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Diet and Territory Size of Butterflyfish in Habitats with Varying Coral Cover and Composition

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DIET AND TERRITORY SIZE OF BUTTERFLYFISH IN HABITATS WITH VARYING CORAL COVER AND COMPOSITION

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Abstract:

Given the highly stochastic nature of larval supply, coral reef fish may often settle in sub-optimal habitats with limited prey. This study examines the foraging and territorial habits of a coral feeding butterflyfish, Chaetodon baronessa, *living in two contrasting habitats with markedly different coral prey. In exposed front reef habitats, where coral prey was highly abundant, C. baronessa was highly selective in its choice of prey and aggressively maintained small territories. In contrast, in back-reef habitats where coral prey was scarcer, C. baronessa was more generalist in its choice of prey, and had larger territories that were only weakly defended. The contrasting habits of C. baronessa in different reef habitats are consistent with predictions of optimal foraging theory, in that dietary specialisation and territoriality are reduced to maximise food intake where prey is less abundant.*

Introduction

Prey acquisition is fundamental to the biology and ecology of all living organisms. Life must be fueled by energy, and any organism's acquisition of the energy is often variable. Species are sometimes presented with a wide range of resources, and in natural settings, consumers are rarely limited to one prey type or foraging location. Assuming that animals have some choice in what they are consuming, these choices are likely to have widely varied consequences (Vincent *et al.*, 1996). Foraging behaviour potentially has far-reaching implications for the well-being and general evolutionary 'fitness' of an animal (Hughes, 1980; Pyke, 1984).

In many groups of consumers, we see a great deal of diversity in morphological and behavioral variations in foraging strategies (Hughes, 1980; Pyke, 1984). Increased diversity within a sympatric group often leads to a corresponding increase in the specialization of individual species with respect to food acquisition (Robinson and Wilson, 1998). In some animals, specialization becomes evolved to an extreme level, with associations very near to obligatory symbiosis.

In some cases, foragers must choose the principal components of their diet or the primary foraging location (Werner and Hall, 1974, Vincent *et al.*, 1996). If we equate dietary breadth to specialisation, then consumers should be specialists when resources are abundant and more generalist when resources are scarce (Werner and Hall, 1974; Pyke, 1984). Optimal foraging theory predicts that a consumer should also specialise on that resource which yields the highest returns (in terms of energy) (Robinson and Wilson, 1998). Thus we would expect a specialist to exclusively consume the optimal resource when it is sufficiently available (Chesson, 1983). In some cases the most profitable prey type is not abundant, and searching to find this prey requires more energy than is returned in its acquisition (Ritchie, 1998). In such cases, it is a trade-off between energy expended to acquire prey and energy gained through consumption of the prey (Vincent *et al.*, 1996). In some situations, it may be more beneficial for a consumer to be a generalist. OFT predicts that animals should be specialists and consume the most profitable food when it is sufficiently available to ultimately return more energy than other prey (Pyke, 1984).

In some situations, it also becomes most profitable for individuals to defend a particular resource, however it may not always be economically viable for an animal to aggressively defend a territory (sensu Brown, 1964; Hixon, 1980; Tricas, 1989). In cases where preferred resources occur in dense patches, animals may find it most profitable to defend a concentrated resource from other competitors. If resources are limited and the animal must cover a wide area to forage, it is then not feasible to expend a large amount of energy defending this large patchy resource (Ritchie, 1998). In areas where resources are highly abundant, it may be profitable to aggressively defend a small territory rich in resources.

Territoriality has been related to dietary specialisation in some species. In some pomacentrids, dietary preferences changed with territory size. Due to increased availability of preferred resources, herbivorous damselfish fed in a more selective manner (Jones and Norman, 1986). In this case, the authors suggested

that food supply was a consequence of territory size rather than a determining factor. However, many studies have attributed territory size to the availability of resources (eg, Irons, 1989; Tricas, 1989, Righton *et al.*, 1998).

Maintenance of a territory must occur in a manner that restricts competitor access. Aggressiveness in a foraging context is predicted to increase in a similar fashion as territoriality. If resources are abundant enough, then individuals need not compete aggressively. However, as resource availability decreases, dense patches of prey may elicit exaggerated aggressive behaviour in a territorial fashion. As aggressive behaviour requires a significant expenditure of energy, this may actually not be a beneficial strategy in situations where energy returns from the aggressive behaviour are insufficient to support the energy expended. These complex trade-offs are thus far usually examined in theoretical and mathematical modelling contexts, as accurate measurement of variables such as those listed above are near impossible to obtain (Vincent *et al.*, 1996; Ritchie, 1998; Robinson and Wilson, 1998).

The triangular butterflyfish, *Chaetodon baronessa*, offers the opportunity to study consequences of foraging behaviour as it exhibits variability in both dietary preference as well as territory maintenance. It can also be observed in a natural setting, allowing for a better understanding of the fishes' natural behaviours.

Methods

This study was conducted between January and April 2000, at Lizard Island (14°40'S, 145°27'E), on the northern Great Barrier Reef, Australia. The foraging behaviour of *Chaetodon baronessa* was studied at each of four sites; South Island, Coconut Beach, Osprey Islet, and Corner Beach. The four sites were purposely chosen to reflect differences in total coral cover as well as differences in coral composition. South Island and Coconut Beach were situated on the south-east side of Lizard Island and directly exposed to the prevailing South East Trade winds whereas Osprey Islet and Coconut Beach were on the north-west side of the island and relatively sheltered. At exposed sites (South Island and Coconut Beach) hard coral cover was in excess of 50% and dominated by the tabular coral, *Acropora hyacinthus*. In contrast, hard coral cover at sheltered sites (Corner Beach and Osprey Islet) was typically less than 15% and soft corals (family *Alcyonacea*) dominated the reef benthos.

The dietary composition of butterflyfish was assessed during feeding observations, in which replicate fish were followed at a distance of approximately one meter, which minimised disturbance of the fish's natural behaviour following Reese (1975). Whilst observing fish, the number of bites taken from each different coral species and other benthic substrates was recorded. Scleractinian corals on which butterflyfish were seen to feed were identified to species, but other substrates were categorised to one of seven general categories (Table 1)

The optimal duration for feeding observations was determined during an initial pilot study, in which ten replicate fish from both South Island and Osprey Islet were observed for a total of 10 minutes. During these ten-minute observations both the cumulative number of different species and cumulative number of bites consumed were recorded at 1-minute intervals. The optimal duration for feeding observations was then determined based on the minimum period necessary to adequately assess dietary composition and also maximize precision in estimates of feeding rates. In all cases, there was no significant increase in number of different prey species consumed after three minutes of observation. Moreover, precision in estimates of feeding rates was relatively uniform for all periods greater than two minutes. Consequently, all subsequent feeding observations were conducted for three minutes.

A total of 50 replicate fish were each observed for three minutes at every site (South Island, Coconut Beach, Osprey Islet and Corner Beach) to assess dietary composition. The proportional use of the main coral species was then compared to their availability at each site, to assess the selectivity of butterflyfish. Selectivity was determined using selection functions following Manly et al. (1993). The availability of coral species was assessed using replicate 10m line-intercept transects, and categories used in the identification of benthic taxa were the same as those used to assess dietary composition of butterflyfish.

To test how aggressively butterflyfish defended their home range against conspecifics, interactions of all butterflyfish were recorded in all observations. Interactions were grouped into two categories, first a "chase" when the observed fish chased away another fish, and secondly, a "chased" category when the individual was chased by another fish. (Data is taken from the 200 individual feeding observations). For all fish observed, incidents were recorded when the subject either chased another fish or was chased. The species of the fish interacted with was also recorded.

In an initial pilot study, fish were observed for a total of 30 minutes to assess territory size. The position of individual butterflyfish was recorded at 45-second intervals. The cumulative home range was then calculated after 7.5, 15, 22.5, and 30 minutes. Analysis of 12 replicate fish in this manner showed no significant difference in territory size after 15 minutes at either site. Consequently, all territory observations were conducted for 15 minutes.

To assess home range of *C. baronessa*, fish were monitored for 15-minute periods. Territory observations were made using several (8-10) metal washers flagged with colored tape. These washers were dropped and moved to fit the boundary of the fish's movement. After 15 minutes, the position of the washers was recorded and measured in a two-dimensional coordinate system. The area of the territory was then calculated using the greatest polygon to fit the recorded boundaries.

Table 1. Benthic categories used in assessing the dietary composition of butterflyfish and measuring prey availability at Lizard Island.

Hard Coral Categories:

Acropora aspera	Diploastrea heliopora	Montipora hispida
Acropora cytherea	Echinopora lamellosa	Montipora hoffmeisteri
Acropora digitifera	Echinopora mammiformis	Montipora monasteriata
Acropora donei	Favia favus	Montipora venosa
Acropora florida	Favia lizardensis	Montipora verrucosa
Acropora formosa	Favia pallida	Other Montipora spp.
Acropora gemmifera	Favia speciosa	Pavona maldivenesis
Acropora grandis	Favia stelligera	Platygyra daedalea
Acropora humilis	Favites abdita	Platygyra sinensis
Acropora hyacinthus	Favites halicora	Platygyra verweyi
Acropora intermedia	Fungia simplex	Pocillopora damicornis
Acropora loripes	Fungiidae	Pocillopora eudouxi
Acropora millepora	Galaxea astreata	Pocillopora meandrina
Acropora monticulosa	Galaxea fascicularis	Pocillopora verrucosa
Acropora nasuta	Goniastrea retiformis	Porites lobata
Acropora robusta	Hydnophora exesa	Other Porites spp.
Acropora sarmentosa	Hydnophora microconos	Povona varians
Acropora secale	Isopora cuneata	Psammacora contigua
Acropora selago	Isopora palifera	Psammacora digitata
Acropora valida	Leptastrea transversa	Sandalitha robusta
Astreopora myriophthalma	Leptoria phrygia	Seriatopora hystrix
Coeloseris mayeri	Lobophyllia hemprichii	Stylophora pistillata
Cyphastrea spp.	Montastrea spp.	Symphyllia recta
Dendronepthea spp.	Montipora efflorescens	Turbinaria spp.

Other categories:

Feather hydroid	Non-Coralline Hard Substrate	Sarcophyta spp.
Lobophyta spp.	Sand	Sinularia spp.

Results

Dietary Composition & Electivity

At South Island, *C. baronessa* included 7 main categories of prey, while using 12 main categories at Coconut Beach (Figure 1). However, it was clear that *C. baronessa* had a diet primarily consisting of *A. hyacinthus* at both sites. At Corner Beach, *C. baronessa* used 11 prey categories with a shift to include *Pocillopora damicornis*, but there was no dominant prey choice. At Osprey Islet, 10 main categories were used; however, there was still no single dominant prey choice. The two most common prey categories were *P. damicornis* and *A. florida* (Figure 1).

Electivity indices indicate that *C. baronessa* uses *A. hyacinthus* at exposed sites (South Island and Coconut Beach) in a greater proportion than its availability (Figure 1). No other coral was selectively eaten at either site. At Corner Beach, *C. baronessa* selectively consumed *P. damicornis, A. florida*, and *Galaxea* spp.; however, total consumption of these corals was not as exaggerated as *A. hyacinthus* at South Island and Coconut Beach. At Osprey Islet, only *P. damicornis* and *Coeloseris* spp. were selectively eaten.

Aggression

C. baronessa was observed to chase fish 32 times at exposed sites (South Island and Coconut Beach) while only chasing fish 10 times at sheltered sites (Osprey Islet and Corner Beach). Data are taken from the 200 feeding observations.

Territory Size

A total of 69 territories were measured. Mean territory size varied at different sites for *C. baronessa* (Figure 2). Mean
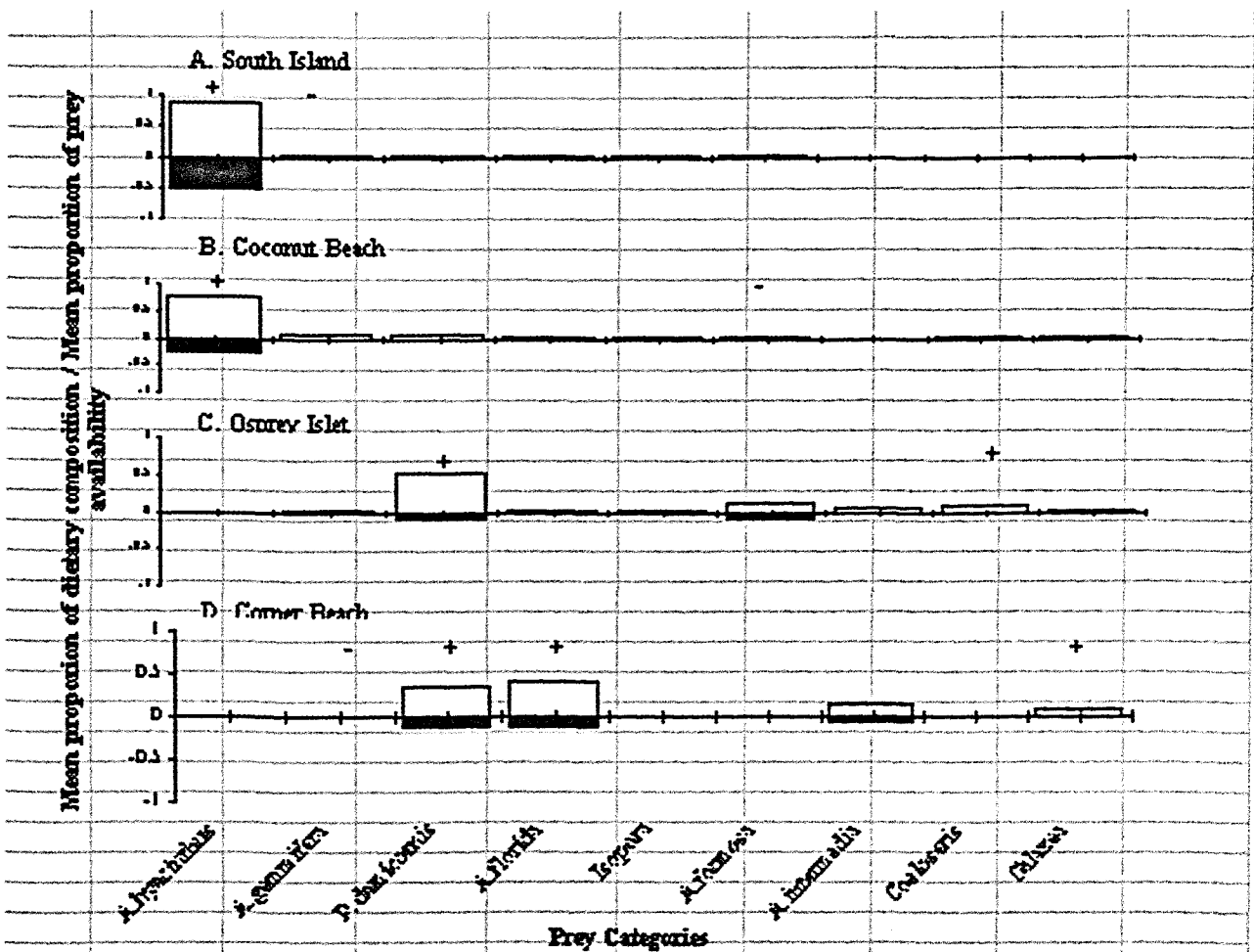

Figure1. Electivity results for selected prey categories used by C. baronessa at four locations at Lizard Island. Positive values (white bars) are proportion of dietary composition based on total number of bites (ie., 1=100%). Negative values (grey bars) are proportion of availability based on total hard coral prey available. "+" symbols indicate taxa which were used significantly more than expected from their availability while "-" indicates significant avoidance of a particular prey category. Data are from three minute feeding observations (n=50).
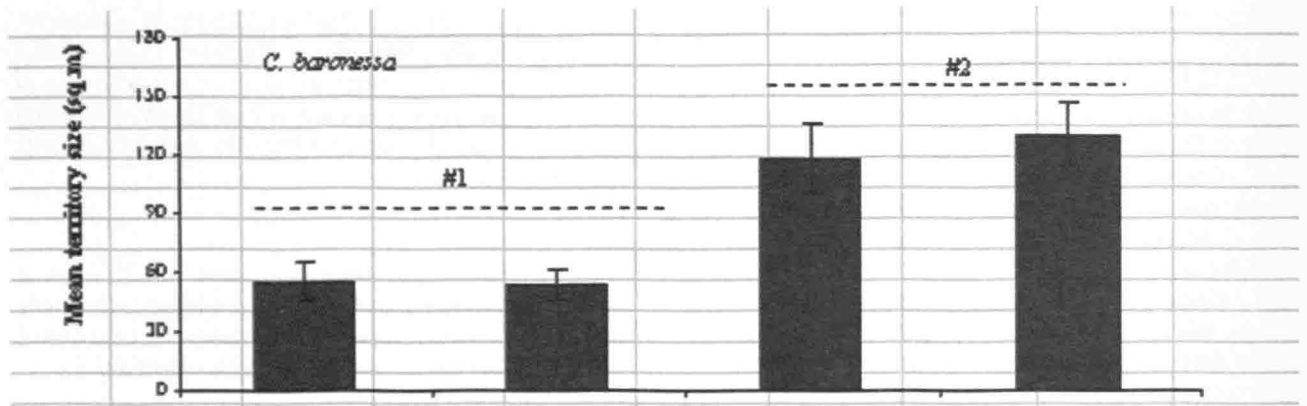
Figure 2. *Mean territory size for butterflyfish from four locations at Lizard Island. Values are means and standard errors of estimates of foraging area (sq.m.) from replicate fifteen minute observations. (n=10). dotted lines indicate homogeneous subsets identified by Tukey's HSD post hoc test.*

territory size at South Island was 55.3 (± 9.3 S.E.) m2 and at Coconut Beach was 53.9 (± 7.7 S.E.) m². Corner Beach and Osprey Islet had mean territory sizes of 112.0 (± 17.8 S.E.) m² and 125.4 (± 16.3 S.E.) m², respectively (Figure 2). ANOVA results for territory size indicate that the difference is significant (p < .001) among sites. The two exposed sites were identified as a homogeneous subset post hoc by Tukey's test, as were Corner Beach and Osprey Islet.

Discussion

OFT predicts that when optimal prey is available in sufficient amounts, a consumer should selectively use this resource (Stephens and Krebs, 1986; Robinson and Wilson, 1998). If *A. hyacinthus* is an optimal resource, then *C. baronessa* is an optimal forager, as these results suggest that *C. baronessa* behaves in an optimal manner – specializing when optimal prey is abundant, and generalizing when optimal prey is not available. Other authors have predicted this 'flexibility' in optimal foragers (eg, Levins, 1962, 1968; Lowe-McConnell, 1996; Robinson and Wilson, 1998).

Foraging behavior may have implications in further areas, such as growth, reproduction, and survivorship (Sale, 1980). It is unlikely that diet alone would be responsible for variation in such major characteristics, but it is an important indicator that subtle variations in habitat (and subsequent variations in condition) could have impacts greater than previously expected. Gradients at larger scales have been documented in other characteristics such as abundance, growth, recruitment, and community structure (*eg*, Ogden and Ebersole, 1981; Done, 1982; Sale, 1984; Bell *et al.*, 1985; Choat and Ackerman, in prep.).

Variation in territory size of *C. baronessa* may also be explained in terms of OFT. Territory size is inversely related to optimal resource availability, while at the same time smaller territories are more aggressively defended. Similar relationships

have been found by other authors and suggest that the resource in question is energetically 'valuable' enough to justify the extra energy expenditure necessary to maintain such rigorous territories (Jones and Norman, 1986; Nakano, 1995; Righton *et al.*, 1998). It is likely that in sheltered sites, aggressively defending small territories is not a beneficial strategy. Perhaps the available prey is of insufficient quality, or perhaps it is an issue of quantity. Larger size of *C. baronessa* territories may be a function of suitable prey availability and basic energetic requirements of the fish (Hixon, 1980; Norman and Jones, 1984; Jones and Norman, 1986; Tricas, 1989; Righton *et al.*, 1998).

In summary, it is apparent that *C. baronessa* shows a difference in dietary preference as well as a difference in territory size. This could be due to a change in the fish's behaviour or due to the availability of prey in varying habitats. Butterflyfish provide an ideal vehicle for testing Optimal Foraging Theory, and further investigation into life history variations and experiments to determine the driving factors behind varying foraging behaviour is necessary to fully realise the implications of these varied behaviours.

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Faculty comments:

Mr. Berumen's mentor, Raj Kilambi, had this to say about his student's work:

I have known Michael Berumen since he enrolled in my Fish Biology class in the spring of 1999. The main course material centered on fish population dynamics. Throughout the semester, I had the opportunity to get to know Michael in a more personal way. I frequently used his assignments as model examples for the class. He worked with a natural inclination for producing neat and accurate work. He treated seriously even minor homework assignments. It was apparent in our discourse that he appreciated the value of the methods we used to study population dynamics more than most students.

Michael Berumen and friend

In group work, including many of our labs, Michael demonstrated a very diplomatic ability to serve as a leader while openly receiving input from all members. Although sound in his own reasoning and problem-solving abilities, he nevertheless encouraged the whole group to consider the issues at hand and contribute ideas. From personal experience, I know that Michael actively seeks advice from other sources and gladly adopts suggestions for improvement in all manners of affairs.

My first experience with Michael's research abilities came soon with the class term papers. For his paper on various aspects of salmon life history he used original data from Australian journals to compare two populations of the salmon. He displayed a thorough understanding of the material and methods used by the researchers in this field. It is highly uncommon to encounter an undergraduate student with the ability to utilize primary sources and handle data in the manner Michael did, let alone encounter a student in his first year of college with this kind of proficiency.

Our conversations always came back to one subject: marine biology. He regularly would want to know how concepts and methods we studied were applicable in tropical or marine environments. He took the initiative to spend the past year in Australia exploring this new field for him. To obtain a strong foundation in the subject he had only independently studied previously, he enrolled in a full load of upper level classes at James Cook University. Having succeeded in these classes, he then arranged to remain in Australia and conduct independent research for a further 7 months.

Michael has returned an even more mature and developed scientist. I am now serving as his honors thesis advisor. His work demonstrates both a capacity for research and a mastery of his topic which involves foraging theory applied to butterfly fish. Recognition for his efforts has already begun as he has had papers accepted for presentation at two major international conferences, one in Indonesia and one in South Africa.

The research, which he has submitted here, represents only a small portion of his accomplishments. What is presented is quality work. This work is the foundation of his thesis in which he greatly expanded on these ideas. He has been recognized not only at these international conferences, but also by USA Today, which named him to the All-USA Academic Team this year. From the standpoint of someone who has spent a great deal of time in the field of fish biology, fish growth and population dynamics, I am confident in saying that Michael is doing great work here. His contributions are doubtless going to be meaningful and continuing in his field..

Morgan Pratchett, the faculty person who supervised Mr. Berumen's research at James Cook University wrote this about him:

I have known Michael for two years, since he enrolled in a final year Coral Reef Ecology course which I teach at James Cook University, Australia. Michael was clearly amongst the top students in this class, demonstrating an unsurpassable depth of knowledge and commitment to study. Michael was also a very well presented and articulate person, which was why I agreed to supervise him while he undertook a research project for the fulfilment of his honours degree.

During the course of his research project I worked very closely with Michael both as much as a colleague as his mentor, and I came to know him very well. Michael displayed considerable aptitude for scientific research, as he adopted a novel and ingenious approach to the research and completed his proposed project with considerable efficiency and apparent ease. Michael's thesis, which explored the ecological cost of differential prey availability for coral reef

dwelling fish, more than fulfilled the requirements for his honours degree and makes a substantial contribution to the field of foraging theory. Michael's research is leading to several major publications in internationally recognized journals, which would be highly commendable even for studens at a Masters of Ph.D. level.

This research has considerable potential to alter the current perception of the role that particular fish play within the dynamics of coral reef ecosystems. I know that Michael had a great deal of difficultly selecting such a small portion of his work to submit to you. His research is broad and encompasses many components, all of which are highly relevant to his topic. I do believe that the piece he has submitted to you is sound and tells a nice story. It mirrors the bigger results which his project has thus far revealed. The research is far from complete, however, and I look forward to participating with Michael in the continued exploration of these areas. His fresh and confident approach to this work convinces me that he will continue to be successful as well.