst adult territories faced higher aggression rates from the adults than those that settled outside adult territories. After settlement, three juveniles that settled away from the ledge expanded their home ranges toward the ledge where there was higher coral cover, but also where they faced higher aggression rates from the adults in that area. They were observed to be more wary in the new area closer to the adults.
New settlers were site attached; in general, unless they moved a very long distance (see below), they were always re-sighted within about a meter of the spot where they settled. While they were still present on the reef, they were reliably relocated each dive. They remained on the reef for an average of 14.7 days, though the duration of their presence was highly variable (std. dev. = 14.7 days; Figure 4.2, 4.3). By the time that diving ceased in August, 12 of the 15 settlers had disappeared from the study site, while three were still present. The mean length of stay is probably an underestimate because of the three settlers that were still present at the end of the study.

Figure 4.2. Histogram for the duration of stay on the reef by *Chaetodon multicinctus*. 
Regression analysis showed a significant inverse relationship between settlement date and length of stay ($p = 0.004$, $n = 15$, $r^2 = 48.8\%$; Figure 4.4), with early settlers remaining in the study site longer than later settlers. The significance of this relationship was not affected by the exclusion of the three fish that were still present at the end of the study or by the exclusion of the early settler from May.
Figure 4.4. Relationship between length of stay and the date of settlement.

Though nearly all of the new settlers remained site attached, two of the 15 settlers were subsequently sighted at different locations. One moved 30 meters and another moved just over 50 meters within the study site. The first of these moved after 19 days on the reef and stayed at the new location for 11 days. It was still present there at the end of the study. The other was not re-sighted again after it moved to the new location. When a settler was not re-sighted, I performed extensive searches of the study site and surrounding areas to determine if it had moved to another location. Settlers that disappeared were presumed to have been lost to predation. Piscivorous scorpionfish,
Scorpaenopsis sp., were abundant in the study area, especially in areas where the juveniles were located, though actual predation was never observed. During the summer of 1997, a peacock grouper, Cephalopholis argus, was seen eating a juvenile, and Dierking and Meyer (unpublished data) have found subadult C. multicinctus in the stomachs of C. argus. Alternatively, settlers may have disappeared by moving several hundred meters outside the study site and surrounding areas. This seems unlikely given the small size of the settlers and the extensive searches; however, I don’t have the data to exclude this possibility.

Pairing behavior was frequently seen amongst juveniles in several different years and locations. Good size data for the onset of pairing behavior are lacking, but it definitely begins by about 35 mm TL, and probably even smaller. At Makaha in 1994, four pairs of the new settlers were seen showing signs of pairing behavior (swimming and feeding together) with other settlers. Nascent pair formation was also seen in 1997 at Kahe Pt. In this case, three solitary juveniles had adjacent home ranges. On one dive, two of the three showed signs of pairing behavior, and on another dive, a different pair of the three showed pairing behavior. None of these pairs persisted.

At Kahoolawe in 1995, pairs approximately 30-50 mm in length were observed defending an area of a few square meters. These small territories were at the borders of or in the interstices between adult territories. They attempted to defend these territories against adults, but due to the large size difference, the adults either ignored the aggression by juveniles or vigorously chased the juveniles. This is similar to Kosaki’s (1999) descriptions of adult C. multicinctus chasing the much larger C. ornatissimus. When the juveniles did attempt to chase or display towards the adults, they tended to not approach...
them as closely. Aggression by juvenile pairs towards other juveniles, either paired or solitary, was also seen. In 1997 at Kahe Pt., a pair was observed successfully holding on to a small territory. The territory boundaries shifted and even enlarged somewhat. However, this pair was located on a small outcrop of reef at the border where the larger reef disappeared into sand flats. In order to attain a full sized adult territory, this pair would have had to expand directly into other adults’ territories. It is unknown if this pair was able to hold on to this territory or expand landward into adult territories. In 1999, a pair about 35-40 mm in length was also observed defending a territory, but again, the ultimate fate of this pair is unknown.

Most pairing behavior by juveniles is directed towards other juveniles. However, solitary juveniles were often seen attempting to follow adult fish. This typically was met with aggression by adults when the adults were paired, but importantly, not in every case. When an adult was alone, it often ignored the juvenile. Only rarely has aggression between solitary juveniles been observed, and even then, it is possible that it could be confused with some sort of pairing or courtship behavior rather than aggression.

Feeding

Kahe Pt. had approximately 37% total coral cover. Of this, 17.3% was *Porites lobata*, 8.5% was *Montipora patula*, 6.4% was *Pocillopora meandrina*, 4.4% was *Montipora capitata*, and less than 1% was other coral species. Approximately half (52%) of the hard bottom habitat was non-coral, while 11% was sand.

Overall, the diets of adults and juveniles of *C. multicinctus* were similar – all fed primarily on coral polyps. Differences, however, were seen in the feeding rates and in
the composition of the diet. *P. lobata, P. meandrina, M. capitata,* and *M. patula* made up
the bulk of the diet of *C. multicinctus.* Adults and large juveniles fed significantly more
than both medium and small juveniles (Figure 4.5, Table 4.1) with over 140 bites per 10
minutes compared to less than 60 bites per 10 minutes for the smaller size classes.
Adults and large juveniles also took significantly more bites on coral than medium and
small juveniles (Figure 4.5, Table 4.1). Adults took the fewest bites on non-coral items.
This was significantly fewer than both large and small juveniles, but only showed a trend
towards being significantly fewer than medium juveniles (*p* = 0.056; Figure 4.5, Table
4.1). On individual corals, adults took significantly more bites than all juvenile size
classes on *P. lobata, M. capitata,* and *M. patula,* with no differences among the juvenile
size classes for those three species. Large juveniles fed the most on *P. meandrina
*(Figure 4.5, Table 4.1). This was largely due to five of the 15 large juveniles having
especially high feeding rates, though the large juveniles still fed at high rates when those
individuals were excluded from analyses. Other species of coral were fed upon
infrequently, and there were no differences in the number of bites on other coral species
for any of the size classes (Figure 4.5, Table 4.1).

Though all size classes fed primarily on coral (approximately 60% and higher),
the proportion of the diet that it composed was variable. Adults had a significantly higher
proportion of coral in the diet than did large juveniles who had a significantly higher
proportion of coral than both medium and small juveniles. The inverse relationship was
true for non-coral food items (Figure 4.6, Table 4.2). There was no difference in the
proportion of the diet composed of *P. lobata* for any of the size classes. Adults, however,
had a higher proportion of both *Montipora* species than all the juvenile size classes, with
Figure 4.5. Feeding rates on different coral species by size class.

Table 4.1. ANOVA results for feeding rates on different coral species by size class. The same letter under Tukey’s multiple comparisons indicates no statistical difference among size classes for that food type. df = 58 for each analysis.

<table>
<thead>
<tr>
<th>Variable</th>
<th>F</th>
<th>P</th>
<th>Tukey’s multiple comparisons</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>adult</td>
</tr>
<tr>
<td><em>Porites lobata</em></td>
<td>10.07</td>
<td>&lt; 0.0005</td>
<td>a</td>
</tr>
<tr>
<td><em>Montipora capitata</em></td>
<td>24.00</td>
<td>&lt; 0.0005</td>
<td>a</td>
</tr>
<tr>
<td><em>Montipora patula</em></td>
<td>16.31</td>
<td>&lt; 0.0005</td>
<td>a</td>
</tr>
<tr>
<td><em>Pocillopora meandrina</em></td>
<td>8.15</td>
<td>&lt; 0.0005</td>
<td>ab</td>
</tr>
<tr>
<td>Other coral</td>
<td>0.63</td>
<td>0.601</td>
<td>a</td>
</tr>
<tr>
<td>Total coral</td>
<td>24.20</td>
<td>&lt; 0.0005</td>
<td>a</td>
</tr>
<tr>
<td>Non-coral</td>
<td>14.97</td>
<td>&lt; 0.0005</td>
<td>ab</td>
</tr>
<tr>
<td>Total</td>
<td>20.69</td>
<td>&lt; 0.0005</td>
<td>a</td>
</tr>
</tbody>
</table>
Figure 4.6. Proportion of different coral species in the diet by size class.

Table 4.2. ANOVA results for proportion of different coral species in the diet by size class. The same letter under Tukey’s multiple comparisons indicates no statistical difference among size classes for that food type. df = 58 for exact analysis.

<table>
<thead>
<tr>
<th>Proportion of diet Variable</th>
<th>F</th>
<th>p</th>
<th>Tukey’s multiple comparisons</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>adult</td>
</tr>
<tr>
<td>Porites lobata</td>
<td>2.07</td>
<td>0.115</td>
<td>a</td>
</tr>
<tr>
<td>Montipora capitata</td>
<td>10.43</td>
<td>&lt;0.0005</td>
<td>a</td>
</tr>
<tr>
<td>Montipora patula</td>
<td>9.76</td>
<td>&lt;0.0005</td>
<td>a</td>
</tr>
<tr>
<td>Pocillopora meandrina</td>
<td>6.37</td>
<td>0.001</td>
<td>b</td>
</tr>
<tr>
<td>Other coral</td>
<td>1.48</td>
<td>0.231</td>
<td>a</td>
</tr>
<tr>
<td>Total coral</td>
<td>34.40</td>
<td>&lt;0.0005</td>
<td>a</td>
</tr>
<tr>
<td>Non-coral</td>
<td>34.40</td>
<td>&lt;0.0005</td>
<td>a</td>
</tr>
</tbody>
</table>
no differences among the juveniles (Figure 4.6, Table 4.2). Again, due to the high feeding rates by large juveniles, they had the highest proportion of *P. meandrina* in their diet. This was significantly higher than adults and small juveniles, but not medium juveniles, and there was no difference among adults and medium and small juveniles (Figure 4.6, Table 4.2). Other coral species made up a small fraction of the diet (<3%), and there were no statistically significant differences among the size classes (Figure 4.6, Table 4.2).

**DISCUSSION**

**Settlement**

The majority of settlement (80%) occurred during the end of June and beginning of July with only a few settlers in May and August. Walsh (1987) examined the recruitment seasonality of several species of fishes in Kona on the island of Hawai‘i. He found that *C. multicinctus* recruited most heavily in July through September and occasionally into October. He conducted this study, however, by visual censuses and stated that he may have recounted the same fish in multiple censuses. Therefore, the juveniles he counted in the fall months may actually have been settlers from earlier months that were still present on the reef. From this study, 20% of settlers from 1994 were still present in August.

The settlement of juveniles into the territories of adults has been noted for several species of butterflyfishes (Tricas 1985, 1986, Fricke 1986, Hourigan 1987, Irons 1989). These juveniles are vigorously chased by the adults, but they are able to maintain
residency within an adult territory by retreating into the small interstices of the reef where the adults can not pursue. As they get larger though, they can no longer hide in the interstices and begin to move over the reef (Tricas 1985, Hourigan 1987). In this study, *C. multicinctus* settled primarily on the fringes of adult habitat but occasionally within adult territories. As they grow larger, juveniles on the fringes of adult territories must encroach further on adult habitat and face higher levels of aggression from adults. The ultimate fate of juveniles at this point in their lives is unclear, since this is also the time when they tend to disappear from the reef.

When juveniles first settle on the reef, they are extremely site attached, rarely moving beyond a square meter. As they get larger, they slowly venture further and further from their settlement site. As juveniles begin moving further over the reef, whether in search of potential pairmates, suitable territories, or to avoid adult aggression, they are more susceptible to predation. Scorpionfish and Peacock Groupers are likely major sources of mortality in this stage of their life. Tricas (1986) reported that Ringtail Wrasses, *Oxycheilinus unifasciatus*, were a major source of predation at Puako on the Island of Hawai‘i, but these fish were rare in my study sites. Juveniles that disappeared from observation during this study probably began to venture further over the reef, where they were either eaten as they moved through unfamiliar territory, or they eventually moved completely outside the study site and surrounding areas. Though juveniles were seen to move over 50 m along the reef, I did survey several hundred meters of reef without re-sighting any juveniles that had disappeared. This suggests that even though they attempted long distance dispersal, they were rarely successful.
Because settlers that arrive on the reef later in the summer do not persist as long as early settlers, this suggests that appropriate habitat for juveniles is limiting. Sites with good shelter from predation and adult aggression are necessary, as well as areas with relatively good coral cover. Though juveniles tend to settle near adults, it is not known if they use the presence of adults as a cue for settlement.

Juveniles and even adults appear to have a tendency to associate with conspecifics. Pairing behavior is seen in fish as small as 35 mm and likely smaller. At this stage, however, pairing is rather fluid as bonds form, break, and reform. Juveniles show pairing behavior with each other, and at times, even try to associate with adults. Adults nearly always chase juveniles vigorously, but occasionally, while solitary, they tolerate the presence of juveniles. It is tempting to think that this might be due to the adult and juvenile being of the opposite sex, but there is no evidence to suggest that adults might be able to tell the sex of juveniles with undifferentiated gonads. Among adults, pairing is presumed to be for life because individual pairs have been observed for many years and because natural territory takeover or mate replacement has never been observed. Upon the loss of their mate, however, adults will form new pairbonds within hours.

Juvenile pairs that persist for any length of time are also territorial. This suggests that successful pairing is related to the establishment of a territory. In adults, males are primarily responsible for territorial defense, while females defend males from other females (Chapter II). In juveniles, it may be that absent a territory, females do not continue to maintain a pairbond with males. This assumes, however, that prior to gonadal differentiation, juveniles behave according to their gender. The association
between pairing and territoriality also explains the lack of aggression between solitary juveniles, as well as, the higher aggression by juvenile pairs. Without a territory and mate for males to defend, and without a male for females to defend, there’s no motivation for aggressive behavior.

The mechanism, therefore, by which juveniles recruit into the adult population involves settlement in areas with good shelter and coral. As they get larger, they expand their home ranges, generally up against adult territories. At this point, they face increased aggression from adults. At small sizes, juveniles begin to associate with other juveniles when present, though these “pairbonds” are unstable. Pairing and territoriality in juveniles appear to be linked. Juvenile pairs attempt to enlarge their territories, but because most of the available habitat is occupied by adults, they encounter adult aggression. Stamps (1994) found that newly settled Anolis lizards are able to gain territories without winning any fights with residents, but merely by persisting in the face of their aggression. Juvenile pairs of C. multicinctus that do gain a territory, likely do so by this method. Juvenile pairs have been observed holding a small territory, however, whether or not they are successful in staying together and holding a territory as adults remains to be determined.

That juveniles gaining territories as adults hasn’t been observed is likely due to the lack of effort by researchers combined with the rarity with which juveniles are successful. Adult habitat for C. multicinctus appears to be completely occupied with adults holding completely adjacent territories (Tricas 1985). Furthermore, the adults are long lived and pair for life (Hourigan 1989). When an adult pair, or only a male, is removed from a reef, neighboring pairs typically take over the removed pair’s territory,
rather than new fish taking over (Hourigan 1987). In a study of more than 30 pairs over four years, Hourigan (1987) found few instances of natural disappearance. One adult female died, and two adult pairs disappeared and their territories were taken over by the expansion of neighboring territories. This indicates that there are very few openings for juveniles to gain a territory and enter the adult population. The level of settlement is more than sufficient to replace lost adults making populations of *C. multicinctus* resource limited rather than recruitment limited. This difficulty for settlers in recruiting to the adult population could be the impetus behind the long distance movements made by juveniles as they search for mates or better habitat. They may be forced to give up attempting to hold a small territory as a juvenile pair.

An alternative tactic for juveniles recruiting to the adult population might involve becoming a floater (Brown 1969, Smith 1978). Rather than attempting to pair with another juvenile and gain a territory by persisting in the face of adult aggression, they could remain single and roam over a large home range encompassing many adult territories. When openings in adult territories become available, they could then compete to take over. One floater was observed (personal observation) at Makaha over several dives. It roamed over several territories and rapidly swam away when residents approached. Though, floaters have been observed, whether they are individuals that never had a mate or individuals that have lost a mate is not known. Kosaki (personal communication) reasoned that there must be large populations of floaters because when he did removal experiments with a single mate, unknown fish frequently replaced the removed fish. Floaters are hard to identify because they necessarily must have very large home ranges. Also, much of the work on *C. multicinctus* has involved finding territorial
pairs and repeatedly watching them on their territory. This makes the detection of an occasional wandering single individual difficult to confirm as a floater. Therefore, though juvenile pairing is the most often seen behavior, becoming a floater may be the predominant method by which juveniles gain entry into adult populations.

**Feeding**

Overall, the diets of adults and juvenile *C. multicinctus* are similar, with coral making up the majority of the food. Even the smallest juveniles fed on coral more than 50% of the time. Differences do exist, however, in the amount of food eaten and in the proportion of coral in the diet. Adults and large juveniles had similarly high feeding rates, while medium and small juveniles fed at significantly lower rates. The proportion of coral in the diet differed significantly among the size classes as well. Adults had the highest proportion of coral in the diet, followed by large juveniles, and then medium and small juveniles. It follows then that the proportion of non-coral items in the diet decreases with size. There were a few significant differences in the species of coral in the diet, but overall, they were quite similar among the size classes.

The reasons for this ontogenetic shift to a higher proportion of coral in the diet are not well understood for *C. multicinctus*. Harmelin-Vivien (1989) found that in two species of obligate corallivores, *C. trifascialis* and *C. lunulatus*, the shift to a completely coral diet, occurred immediately upon metamorphosis. This study, however, was based entirely on gut content analysis and did not include behavioral observations of feeding in the wild. Jon Lee (unpublished data) examined the gut contents of an unspecified number of juvenile *C. multicinctus* and found that all had greater than 99% coral tissue,
even though up to 40% of their bites are on non-coral items. The apparent lack of non-
coral items in the gut contents may reflect sampling behavior or a juvenile’s poor ability
to catch such prey.

The lower percentage of coral in the diet of smaller fish must be due to either
differences in the food preferences of smaller fish or differences in the availability of
coral to those fish. Though adults and juveniles of *C. multicinctus* show a preference for
*P. meandrina* (Hourigan 1987, 1991; Tricas 1989b, Lee unpublished data), they are on
whole generalist corallivores. Since juveniles show a similar pattern to adults in the
composition of coral species in their diet, if a different food preference by juveniles
explains the lower percentage of coral in the diet, it likely is a relatively stronger
preference for non-coral items in general, rather than against any particular species of
coral. Since coral tissue is a relatively nutrient poor food resource, juveniles may prefer
non-coral items for the early part of their life history when rapid growth is essential both
for territorial defense reasons and to avoid predation (Tricas 1989b). Even though they
have very little non-coral in their guts, the little that they do get may be nutritionally
important. Lee (unpublished data) found that in experimental food offerings, juvenile *C.
multicinctus*, would eat small crustaceans. Hourigan (1991) found that for the specialist
corallivore, *C. quadrimaculatus*, juveniles ate a higher proportion of the less preferred
corals in both laboratory and field behavioral experiments. He did not, however, report
feeding data for non-coral items.

Alternatively, the higher proportion of non-coral in the juvenile diets may be the
result of a low availability of preferred corals. Because juveniles have a very small home
range relative to adult territory size, corals may not be sufficiently abundant for them to
take in as much coral as adults. As they get larger and begin to expand their home range, they also increase the proportion of coral in their diet. Corals may also be unavailable to juveniles if the few corals that they have access to in their home range are heavily predated upon. Gochfeld (2004) found that predation on corals increased polyp retraction times and nematocyst densities, which then decreased the palatability of and feeding rates on these corals.
CHAPTER V
TERRITORIAL AGONISTIC BEHAVIOR

INTRODUCTION

Adults have been shown to have a variety of effects on the settlement of larvae for many different species of fishes (e.g., positive effects, Sweatman 1985; negative effects, Almany 2004; no effect, Steele et al. 1998). Other juveniles may also affect settlement (Booth 1992). For C. multicolor, it is unknown if adults serve as an attractant or deterrent to the settlement of larvae, though recruits of C. multicolor do tend to settle near adult territories. What is known is that adults are very aggressive towards juveniles (Tricas 1985, Hourigan 1987, Reese 1991). This aggression has a large impact on the lives of juveniles, but little work has been done on the effect of settlers on adults.

Natural territory turnover for C. multicolor has rarely been observed (Hourigan 1987). In one case, a female pairmate died and was quickly replaced by another adult. In another case, two separate pairs disappeared, and their territories were taken over by the encroachment of neighbors' territories. Resident territorial holders were always able to repel intruders, and territory usurpation or natural mate switching was never observed, though mate switching did occur during individual removal experiments (Hourigan 1987). Whether these methods for turnover are the norm or not is not well understood. The replacement of individuals or pairs by existing adults would seem to preclude juveniles from entering the adult population. However, since adult territories are
contiguous, changes in one territory can affect neighboring territories and create a
domino effect that eventually opens up space in other parts of the reef (Hourigan 1987).

It may be that neighboring adults represent a short-term threat to the fitness of a
territory holder in terms of occasional sneak spawnings or partial territory usurpation.
Newly settled juveniles on the other hand may represent a more severe long-term threat if
they might eventually crowd out a territory owner. That residents were always able to
repel intruders and natural openings in the adult population were rare suggests that
juveniles could be a significant threat and may explain the extraordinary aggression
shown towards them.

Previous descriptions of aggressive behavior in butterflyfishes have noted the
overall low levels of aggression and that territorial species are able to maintain their
territories with relatively low intensity agonistic displays (Reese 1975, Ehrlich et al.
1977, Roberts and Ormond 1992). These studies, however, lacked a detailed description
of the types of behavior demonstrated by the fish in agonistic interactions (but see Yabuta
(2000) for a description of aggressive behaviors in *C. lunulatus* and Hamilton and
Peterman (1971) for a description of color changes in *Chaetodon lunula*).

The purpose of this study is to describe the aggressive behavior of adult *C.
*multicinctus* territory owners towards different intruders into their territory. By
understanding the aggressive behavior of territorial owners towards different types of
intruders, we gain insight into the selective pressures affecting their territorial behavior.
Furthermore, an understanding of the threats to resident territorial owners has
implications for our understanding of mate guarding and the degree of sexual competition
among adults.
METHODS

In order to describe the agonistic behavior shown by territory holders toward intruders, an unfamiliar fish was placed in a one-gallon glass jar with a mesh covering and weighted bottom. The unfamiliar fish were captured from distant locations and housed at the Hawai‘i Institute of Marine Biology. They were brought to the experimental location, placed in the bottle, and the bottle was then placed in the territory of an adult pair. The resulting interactions were captured on videotape. A total of 13 introductions were filmed. Two adult and two juvenile introductions were videotaped in the spur and groove habitat outside the barrier reef in Kaneohe Bay on Oahu, and four adult and five juvenile introductions were videotaped at Kahe Pt. during July and August of 1996. The introductions were videotaped up to 20 minutes, but the length of the introduction varied depending on the behavior of residents, water conditions, tape length, battery power, and the presence of sharks. A total of almost three hours of footage was taken, with an average of about 13 minutes per introduction. Because the purpose of this portion of the study was to make qualitative descriptions, I was not concerned with the varying lengths of the introduction times. I did not describe the behavior of the bottled fish because they tended to stay stationary in the bottle and react more to being held in the bottle rather than to the resident fish. This did not, however, prevent resident fish from interacting with the intruder. These videotaped introductions were supplemented with anecdotal observations of natural aggression.

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RESULTS

Adult Introductions

The most common aggressive interactions by *C. multicinctus* seen in the wild are parallel swimming (two fish swim parallel to each other with fins erected and the head tilted down slightly) and chasing. These behaviors, or attempts at these behaviors, are also seen in the bottle introductions, with the main difference being that the intruder fish cannot move with the resident in a parallel swim or towards or away in a chase while in the bottle.

When an adult was introduced into a territory, the resident fish rapidly approached the bottle. When two residents approached the bottle, they both displayed, but in general, one of the two was more vigorous in its displays. The more vigorous of the two was presumably the male since males will more often chase females than vice versa and since male aggressive displays are generally more intense (Hourigan 1987).

The most common display was a Rounded Fin Display, or RFD (Figure 5.1). In this display, the soft dorsal and anal fins are fully erected, but the dorsal and anal spines and pelvic fins are held against the body. When the fins are erected, more of the stripes on the side of the fish can be seen, because the striping often extends from the side of the body up onto the dorsal fin. Because there is individual variation in the length of the stripes, the apparent elongation of the stripes varies from fish to fish. Also, in the normal fin position, the posterior dorsal fin and anal fin are nearly continuous with the caudal fin, but during the RFD, there is a separation between them. While performing an RFD, the
Figure 5.1. Fin displays by *Chaetodon multicinctus*. A) Normal fin position. B) Rounded Fin Display (RFD). Note the extension of the stripes towards the dorsal surface and the separation between the caudal fin and the posterior dorsal and anal fins. C) Rounded Fin Display with darkening on the rear half of the body and the posterior dorsal and anal fins. D) Full Spine Display. All spines and fins are erected.

displaying fish swims with its head tilted slightly down. It uses its pectoral fins for propulsion, and the caudal fin and body are held rigid.

The RFD is seen during the parallel swims performed by *C. multicinctus* in the wild. During the bottle introductions, the residents rapidly approach the bottle head on,
gave a quick snap of the tail, then turned laterally and performed the RFD. Since the intruder fish could not engage in a parallel swim, the resident continued to circle back around and repeat the sequence. This behavior often sped up during the course of the introduction and appeared to be the result of the resident fish becoming more agitated.

Often upon approaching the bottle, the resident fish darkened the posterior dorsal and anal fins, as well as the spaces between the stripes on the rear half of the body (Figure 5.1). This color change tended to co-occur with the RFD. In general, the color change took place for only a few moments at first contact, rarely lasting longer than 60 seconds. This darkening was also seen during the mate choice trials (Chapter III). When a stimulus fish was first placed in the tank, the experimental fish often darkened as it approached the other fish. This was only seen for a short time as well. The only observation of a prolonged color change came from an observation in the wild of two adult fish in a particularly aggressive and prolonged fight lasting many minutes.

During one of the adult introductions, a solitary resident approached the bottle first before being joined by its pairmate. By itself, the solitary resident seemed very timid. It did not approach the bottle closely nor did it show any obvious RFD’s. As it swam slowly in the vicinity of the bottle, it often tilted its dorsum away from the bottled intruder. When it was rejoined by its pairmate, the overall level of aggression stayed relatively low, with few instances of RFD’s. The sexes of the fish were unknown. It was difficult to compare the relative sizes of the three fish, but they seemed to all be of a similar size, or if anything, the intruder was slightly smaller. Also, the borders of the resident pair’s territory were not marked, so it is not known where the intruder was
placed relative to the territory’s boundaries. In another incident that was not filmed, a relatively small resident pair could not be induced to chase or display at an adult intruder.

Another behavior that was performed primarily during adult introductions was a Head Bounce. During this behavior, the resident would tilt its head down until it was vertical and then move at the substrate as if it was feeding. It was difficult to distinguish this from normal feeding behavior, except that in a few instances, the fish performing the Head Bounce could clearly be seen not biting the substrate. This behavior was most often seen early during the introduction.

**Juvenile Introductions**

When juvenile intruders were introduced into a pair’s territory, the residents always responded very rapidly. As they approached, RFD’s were performed as above. The duration of the display, however, was very brief. They very quickly performed an RFD, if at all, and then went into a Full Spine Display, or FSD (Figure 5.1). This display was very similar to an RFD, except that the dorsal and anal spines were erected as well as the pelvic fins.

In general, most movements were much faster than with adult intruders, and the residents appeared to be much more agitated. The typical response to a juvenile intruder was to perform an FSD, while rushing directly at the bottle rather than alongside it as the residents did with adult intruders. They generally stayed close to the bottle, oriented towards it, and their body would often twitch as they faced the intruder. This body twitching was very similar to the snapping of the tail seen with an adult intruder, but rather than it leading into a parallel swim or RFD, the resident held its position facing the
bottle. Sometimes, they would perform this behavior while rapidly swimming in a tight circle next to the bottle.

Also during the juvenile introduction, residents were often seen to tilt their dorsum towards the bottle with the spines fully erected. This tended to occur later during an introduction after apparent attempts to chase away the juvenile were unsuccessful. In the wild, this behavior has been seen only in the most intense bouts of aggression and resulted in scales being dislodged from the opponent fish (Hourigan 1987).

Another behavior observed mostly during the juvenile introductions was pelvic fin flicking. This tended to happen early in the trial while residents were circling the bottle and performing RFD’s. While doing so, they would very rapidly extend then retract their pelvic fins.

**DISCUSSION**

At first glance, it would appear that the resident territorial fish are showing higher levels of aggression towards the juvenile intruders. The attempts at chasing, the extended spines, and the overall apparent agitation of the residents during a juvenile introduction suggest a more aggressive response. It would be tempting to conclude therefore, that juveniles represent a larger long-term threat to a territorial pair. However, the different responses and apparent differences in the intensity of aggression to adult and juvenile intruders could be the result of several not necessarily mutually exclusive factors.
Fights with other adults carry a higher risk of injury than fights with juveniles. The overall lower intensity of displays directed towards adults may be the result of a motivational conflict between attacking the intruder and swimming away from a dangerous opponent (Tinbergen 1959). In an evolutionary sense, fights that are settled via a lower risk display rather than a full fight are favored (Krebs and Davies 1993). Adult intruders may actually represent a larger threat to a territorial pair, but because of the higher risks involved, a more intense display is not seen.

Occasionally, resident pairs showed very low levels of aggression toward an adult intruder or would not display at all. In some of these cases, it was likely due to a larger intruder that was placed in the territory and the resulting motivational conflict it caused in the resident. A similar pattern is seen when adult *C. multicinctus* react to intrusions by the much larger corallivore, *C. ornatissimus* (Kosaki 1999). Alternatively, since territory boundaries were not marked before introductions, the occasional low levels of aggression may have been due to the bottle being accidentally placed at the border of the residents' territory rather than intruding into the resident’s territory. That these incidents involved lower intensity displays, it does not necessarily follow that lower apparent levels of aggression are due to a lower threat by a large intruder to a resident pair’s territory.

Yabuta (1999, 2002) described agonistic behaviors in *C. lunulatus* that are also used for partner recognition. He described a tail-up display used when pairmates greet each other after being separated that is very similar to the Rounded Fin Display seen in *C. multicinctus*. He felt that reuniting pairmates were in a state of motivational conflict because they could not distinguish their pairmate from an intruder. The result of this tail-up display is a reduction of escalated fighting between pairmates in the cases of uncertain
partner recognition. Driscoll and Driscoll (1988) reported that *C. multicinctus* engaged in a fast swim behavior when reuniting after a separation. Though they do not describe it in details, reuniting pairs often swim rapidly toward each other and perform an RFD (personal observation). It may be that RFD’s are not seen with juvenile intruders because the resident fish lacks the motivational conflict that results in an RFD. This lack of a motivational conflict may be because there is no fear response to the smaller fish or because the resident can be sure that the much smaller fish is not a pairmate. Without a motivational conflict, the resident immediately escalates to a high intensity display. It is therefore possible, that juvenile intruders are a lower threat to a resident pair, but they receive a more intense display (FSD) because of the lack of a motivational conflict.

The data from this study are not sufficient to clarify whether adult or juvenile intruders represent a larger threat to a resident pair. An additional aspect of territorial behavior that this study did not examine is the difference between adult neighbors and non-neighbors. Territory owners often respond less aggressively to intrusion by familiar neighbors than to intrusions by strangers, a phenomenon known as the dear enemy effect. This has been shown to be true in some birds (Lovell and Lein 2004) but not others (Lachish and Goldizen 2004), while Myrberg and Riggio (1985) demonstrated the effect in a territorial damselfish. Neighboring adult and strange adult intruders may present different threats to a resident. Neighboring adults may encroach on the territory or occasionally sneak spawnings, but total usurpation of the territory seems unlikely. A single non-neighbor intruder such as a floater, however, is a potential threat in many ways. They may steal food as they pass through a territory, they may sneak spawnings during the reproductive season, or they might evict one of the territory holders and
replace them. Each of these represents an increasing threat. A settling juvenile represents little immediate threat in terms of food or sneak spawnings, but if it pairs and persists in the area, it may eventually crowd out the adult residents. Clearly losing a small portion of food or a few fertilizations to sneakers is not as severe a threat as losing one’s territory and mate entirely. In order to gauge the relative threat of each of these events, we need to know the frequency with which they occur. Data on the percentage of successful sneak spawnings and the identity of sneakers, the frequency of natural territory turnover, the frequency of natural mate replacement, the population density of floaters, and the stability of territory boundaries between neighboring territories would help to evaluate these threats.

The darkened appearance during many of the encounters (intruder introductions, mate choice trials, and observations in the wild) seems to occur during periods of heightened intensity. However, they did not occur consistently enough to warrant further generalization. The Head Bounce display may be an advertisement of territorial ownership by simulating feeding behavior.

Tricas (unpublished data) has recently reported that C. multicinctus produces sounds during aggressive displays. Many of the behaviors seen during these intruder introductions may also involve auditory communication. He found that the pelvic fin flicking and tail snaps produce distinct sounds. He also documented pelvic fin flicking with adult intrusions. The functions of these different sounds remain to be experimentally tested.
CHAPTER VI
CONCLUSIONS

The main conclusions to be drawn from this study are:

- Monogamy historically has been defined in many ways. It is important to distinguish between genetic monogamy (shared genes), social monogamy (shared space), and pairbonding (shared time).

- Though both sexes of *Chaetodon multicinctus* will attempt bigamy, social monogamy is constrained by same sex aggression by both sexes. In addition, the large territory sizes relative to body size and the large amount of time spent feeding are likely further constraints.

- Female-female aggression is likely mate guarding because they were only observed to show aggression when in the presence of their mate. Since females cannot hold a territory alone but males can, they are likely defending males and their territory holding capabilities.

- Males are primarily responsible for defense of the territory. Male-male aggression is likely a combination of territory defense and mate guarding. They showed a higher probability of aggression when with the mate, but also showed high aggression without the mate. Males likely guard females for mating and for the increased fecundity from feeding on their territory.

- Pairbonding is the result of movements toward the pairmate by both sexes, though females were primarily responsible for maintaining proximity in the pairbond. These
movements toward the mate can be for the purposes of either mate guarding or the increased feeding rates while with the pairmate.

- Whether or not social monogamy is a constraint or is mutually beneficial depends on female growth rates. If females grow approximately 7% longer by being the sole female on a male’s territory, then social monogamy may be evolutionarily beneficial to the male. If female growth rates or fecundity do not increase significantly with territory size or quality, then social monogamy may be evolutionarily beneficial to the female.

- Female defense of males is an important determinant of the social system of *C. multicinctus*.

- Males, but not females, spent more time with larger mates in mate choice experiments.

- Females may not be choosy because they choose some male trait other than size, such as territory quality, or because *C. multicinctus* is sex-role reversed.

- Behavioral dimorphism in *C. multicinctus* (e.g., males defend the territory more, females feed more) is likely due to sexual selection.

- Males and females pair assortatively by size. This is likely due to a non-sexually selected process where pairing within a cohort carries over from year to year. It may also be reinforced by intrasexual competition among females.

- Juvenile *C. multicinctus* settle among or near adult territories. They then expand their home ranges into adult areas as they get larger. The inability to expand may lead to long distance dispersal.

- The majority of settlers observed in 1994 did not survive.
• Pairing behavior begins at small sizes and may be linked to territorial behavior.

• Juveniles likely gain territories as adults by persisting as a juvenile pair long enough to carve out a space among adults or by becoming a floater.

• Habitat appears to be limited for juveniles as evidenced by the fact that most do not survive and that the earlier settlers survived longer.

• Adult populations do not appear to be recruitment limited. The majority of adult habitat is occupied, adults are long-lived and so there are few openings, recruitment levels are high, and most juveniles do not successfully recruit to adult populations.

• All ages of *C. multicinctus* feed primarily on coral. As they get older, the proportion of non-coral items in the diet decreases.

• Adults perform higher intensity displays toward juvenile intruders compared to adult intruders. This may be the result of a motivational conflict produced by an adult intruder, a lack of pairmate recognition behavior performed towards juveniles, or a reflection that new settlers pose a higher threat to residents compared to adults.

**RECOMMENDATIONS FOR FUTURE RESEARCH**

Many of the conclusions regarding the evolution of social monogamy and pairbonding are based on observational and correlational data. This is in part necessitated by the logistical difficulties of making the necessary field manipulations. However, some difficult but interesting experiments could be attempted. Either through removals of fish or by transplanting fish to another reef, manipulating the sex ratio could help
clarify the proximate constraints on social monogamy. If males are removed, we would predict to see increased female-female competition for males. This may result in some females being displaced and becoming floaters, or females becoming territorial and splitting up a male’s territory, or the formation of threesomes with an alpha and beta female if they are not able to exclude each other. If females are removed, male-male competition may not increase since they are constrained by territoriality, but we would probably see females moving over multiple male territories.

Tests of mate guarding as the primary constraint on social monogamy could be achieved by hormonally reducing aggression rates. Reducing female aggression may allow for polygyny to develop, and reducing male aggression may break down territoriality and cause females to no longer maintain a pairbond. Mate guarding could also be further examined by looking at differences in the pairbond behavior relative to the experimentally manipulated size or quality of a mate.

Though the proximate causation of the social behavior of C. multicinctus has been fairly well worked out in this study, some questions about the ultimate causation remain. Specifically, is social monogamy evolutionarily favored or is one or both sexes constrained to monogamy? In order to answer this, we need to understand the relationship between territory size or quality and female growth rates or fecundity. This information is necessary to find out if it’s more beneficial to a male to have one or two females on his territory and if it’s beneficial to a female to be able to forage on multiple territories. Laboratory studies or large manipulations as above may help to answer this.

The temporal variation in pairbonding is another potentially interesting area of research. When a female is getting ready to spawn, she may spend more time away from
the male in an attempt to attract multiple males to spawn. Likewise, if a female is not ready to spawn, a male may spend more time away from her in search of other females that might be ready to spawn. Understanding changes in pairbonding behavior around spawning times may also shed light on the evolution of bright colors in a monogamous fish sensu Hamilton (1990). Differences between breeding and non-breeding seasons could be interesting, as well as differences based on fish size, habitat, or territory size.

The relationship between male size and territory size or quality remains to be conclusively explained. Tricas (1989a) found a relationship between male size and territory size in some cases but not others. Since territory size is affected both by coral cover, coral composition, local topography, and intruder pressure, a method of standardizing territory measurements is needed. Perhaps if we measure territories in terms of the number of calories available per fish, we may be able to describe a more definite link between male size and territory size that is not confounded by these other variables.

The effect of territory quality on pair behavior is also an area that is ripe for exploration. Researchers who have spent any time watching C. multicinctus have learned to identify the sex of the fish by watching their behavior – males are more aggressive and swim higher off the bottom, whereas females feed more. How this division of labor varies and is affected by environmental conditions has not been explored. At Puako, I found the fish very easy to sex behaviorally, but could not sex them reliably at Kahe Pt. The main differences between the area of Puako where I worked and Kahe Pt. is that Puako has small territories with high densities of the least preferred coral *Porites compressa*, whereas Kahe Pt. has larger territories and lower overall coral cover but with
higher proportions of more preferred and/or calorie rich corals such as *Pocillopora* and *Porites lobata*. At Puako, there was no difference between the sexes in feeding rates, but at Kahe Pt. there was a significant difference (Table 2.4, Figure 2.1). Aggression was higher at Puako (Table 2.5). The larger territory size at Kahe Pt. may explain the lower aggression there simply as a matter of encounter rate with neighbors. The different feeding rates between the sexes there may be difficult to detect observationally and so they are hard to sex behaviorally. At Puako, with the lower quality food, it might be expected that the feeding rates would differ between the sexes since the females need to eat more to produce eggs (Hourigan 1987). The lower quality food that predominates in the territories, though, may require the male to feed more to the point where his feeding rates match the female’s. On the other hand, it may be that the total caloric value of the territory is higher, even though it is smaller and has less preferred coral, since the coral cover is so high and so females do not have to feed at higher rates to increase their fecundity. The higher aggression rates at Puako are perhaps what makes it easier to sex the fish behaviorally rather than feeding rates. The effect of different coral compositions within a territory on growth rates would also be useful.

Regarding mate choice, one aspect of mate preference that I wanted to explore but did not run enough trials was comparing the preferences of each sex for its mate versus another fish of the same sex that was the same size or larger. This may potentially shed some light on the evolutionary favorability of social monogamy and pairbonding, as well as whether experience as a pair affects reproductive success. Using male aggression levels as a variable in female choice tests would be useful as well. If territory quality is what is important about males to a female, his aggression levels may be more important
than his size. If aggression levels could be measured and controlled for in a mate choice experiment, this would greatly help our understanding of sexual selection in *C. multicinctus*.

The mechanisms of territory acquisition and the threats to territory holders also remain to be fully clarified. If juveniles could be followed from settlement to adulthood, that would be ideal, though it would take a brave graduate student to undertake this task. It would also be interesting to examine the timing of gonadal differentiation and how it correlates with the onset of territorial and pairing behavior. Other information on the percentage of successful sneak spawnings and the identity of sneakers, the frequency of natural territory turnover, the frequency of natural mate replacement, the population density of floaters, and the stability of territory boundaries between neighboring territories would help to evaluate the threats to territory holders. These would all take long term monitoring and/or an intensive observational effort. Model bottle experiments in which a neighbor or a strange fish is introduced into a territory might help to clarify whether neighboring adult pairs or solitary floaters represent a greater threat to resident pair.

Some current research on UV vision and sound production by George Losey and Tim Tricas respectively provide interesting ideas for future research. The appearance of corals in the ultraviolet may help us better understand feeding in *C. multicinctus*. This may in turn affect territorial behavior and pairbond behavior. The dark coloration seen during the model bottle introductions may contain further signals in the UV. Sound production by *C. multicinctus*, may influence pairbond dynamics, aggressive responses, and mate choice.

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