Comparative life history traits across the family Chaetodontidae in French Polynesia

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Abstract
Nine species of butterflyfish were tagged and observed in Moorea, French Polynesia over a period of four weeks. Feeding and home range sizes, fidelity to night sleeping location, and group size were observed and quantified. All factors significantly differed among the target species. Additionally, these life history traits could be combined and used to segregate species into groups, which suggests that behavior can be used to separate different species into their respective ecological niches.

Introduction
Butterflyfish (family Chaetodontidae) include over 114 species in 10 genera and form an intricate part of the coral reef ecosystem (Allen et al., 1998). Because butterflyfish are abundant and speciose on shallow reefs, their behavior has been the focus of numerous studies (Motta et al., 1989). Inhabiting several niches within this ecosystem, there are similarities as well as differences in behavior among species and many studies have therefore investigated whether differences in behavior can be invoked as an explanation for species coexistence. For the purpose of this paper, niche will be used to describe not only the particular habitat species occupy, but also the different behaviors and life history traits that perpetuate that particular role. Differences in behavior could be the result of variation in feeding, territoriality, pair bonds, mate availability, competition, predation, and resource partitioning. The structure of the reef has also been implicated as a factor affecting space partitioning and interactions among butterflyfish (Bell et al 1985; Bouchon-Navaro 1986).

Depending on the diet of the species, feeding behaviors, and thus feeding ranges, can differ dramatically. For example, *Chaetodon trifascialis* inhabits a territory that can be as small as a single head of *Acropora sp.* (Hourigan 1989), while other planktivorous species are known to have very large home ranges, up to several hundred square meters. (Motta et al.,
Studies have also been done to investigate how fish maintain their territories and home ranges; these studies have suggested that fish may map their area by relying on visual cues and following predictable routes in the morning and evening, which implies a daily routine (Reese 1989). Additionally, studies have found this daily routine included a particular sleeping location within the home range (Hourigan, 1989). However, no studies mapped these home ranges and related them to sleeping areas.

In addition to questions relating to spatial division of reef habitat, there has been great interest in the social structure of butterflyfish. It has been suggested that butterflyfish may live in a pair for many years (Hourigan, 1989). This led researchers to believe that butterflies may pair for their entire lives (Motta et al., 1989). Pair fidelity seems to be very strong in these fish and studies have suggested explanations for this fidelity, including increased reproductive success, territoriality, and defense. Studies have also indicated that pair bonding may be dynamic; when one individual in a pair was removed it took an average of 1-5 days for mate replacement (Hourigan 1989). Still little is known on the strength of this relationship across the family.

Thus, an interspecific study of spatial and social behavior in butterflyfish is warranted. The overall goal of our study was to compare a suite of behaviors across taxa that co-exist on shallow reefs in Moorea. Specifically we asked:

1) What is the typical group size within species and does this vary among species?

2) Do home ranges vary as a function of species?

3) Do individuals always sleep in home ranges and do sleeping locations vary temporally?

4) Do these criteria correlate with each other to form a framework by which life histories may be used to distinguish between species in a similar habitat?
Materials & Methods

Study Site
The site chosen for this study was a fringing reef, White House Wall, Opunohu Bay, Moorea, French Polynesia. This site is characterized by a shelf composed primarily of Porites lobata and Porites rus with a maximum depth of 3 m, combined with a steep wall of rock and dead coral descending to approximately 15 m. The actual study site ranged from the north to the south side of the wall between 1 and 12 m in depth. The site was chosen for its logistical ease and diversity of butterflyfish.

Species
Nine species in the family Chaetodontidae were used in the study:

Chaetodon citrinellus: Speckled butterflyfish are common in areas with patchy corals. They are usually paired and feed on coral polyps, benthic invertebrates, and algae.

Chaetodon lunula: Raccoon butterflyfish are primarily found on exposed rocky areas. They are occasionally paired, primarily nocturnal and feed on coral polyps, invertebrates, and algae.

Chaetodon ornatissimus: Ornate butterflyfish are common in coral reef areas. Adults are occasionally paired and feed exclusively on coral tissue.

Chaetodon reticulatus: Reticulated butterflyfish are found in areas of rich coral growth in exposed areas. They are occasionally paired and feed primarily on coral polyps.

Chaetodon trichrous: Tahiti butterflyfish are found primarily on lagoon reefs. They are usually paired and feed on primarily coral polyps.

Chaetodon trifasciatus: Red-fin butterflyfish are found in coral rich areas of the lagoon. Adults are usually paired and feed exclusively on coral polyps.

Chaetodon vagabundus: Vagabond butterflyfish are found in a variety of habitats. They are usually paired and feed on invertebrates, coral polyps and algae.

Forcipiger flavissimus: Long-nosed butterflyfish are usually found in the lagoon near ledges and caves. They are found solitary or in small groups and feed on benthic invertebrates.

Heniochus chrysostomus: Pennant bannerfish are found in coral rich areas on seaward reefs. They are usually solitary or in small groups and feed on coral polyps.

(Lieske 1999).
General Survey Design

Fishes were tagged and monitored for a period of four weeks during the months of November and December, 2004. During three nights, 9 *Chaetodon citrinellus*, 4 *C. lunula*, 5 *C. ornatissimus*, 8 *C. reticulatus*, 6 *C. trichrous*, 6 *C. trifasiatus*, 11 *C. vagabundus*, 10 *Forcipiger flavissimus*, and 5 *Heniochous chrysostomus* were tagged and released (84 total). The tags consisted of nickel fishhooks threaded with different color patterns of beads. Fish were captured at night, using aquarium nets and were held while the hook was attached through the dorsal muscle of each fish. The following data were recorded: Species of fish, bead color, depth, and whether the target fish was solitary or paired. Location of capture was marked on the reef by the use of flagging tape labeled with site location and number. Later, these flags were mapped for future reference.

Group size

Data for average group size was collected over the course of ten dives during the study period, by extensive observations of the nine target species, both tagged and untagged, at White House Wall and West Opunahu. Fish were recorded as being solitary, paired, or in groups from three to six individuals, according to species.

Home range estimation

Home ranges were estimated by chasing tagged fish to the farthest points in a series of directions to map a perimeter, assuming that the fish would stay within their home range. Weighted flags were dropped at these locations, giving boundaries to the area. The flags were adjusted as further observations revealed an expansion of the fish’s range if necessary. Measurements were then taken from the original tagging site to the closest flagged point in the perimeter of the area, to determine proximity of initial sleeping location to home range.
Measurements were also taken from points opposite of each other for both length and width to approximate the home area.

**Fidelity to sleeping location**

To determine whether the fish showed fidelity for their sleeping location, observations were made on five nights over the period of the study noting whether or not tagged fish returned to the flagged area in which they were first located. If they were found away from the original tagging location, it was also recorded so that mortality of the fish was ruled out.

**Results**

**Group Size**

Two aspects of group size of the nine target species were examined: The likelihood that a group of size N would be observed, and the likelihood that an individual fish would be found in a group of size N. On 10 days during the study period, fish were observed and the group size noted. These data were then examined using a Tukey a-posteriori ANOVA analysis.

For average group size (the average number of individuals in all groups observed), we found a strongly significant difference among our nine target species (p=0.000). The Tukey analysis revealed three catagories for average group size; low (A), medium (B), and high (C) (figure 1). For all the categories of group size, there was no significant difference between species within the group, but the difference in fish among categories was statistically significant with some overlap. The species of fish included (in ascending order) in grouping A were: *C. ornatissimus, C. reticulatus*, and *C. vagabundus*; for grouping B, *C. vagabundus, H. chrysostomus*, and *C. lunula*; and for grouping C, *C. lunula, F. flavissimus, C. trifasciatus, C. citrinellus*, and *C. trichrous*. With respect to the likely size of the group a fish would be
found in, there was also a highly significant difference among species (p=0.00). There was a rough grouping of species, but clear significant differences were not found among groups and the analysis suggests more of an overlapping progression among species (figure 2).

**Figure 1**

![Graph showing group size by species.](image1)

Fig. 1 shows the average group size by species. Black lines above groups of bars shows statistically different groups. Standard error bars are included. Fig. 2 shows likely group size for individual fish. Black lines above groups of bars show statistically different groups, but no distinctive groups are evident. Standard error bars are included.

**Home Ranges**

Data collected allowed us to calculate home range for 5 of our 9 target species. These areas are assumed to be feeding ranges which the fish inhabit during the day, as part of an overall home range. We also recorded the distance between the original tagging location and the edge of the suspected feeding range to develop a more accurate understanding of overall home range size. The data was analyzed using a Tukey a-posteriori ANOVA and graphed on a log scale. For this analysis we are considering p-values > 0.10 significant. This showed that the differences in average area of the feeding ranges was significant among species (p=0.023 figure 3). We found that there was a highly significant difference between *C. vagabundus* and *C. trichrous* (p=0.012), as well as a suggested difference between *C. vagabundus* and *C. citrinellus* (p=0.194). A difference among species was also found with respect to distance from original tagging site to speculated feeding range (p=0.012 figure 4). Significant
differences were found between *C. citrinellus* and *C. reticulatus* (p=0.068), between *C. citrinellus* and *C. trichrous* (p=0.009), and a weak significance was observed between *C. trichrous* and *C. vagabundus* (p=0.102).

Figure 3

![Figure 3](image1.png)

Fig. 3 shows the average log area of speculated feeding ranges by species. Standard error bars are included. Fig. 4 shows the average log distance from original tagging site to closest location on the perimeter of suspected feeding range. Standard error bars are included.

*Sleeping Location Fidelity*

During the course of the study, data was collected on five nights for seven species. The presence or absence of fish at original tagging/sleeping location was used to calculate the percentage of fish that returned to original location, and then analyzed using a Tukey a-posteriori ANOVA. The analysis showed that there was a significant difference among species in fidelity to sleeping location (p=0.069), but a high significance was found only between *C. ornatisimus* and *F. flavissimus* (p=0.032 figure 5).
Fig. 5 shows the percentage of time that fish were observed returning to their original tagging location on consecutive nights. In this graph *F. longirostris* is actually *F. flavissimus*. Standard error bars are included.

*Species Discrimination*

We looked for relationships between behaviors in attempts to distinguish species on the basis of life history traits. No significant correlation was found when using a multi-variable plot with home range, night fidelity, and group size. However, two bi-variable plots of log area and log distance, and night fidelity and range area, both as a function of species, revealed a rough grouping of individuals within species, and a spread between separate species respectively. (figure 6 and figure 7).
Fig. 6 shows the log of the assumed feeding range area plotted against the log of the distance from the original tagging location to the closest part of suspected feeding area. The rings group individuals by species based on results in this criteria. Fig. 7 shows a bi-variate plot of night fidelity and group size. The means of this data was compiled into one point per species showing how the species can be separated.

**Discussion**

In this study, we set out to address the following questions:

1) What is the typical group size within species and does this vary among species?

2) Do home ranges vary as a function of species?

3) Do individuals always sleep in home ranges and do sleeping locations vary temporally?

4) Do these criteria correlate with each other to form a framework by which life histories may be used to distinguish between species in a similar habitat?

We found that suspected feeding ranges vary among species and think this may be related to maximum body size and feeding behaviors, under the assumption that larger fish can better defend a larger area. *Chaetodon vagabundus*, the largest species for which range data was collected and analyzed, also has the largest overall feeding range, while *C. citrinellus* and *C. trichrous* both have the smallest body size and the smallest feeding area. Interestingly the pattern is not consistent for the distance from sleeping location data. *Chaetodon trichrous*, which is one of the smallest fish with the smallest range, appears to travel the furthest distance from its sleeping location; *C. vagabundus*, which has the largest feeding area, travels the shortest distance from its night shelter. The major inconsistency is between *C. trichrous* and *C. citrinellus*, where both have small body size and a relatively small feeding area, but *C. citrinellus* stays within a close proximity to its daily feeding area and *C. trichrous* as previously stated, travels a relatively much larger distance. It may be that a larger distance between feeding and sleeping locations is evidence of an overall larger home range, where
sleeping and feeding regions are separated (with a possible daily “commute” between the two), whereas a closer proximity of sleeping location to feeding range suggests that the fish remain in approximately the same area during both the day and night. Ultimately, we believe that range varies among species due to a summation of each species’ different life history traits, but that such differences and possible patterns would become more clear with a higher number of replications for each species included in the study.

Analysis of night fidelity to sleeping location was intuitively different among species, but the only statistical significant difference was between *C. ornatissimus* and *F. flavissimus*, whose return rates ranged from approximately 10% to 70% respectively. We found that both *H. chrysostomus* and *C. ornatissimus* had the lowest rate of return to their marked sleeping location. Our observations suggest that it is logical to assume this due to both species possessing at least a degree of nocturnal behaviors (night observations found both to be more active at night than other species – they proved difficult to catch for tagging purposes). To some degree discrepancies in the measured fidelity may be attributed to errors in our sampling method (i.e. difficulties in locating fish due to reef structure, time restraints, air restraints, etc.)

Data for group size was collected in two different data sets. We recorded the number of groups of each size N (each group was recorded as 1 entry of group size N), and the number of individuals and the respective group in which they were found (a pair was recorded as two separate fish each in a pair). These two sets of data gave us different information. The first, gave us the average group size for each species and the second, gave us the most likely group size an individual would be found in. Resulting from the difference in data collection, the two sets did not correlate with each other, but the analysis appeared to be consistent with our observations and expectations.
Average group size was organized into a three-tier model. The first tier was those species with a low average group number (approximately 1.5). These were fish that were often sighted alone and occasionally paired (C. ornatissimus, C. reticulatus). The second group was those with an intermediate group size (approximately 1.75) and consisted of species whose observations were rarely consistent for group size (fish were found in groups ranging anywhere from 1 to 6 individuals, such as H. chrysostomus). The third and final group was those species with the largest average group size (approximately 1.9), including fish that were consistently observed in pairs (C. trichrous, C. citrinellus, C. trifasciatus). We assume that a high average group size may be a result of high pair fidelity in these species.

Our second data revealed little relation between species, despite being highly significant overall. We attempted to distinguish different groups here as we did previously for average group size, but the data seemed to suggest more of an overlapping progression through the species. However, it was still pertinent to our study and analysis. Species with the highest values for likely group size tended to be those found in the largest aggregations. H. chrysostomus could be found in larger groups, up to five or six individuals, and F. flavissimus was most often found in groups of three. Species with the lowest values for likely group size were the same as those for average group size. This is consistent with our assumptions because solitary observations will not be amplified and those of larger groups are. It is therefore easier to identify those species that are more often found in a larger group.

But can these findings be used as a basis of species classification, or at least identification? Our results suggest that species can be distinguished from each other on the basis of differences in their life histories. Bi-variable plots of log area and log distance as a function of species, showed that segregation on the plot was representative of species, that is, individuals were grouped together according to their species based on these characteristics (figure 6). The plot of night fidelity to group size as a function of species, showed a distinct
spread of the species across the range of available niches in the habitat of study. This result suggests that certain species exhibit behaviors that remain consistent with each other across the continuum of possible life history traits. For instance, *C. trichrous* exhibits several consistent behaviors such as high sleeping location fidelity, high pair bond and small range size, these behaviors can be correlated with each other to form a profile of the species. At the same time, certain species appear to be less predictable in their behaviors and these behaviors often do not relate to each other logistically. *C. reticulatus* appears to display relatively unpredictable patterns across the suite of behaviors. While this unpredictability makes it difficult to understand the underlying factors that govern these behaviors, they still set the species apart from the others based on the profile these behaviors create. These profiles could be related to the niches these species occupy and also distinguish them from other species using this niche coupled with additional behaviors and environmental factors governing life histories. This study was successful in showing that a spread of species could be produced combining home range area, fidelity to sleeping location, and group size, however, we could not define species solely on the basis of life history traits that we analyzed.

**Future Research**

Though we were able to successfully characterize different behaviors and use them to potentially distinguish different species, we were only able to do so for a limited number of our target species. In order to see the “big picture” a more intense study needs to be conducted including a greater number of species, a wider array of life history traits sampled, more replicates, and a longer study period. The more traits sampled and more replicates gathered, the higher the degree of separation that could be used to distinguish species from one another and lead to a better understanding of the family as a whole. Additionally, studies
in different habitats would better characterize the species behavior on a larger spatial scale. This may help us to understand subtle differences between various habitats.

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Literature Cited


