NETWORK ANALYSIS OF THE TAHITIAN RAY (*HIMANTURA FAI)* IN MO'OREA, FRENCH POLYNESIA: IS THERE SOCIAL STRUCTURE TO THE FEEDING FRENZY?

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*Abstract. S*ocial structure is key to a species' biology and ecology. Relations within a population can have important fitness consequences, but only recently have researchers been able to explicitly measure and quantify these relationships through network modeling. Social network analysis is the study of social groups as networks of nodes connected by social ties. In this study, network analysis is implemented to determine that there is a social structure within an aggregation of *Himantura fai* at feeding excursion sites. An ethogram defining *H. fai* behaviors is compiled. A sum of interactions network is subdivided into five behavior networks to allow for further quantification of the relations within the aggregation. Size, color, and sex are found to be correlated to dominance, and an order of dominance is determined, with large females at the top and the smaller of both sexes at the bottom. To address the confounding factor of human presence at the study sites, the effects of feeding excursions on *H. fai* behavior are investigated. The variation and frequency of interactions between individuals increase with the presence of a feeder, but the amount of time spent interacting with at least one other individual is unaffected by human presence. Overall, this study investigates the effects of feeding excursions on *H. fai* behavior and utilizes a relatively new analytical tool to determine the social structure of *H. fai*.

Key words: elasmobranch; feeding excursion; animal behavior; network modeling; dominance; batoid; Myliobatiformes; Dasyatidae

INTRODUCTION

The social structure of a population plays a key role in many aspects of a species' ecology and biology. It influences a species' genetic makeup, the spread of disease or parasites, and the ways organisms communicate and exploit their environment. The study of social structure in non-primate animals has received little attention because of the difficulty in abstracting social structure from the description of association patterns between individuals (Lusseau *et al*. 2005). Network analysis, however, has been shown in recent parallel studies on other non-primate organisms to be an effective tool that facilitates inference about social structure in a group. Network models have been used in a variety of fields, originating in mathematical graph theory and expanding to the study of sociology, business, markets, political science, ecology, epidemiology, and more recently, ecosystem ecology. This relatively new method of analysis has seen little application to animal systems, but has potential to be a useful tool in quantifying relational data for understanding overall structure and the roles of individuals within a group, or network (Wey *et al*. 2007). In this study, a social network analysis was performed to evaluate whether *Himantura fai* feeding behaviors are socially structured.

In Mo’orea, French Polynesia, shark and ray feedings are a major tourist attraction. Ecotourism is a rapidly growing industry, as humans are fascinated by nature and have a high willingness to pay for the ability to observe wildlife up close in their ‘natural’ habitat (Vignon *et al*. 2010). The effects of wildlife feeding excursions are controversial. Excursions spread awareness, promote conservation, and generate economic benefits for the non-consumptive utilization of wildlife. However, due to an increased density of individuals in a small area, long-term feedings are suspected of impacting local ecosystems, altering natural behaviors and populations, increasing parasitic loads, and engendering dependency and habituation towards humans (Orams 2002). While the effects of feeding excursions have recently become focal topics in academic literature, the effects on behavior has yet to be quantified (Gaspar 2008).

Elasmobranches in general tend to organize themselves into loose aggregations with sexual and size segregation (Silliman and Gruber 1999). However, rays are usually depicted as solitary in nature as, for most species, individuals are regularly sighted alone (Carrier *et al*. 2004). *Himantura fai (Myliobatiformes:Dasyatidae),* commonly known as the Tahitian ray or the pink whipray, is the only species in the Indo-Pacific region to regularly be sighted in groups (Vaudo and Lowe 2009).

Despite a high ecotourism focus on rays, these elasmobranch mesopredators have largely been overlooked in the academic field. Relatively few studies of elasmobranch community structures exist, and no studies of ray social structures have been published (Vaudo and Lowe 2009). Network analysis is a promising tool for the study of sociality in *H. fai*. In this study, this recently developed analytical technique will be applied to *H. fai* interaction behaviors during feeding excursions. Since this species is commonly seen in groups, there exists the possibility of a social structure among *H. fai* in natural conditions. For this study, feeding excursion sites were chosen due to the daily recurring aggregation of individual rays in one area, which provided an opportunity to study a large volume of interactions and high density of individuals in an easily accessible, shallow site with clear visibility.

The first step in this study was to define social behaviors by compiling an ethogram for *H. fai*. Interaction frequencies in the presence and absence of a feeder were analyzed to determine whether feeding excursions change the frequency and types of interactions between individuals. It was hypothesized that feeding excursions increase the incidence and variety of interactions between individuals. Second**,** a network analysis was conducted to evaluate whether feeding excursions result in an active social association or a simple spatial aggregation of *H. fai*. The null hypothesis was that there is no social structure; intraspecific interactions are solely a result of close proximity to others to obtain food. The alternative hypothesis was that there are social relationships within the group, suggesting an active social association among *H. fai.*

METHODS

Study organism

H. fai has a dorsoventrally flattened body, enlarged pectoral fins, fine-tune senses, and a venomous spine at the base of a long, whip-like tail (Figure 1). This benthic ray is found in the Indo-Pacific region off the intercontinental shelf, often near coral reefs about 200-300 meters offshore and usually in subtidal sand microhabitats (Vaudo and Lowe 2009). They can be found up to 40 meters deep (Gaspar *et al*. 2008).

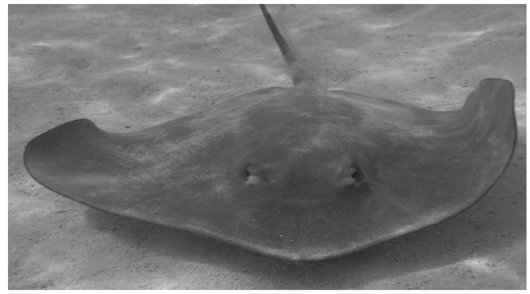

FIGURE 1: *Himantura fai*, Taken by E. Furst

In elasmobranches, females tend to mature to a larger size than males. One can determine whether a male is mature based on degree of clasper calcification (Vaudo and Lowe 2009). Rays also have dental sexual dimorphism, with males developing sharp teeth during mating season. During mating,males grasp onto the females, and bite to aid in staying mounted. Females have thicker skin associated with this mating behavior, and mating scars create distinct patterns unique to each individual (Roy Caldwell, UC Berkeley, personal communication).

While many species can occasionally be observed resting in groups, *H. fai* is the only species in the Indo-Pacific region to be found regularly, with more than 40% of sightings, in groups. Individuals were considered a part of a group if they were less than 1 m from another individual (Vaudo and Lowe 2009).

Elasmobranches are generally solitary foragers, and are very opportunistic in what and how they acquire prey. Rays typically forage for invertebrates on the sea floor, locating prey through electrosensory and olfactory senses (Jordan 2008). Their mouth consists of a bony plate, a sucker, and jaws powerful enough to crush shellfish such as clams, mussels, and bivalves. They feed by biting pieces of sessile invertebrates, excavating buried prey by rhythmic flapping of the rostrum and pectoral fins, or by hydraulically mining prey by jetting water through the mouth. It is rare for rays to prey on fish in the water column (Carrier *et al*. 2004). Chondrichthyes in general are nocturnal foragers, but adapt to seasonal changes in feeding patterns due to their opportunistic tendency for prey capture (Motta 2001). At both feeding sites, *H. fai* are fed small pieces of tuna, mackerel, or chicken by hand (personal observations).

Study sites

Two sites were examined in this study (Fig. 2). At site 1, a lagoon near the motu Tihura (17˚29′17.64″ S; 149˚54′1.60″ W), ray and shark feeding excursions occur daily. At site 2, below the balcony of Te Honu Iti, a restaurant in Cook's Bay (17˚30′17.95″ S; 149˚49′8.39″ W), a worker feeds rays around 8 pm daily, except Sundays. Both sites have a group of *H. fai*, ranging from 8-18 individuals, which visit daily (personal observations).

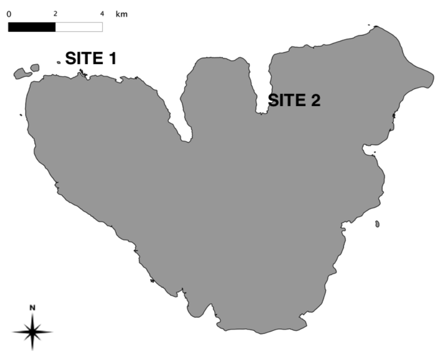

FIGURE 2: Map of Study Sites, Labeled

Effects of feeding excursions on H. fai behaviors

An ethogram was complied to denote the typical behaviors among the *H. fai* group (Table 1, see appendix). This ethogram was defined off of observed behaviors, and is not meant to be interpreted as significantly distinct in meaning for *H. fai*. The ethogram was presented to three fellow researchers, and tested in the field to ensure that the defined behaviors are objective and repeatable.

All types of behaviors were viewed at site 1, due to the increased water depth and increased number and variability of rays. A weighted tripod was systematically dropped within 4 meters of the anchor, and video was later analyzed to determine the frequency of each behavior observed, including the percentage of time individuals were solitary or absent. Rare competition or cooperation behaviors unlikely captured in this video snapshot were noted when witnessed. The times of feeders' arrivals and departures at the site were recorded and cross-linked to the video analysis to determine how the presence of one or more feeders influences *H. fai* behaviors. Analysis for the effects of feeding excursions on behaviors was conducted using JMP (JMP, Version 9).

Estimating social structure of H. fai

All behavioral observations at site 2 were conducted at night since that is when the feedings took place. The site was limited by the availability of light, and thus the area of interest was chosen to be a 17 x 15 m^2 plot of shallow water lit by the restaurant. Eight individuals at site 2 were chosen as focal individuals. All rays that regularly visited the site and could be identified to an individual level were included as focal individuals, but identification was limited by the ability to distinguish between individuals with the unique dorsal patterns of nicks, lesions, and mating scars. One focal individual was chosen upon arrival at the site and was tracked until feeding occurred, resulting in between 1 and 1.5 hours of observations for each focal individual. The focal individual's behaviors towards others and others' behaviors towards the focal individual within this area were recorded, along with the duration of each interaction. All individuals that interacted with the focal individual, but could not be identified to an individual level, were clumped into an "other" category.

Network analysis was used to determine the social structure at site 2. Network parameters, including individual's centrality (structural importance to the group), indegree (the number of ties directed towards an individual), outdegree (the number of ties originating from the focal individual), and node degree (the total number of ties an individual has) were extrapolated from the network analysis (Wey *et al*. 2007). These parameters were used to determine if there is a social structure within a feeding site aggregation. All network analysis was done in R (Ihaka and Gentleman 1996) using the igraph package version 0.5.4 (Csardi and Nepusz 2006).

Proxy for dominance

At site 2, the percentage of food each focal individual obtained was used as a proxy to indicate dominance, as food is limited in supply and can be assumed to be desired by all individuals in the aggregation. During the feeding, the amount of fish consumed by each identified individual was recorded. This data was then cross-analyzed with each individual's size and color to determine if these physical characteristics were correlated to dominance.

At site 1, the same methods were repeated to determine if there is a structure of dominance within a larger, more variable, and mixed-sex aggregation. The sex and size of the individuals that surfaced for feeding directly from a feeder's hand were recorded. Focal sampling was utilized when multiple feeders were present. Analysis for determining dominance was conducted using JMP (JMP, Version 9).

Results

Effects of feeding excursions on H. fai behaviors

H. fai are predominantly solitary while swimming. For example, all sightings were of mobile individuals and *H. fai* were observed as lone individuals in 90% of sightings outside of feeding excursions; 10% of sightings were of two interacting individuals (Fig. 3).

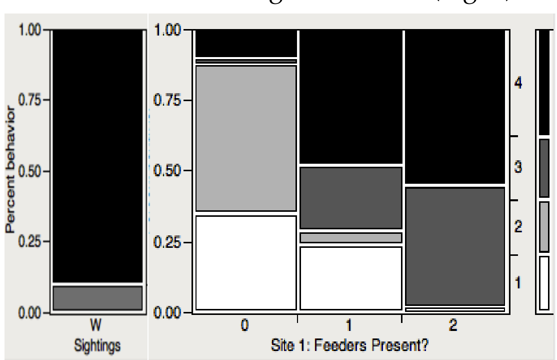

FIGURE 3: The Effects of Feeding Excursions on *H. fai* Behavior. The behaviors were categorized on the y-axis, where 1(white) represents an isolated individual, 2 (light grey) represents two or more individuals burrowing in close proximity, 3 (dark grey) represents two or more individuals interacting while mobile, and 4 (black) represents a mobile solitary individual. The continuity bar on the left represents behaviors reported during sightings outside of feeding excursion sites, where N= 21 individuals sighted. The continuity bars on the right represent behaviors observed at site 1. On the x-axis, 0 represents no feeders present, 1 represents a feeder being present but not adjacent to the individuals being monitored, and 2 represents a presence and close proximity to a feeder. N = 5.7 hours for 0, N= 2.2 hours for 1, and N= 1.7 hours for 2. Observation time for 0 was roughly tripled due to the large percentage of time recorded with no individual captured on screen.

The addition of feeders to a site increases *H. fai* mobility, but does not significantly alter the percentage of time individuals interact with others (Fig 3). However, the number of individuals one individual interacts with increases from an average of 1 to between 2 and 11 individuals when a feeder was present. With no feeders present at site 1, 45% of individuals were solitary, and 12% were mobile. 55% of individuals burrowed in close proximity to others, creating subgroups ranging from two to eight individuals. With a feeder present in the water, 72% of individuals away from the feeder were solitary, and 71% mobile. Directly adjacent to the feeder, 57% of behaviors were solitary, and 98% of individuals were mobile. There was a significant difference between *H. fai* behaviors depending on the proximity to and the presence of a feeder (ChiSquare Test, Pearson, df=6, X^2 =182.691, p=<.0001).

The addition of a feeder increases the variety of behaviors that *H. fai* exhibit (Fig 4). Six behaviors were witnessed when no feeder was present but sixteen behaviors were witnessed when individuals were in close proximity to a feeder.

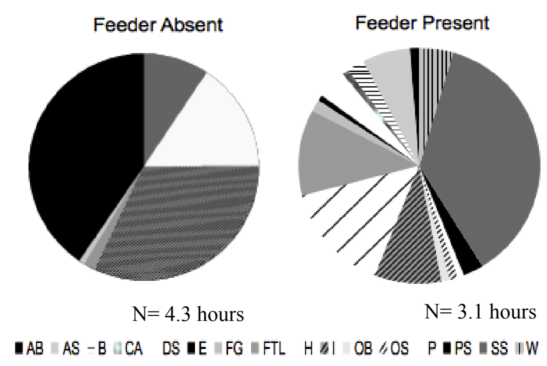

FIGURE 4: Variety of *H. fai* Behaviors in the Presence/ Absence of a Feeder. Each of the abbreviations above represent a unique behavior (see appendix, Table 1). A total of 9.6 hours of observations were analyzed. The number of hours (N) listed above excludes the time when no individual was recorded.

Estimating social structure of H. fai

There is a social structure within an aggregation of *H. fai* (Fig. 5). The width of the edges, or lines, represents the amount of time two individuals spent together. For example, ray 0 and ray 1 spent the most time interacting with each other, whereas ray 3 and 4 spent minimal time interacting. The absence of an edge represents the lack of interactions, as is the case between ray 0 and 4. No individual has a significantly greater centrality to the aggregation than the others, as the node degree for all individuals is between 5 and 7. See appendix for the matrices of data used in this network analysis (Table 2, see appendix).

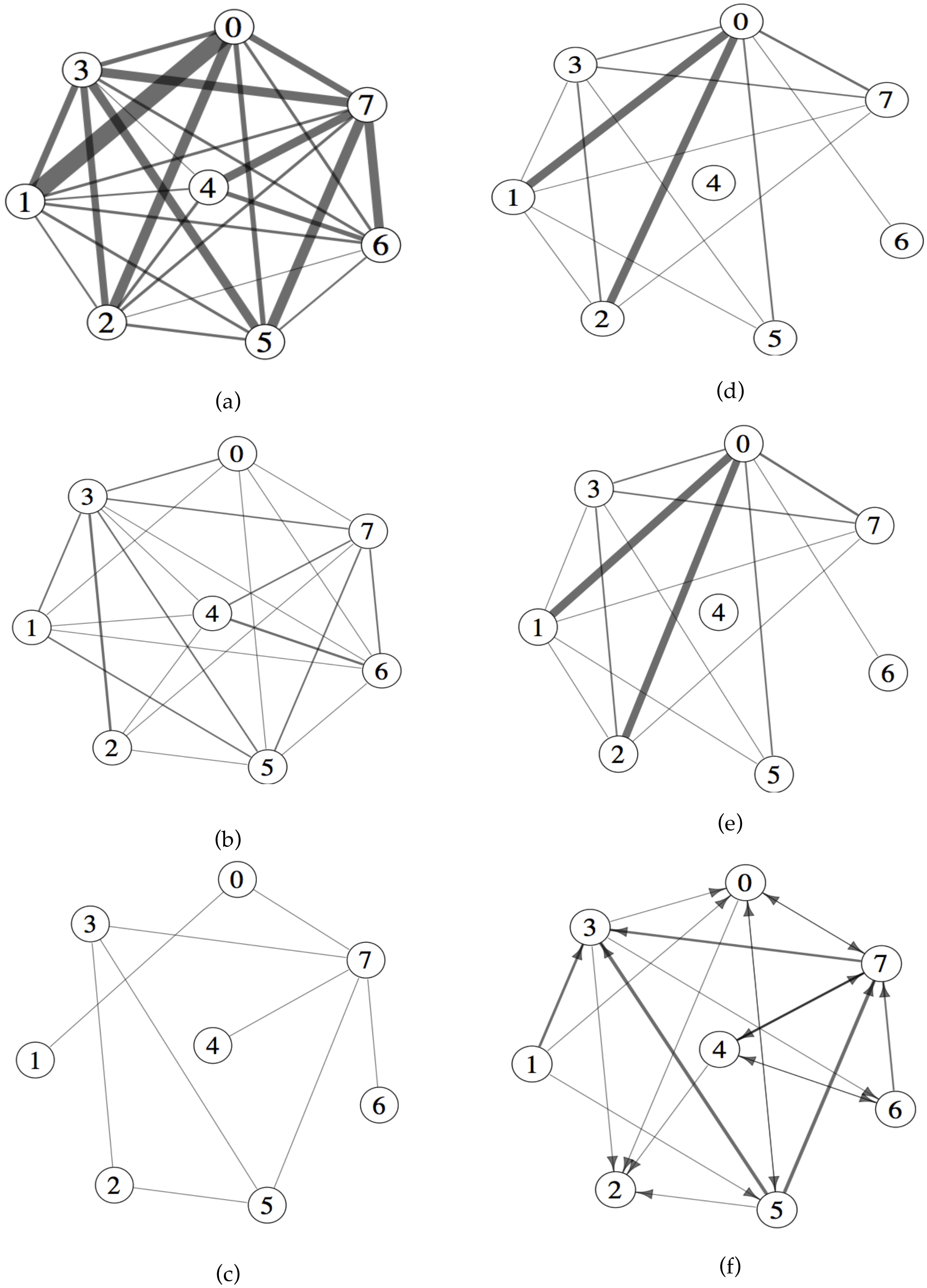

FIGURE 5: Social Networks for One Aggregation of *H. fai*. Eight focal individuals from site 2 were included in the social network analysis, each represented and labelled within a node. All networks visualize the relations among the individuals, with a thicker edge, or line, representing a greater amount of time two individuals spent together. The distance between nodes, or individuals was standardized to a Fruchterman Reingold layout as a visual preference. Fig. (a) through (e) are undirected, in which the interactions are communicative and symmetric. (**a**) Social Network for the Sum of Interactions, Undirected. (**b**) Social Network of AS Interactions, Undirected (**c**) Social Network of OS Interactions, Undirected. **(d)** Social Network of AB Interactions, Undirected **(e)** Social Network of OB Interactions, Undirected (**f**) Social Network of FTL Interactions, Directed. The arrow originates from the individual initiating the behavior.

The trends observed by graphically subdividing the sum of interactions network into five behavioral categories allows for the quantification of specific relations between individuals (Fig. 5b-f). For example, ray 2 and ray 5 only interacted while mobile, and did not associate in burrowing behaviors (Fig. 5b-e). Follow the leader interactions between this pair were unidirectional and initiated by ray 5. Other pairs, such as ray 4 and ray 6, have a bidirectional FTL interaction (Fig. 5f, table 1, see appendix).

Individuals within an aggregation have different measures of indegree and outdegree. (Fig. 5f). For example, ray 1 has an indegree of zero as no ties are directed towards this individual. This quantifies the data that no focal ray followed behind ray 1 while mobile. Ray 1 has an outdegree of 3, directed towards rays 0, 3, and 5, as ray 1 followed these individuals when mobile. Contrary to ray 1, ray 2 has an outdegree of zero and the maximal indegree within the aggregation. This quantification portrays that ray 2 did not initiate interactions with others, but others initiated interactions with ray 2 when mobile. Rays 0, 2, and 7 have the maximum indegree of 4, denoting that other individuals initiated interactions with these individuals the most. There are bidirectional ties between rays 4 and 6, rays 4 and 7, and rays 0 and 7 (Fig. 5f).

Proxy for dominance

Some specific individuals consume more of the food provided than do others (Fig. 6). For example, individuals 2 and 12 consumed significantly more fish than the other individuals. Larger individuals consumed significantly more than medium or small individuals. A large male was defined as approximately 1 m across, a mid-sized male was defined as between 0.8 m and 1 m across, and a small male was defined as a male between 0.6 m to 0.8 m. All the large individuals were light or pink-tinted grey, while other individuals ranged between true grey and black in color. All individuals at site 2 were males.

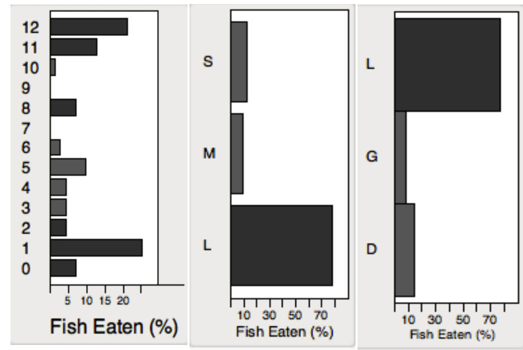

FIGURE 6: Association of Size and Color on the Percentage of Fish Consumed by Individuals at Site 2. On the y-axis, each number represents an identified individual (left). Specific individuals consume significantly more than others (left), and tend to be large in size (middle) and light in color (right). Legend: S= small, M= medium, L= large (middle). L= light in color, G= grey, and D= dark in color (right).

Females consume more fish than males when both sexes are present within an aggregation (Fig. 7). A large female was defined as a female between 1 m and 1.2 m across, a large male was defined as approximately 1 m across, a small female was defined as less than 1 m across, and a small male was defined as a male between 0.6 m to 0.85 m. Small individuals of both sexes never hovered at the surface to be fed by hand, and remained on the sea floor below.

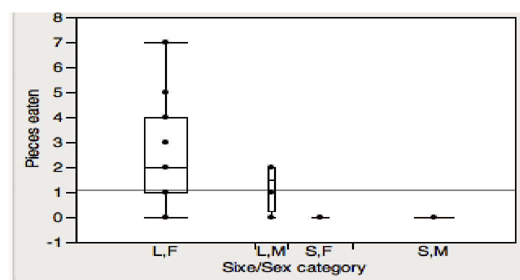

FIGURE 7: Size and Sex of Individuals Surfacing for Feeding by Hand at Site 1.

Males come to the surface for feeding significantly less often than female individuals do (Logistic Regression Test, df=1, X^2= 6.43, p=.01). Males only hovered at the surface to obtain food from a feeder when there were many people in the water and groups of tourists larger than 20 people occurred less than 20% of the time (Fig 8).

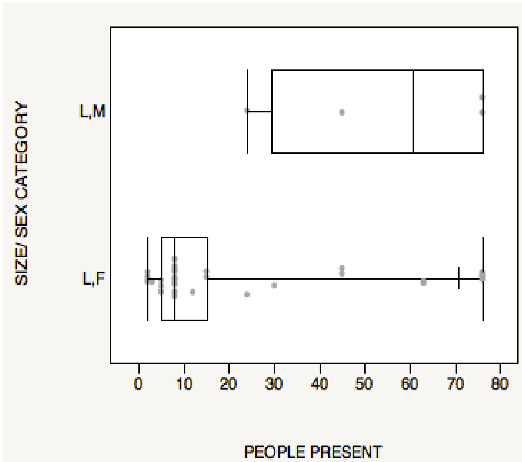

FIGURE 8: The Effects of the Number of People at Site 1 on the Type of Individuals that Surface. L,F represents a large female individual coming to the surface to feed directly from a feeder's hand, whereas L,M represents a large male. No small individuals were included in this figure as none surface to be fed.

Discussion

Effects of feeding excursions on H. fai behaviors

Feeding excursions do affect the behaviors of *H. fai* (Fig. 3). As *H. fai* can burrow at water depths that are difficult to observe, this study could not address whether individuals in truly natural conditions burrow in aggregations. However, when no feeders were present at site 1, and thus in the most natural-like conditions where individual rays can easily and repetitively be observed, individuals would tend to burrow in aggregations, ranging in size from two to eight individuals (55% of recordings, Fig. 3). With the addition of feeders to the site, *H. fai* become significantly more mobile (Fig. 3). Although in natural conditions *H. fai* tend to be swimming alone when sighted (Fig. 3), individuals are not typically solitary when mobile while a feeder is present. Also, the average number of other individuals that one interacts with increases two- to eleven-fold with the addition of a feeder to the site. This increased rate and number of interactions with others while mobile is hypothesized to be due to the limited area available near a feeder. Along with the increased number of intraspecific interactions, 10 additional types of behaviors were witnessed with the addition of a feeder to the site (Fig. 4). This suggests that feeding excursions in Mo'orea do alter the behaviors of *H. fai,* do increase the number of other individuals one interacts with, but do not alter the amount of time one individual spends alone or the amount of time spent interacting with at least one other individual.

In conclusion, feeders do have an effect on *H. fai* behavior. The effects of feeding excursions on a species are a controversial topic, as there are arguably a similar amount of positive and negative effects generated. The conclusion that feeding excursions in Mo'orea do alter the behaviors and the number of interacting individuals, but do not alter the overall amount of time spent interacting with others should not be considered a significant addition to this on-going debate. *H. fai* are opportunistic feeders that are exploiting their environment in this means, and no positive or negative conclusions will be drawn from this study. However, it is important to understand one more piece to this debate, and continue to determine whether feeding excursions are affecting the ecosystems in a significant manner.

Estimating social structure of H. fai

There is a social structure in an aggregation of *H. fai* (Fig. 5). The weighted edges demonstrate that one individual spends a greater amount of time interacting with specific individuals over others. There is an active social association among *H. fai* rather than a simple spacial aggregation of *H. fai*, as the ties between individuals differ from those expected if random.

No individual has a greater centrality to the aggregation's social structure when analyzing the presence or absence of relations to others (Fig. 5a). However, certain individuals, such as ray 0 and ray 1, spend an disproportionally greater amount of time interacting with others, which could suggest these individuals visit the site more regularly, have a more dominant position in the aggregation, or have a greater centrality in respect to time invested in relations with others.

Graphically subdividing the sum of interactions network into five behavioral categories allows for the quantification of specific relations between individuals (Fig. 5b-f). One can assess the amount of time individuals spend interacting while mobile versus burrowing. For example, ray 0 and ray 1 spend a great amount of time burrowing in close proximity but do not associate to a great extent otherwise. In this particular case, both ray 0 and ray 1 are larger, more dominant males who burrow adjacent to the feeding station. This suggests that ray 0 and ray 1 spend a great amount of time burrowing in close proximity due to similar dominant positions within the aggregation, but do not tend to associate much beyond this role. Network analysis of the Follow The Leader behavior allows for the quantification of a relation's directionality between individuals. Bidirectionality within the FTL interaction network suggests a mutual association and the possibility of a similar position within the group. Variation in directionality reveals that individuals within an aggregation have different measures of indegree and outdegree (Fig 5f). The ability to analyze Follow The Leader interactions using a directed network adds another level of complexity to the social structure among *H. fai.* Each network reveals additional intricacies of the relations among the eight focal individuals and adds to an understanding of the overall social structure.

Proxy for dominance

There is a clear structure of dominance at both an individual and group level (Fig 6-8). The amount of fish consumed by one individual was used as a proxy for dominance, as it is limited in supply and can be assumed to be desired by all individuals within an aggregation. In the single-sex aggregation at site 2, the larger, lighter colored male individuals consumed significantly more than the others, with specific individuals within that category consuming the majority of the fish provided (Fig. 6). With both sexes present within an aggregation, large females were the most dominant, followed by large males, and lastly by the smaller individuals of both sexes (Fig. 7). This was determined by the individuals that would surface to feed directly from the feeder's hand. Large females would surface regardless of how many feeders were present, whereas large males would only surface if there were many feeders (Fig. 8). Small females and small males never come to the surface to be fed, and only consume the fish that is secondarily dropped to the sea floor. Therefore, dominance within an aggregation is influenced by sex and size, and is correlated to color.

Significance/ Future research

Social network modeling and the use of a proxy for dominance has revealed a social structure within an aggregation for *H. fai.* Determining the social structure in an aggregation plays a key role in understanding the species' ecology and biology, as social structure influences the possible paths for the spread of disease or parasites, the group's genetic make-up, and the ways individuals exploit their environment (Lusseau *et al*. 2005). Just the knowledge of sex segregation within some but not all aggregations influences the design for conservation plans, or for the management of aquatic ecosystems (Clark 1993; Bodin *et al*. 2006). Although this study analyzed only one sex-segregated aggregation with network modeling, it portrays the feasibility of expanding the use of this analytical tool to other sites, a mixed sex aggregation, or an aggregation with other species of batoids. This study is one more addition to the recent pool of literature that is expanding the use of network modeling into the field of animal behavior (Armand *et al*. 2011; Croft *et al*. 2005; Cross *et al*. 2005; Girvan and Newman 2002; Hock *et al*. 2010; Jacoby *et al*. 2010; Kasper and Voelkl 2009; Krause *et al*. 2007; Krause *et al*. 2009; Lusseau 2003; Lusseau *et al*. 2006; Oh and Badyaev 2010; Pinter-Toth and Griggio 2011; Sih *et al*. 2009; Vital and Martins 2011; Wey *et al*. 2008; Wollman *et al*. 2011).

As there is a relatively small amount of academic literature available on rays, there are many topics yet to be researched (Vaudo and Lowe 2009). The following are suggested topics for future studies: For *H. fai*, how far do individuals migrate from the feeding sites? Does this social structure hold true in an all female aggregation, or when more than one sex is present? Does the dominance structure in this study hold true across seasons, or is female dominance dependent on the mating season? What are the interspecific interactions between *H. fai,* black-tipped reef sharks, Great Crested Terns, and the many species of fish that are attracted to the feedings regularly? Finally, it would be of particular interest to perform a cross-species network analysis to compare the social structures among *H. fai* and other batoid species. As *H. fai* are the only species in the Indo-Pacific region to regularly be sighted in groups (Vaudo and Lowe 2009), do *H. fai* aggregations have a more defined social structure?

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APPENDIX A

TABLE 1: Ethogram of *H. fai* behavior

Behavior	Abbre	Description
Eating	E	Ingesting food; obtained by hand or by flapping pectoral fins to excavate food/prey off sea floor
Food Guarding	FG	Covering food with one's ventral surface; spine is elevated and pectoral fins are touching the substrate floor at all points.
Carrying	C	Carrying food from one point to another by hiding food underneath the spine on the ventral side and clamping the food in between one's pectoral fins when swimming. Usually occurs during food guarding and pushing displays.
Pushing	P	One individual forcefully swims face-forward on top of an individual food guarding.
Overlapping settling	OB	One individual settling with a portion of their pectoral fins physically touching another's pectoral fins for >2 seconds
Face-to-face settling	FTF	One individual settling within 1.5 meters of another, oriented facing each other.
Adjacent settling/ burrowing	AB	One individual settling within 1.5 meters of another, oriented away from each other (stinger to stinger, fin to fin, fin to stinger, face to fin, face to stinger, etc.)
Directional swimming	DS	Swimming directly towards a food source
Solitary Swimming/	SS	The act of one individual swimming alone. Can be straight, turning, or tilted swimming.
Overlapping swimming	OS	Two individuals' pectoral fins touch while swimming; can be instantaneous.
Adjacent swimming	AS	Two individuals swimming within a 1 meter range and at the same depth.
Parallel swimming	PS	Two individuals swimming aligned vertically in the water column at different depths within 1 meter of one another.
Follow the leader	FTL	Two individuals swimming face to stinger in the same direction, either in a line or circle.
Hovering	H	One individual staying at the water surface for at least 30 seconds; usually close to a person with food.
Begging	B	One individual hovering close to a person and flapping one's pectoral fins on the potential feeder.
Isolation	I	Settling on the sea floor away from the feeding site and more than 1 meter away from other individuals; usually involves covering oneself with sand through pectoral flapping ("burrowing").
Waiting	W	One individual settling for 1+ seconds, to either allow for another ray to pass, or to settle at the base of a person's feet.

TABLE 2: Data Matrix for Sum of Interactions Network. Focal individuals are represented by the numbers 0 through 7 in the first column, and the ray being interacted with are represented by the numbers 0 through 7 in the first row. The total time pairs spent interacting is given in the matrix. **(a)** Matrix for the Sum of Interactions **(b)** Matrix for AS Interactions **(c)** Matrix for OS Interactions **(d)** Matrix for AB Interactions **(e)** Matrix for OB Interactions **(f)** Matrix for FTL Interactions

	0	1	2	3	4	5	6	7
0	0	1106	0	208	63	204	186	508
1	804	0	0	34	0	77	152	223
2	545	100	0	422	223	318	67	167
3	255	626	228	0	0	832	208	959
4	3	86	38	61	0	28	236	494
5	337	221	1	60	17	0	59	0
6	91	121	0	93	305	133	0	0
7	185	54	0	4	391	507	443	0

(a)

	0	1	2	3	4	5	6	7
0	0	117	0	108	33	31	16	57
1	2	0	0	10	0	47	63	18
2	9	15	0	240	74	123	24	28
3	55	141	20	0	0	200	90	218
4	0	35	14	32	0	17	94	157
5	101	105	0	5	16	0	7	0
6	41	42	0	16	193	57	0	0
7	23	1	0	0	80	91	123	0

(b)

	0	1	2	3	4	5	6	7
0	0	54	0	13	6	25	26	36
1	9	0	0	19	0	17	30	17
2	12	20	0	57	21	68	15	18
3	16	16	7	0	0	75	21	70
4	3	12	5	10	0	6	11	34
5	23	2	1	0	1	0	1	0
6	7	16	0	10	15	10	0	0
7	52	8	0	4	43	46	69	0

(c)

	0	1	2	3	4	5	6	7
0	0	354	0	28	22	82	85	287
1	640	0	0	0	0	5	32	84
2	432	38	0	1	35	23	27	50
3	137	141	163	0	0	87	12	207
4	0	0	0	0	0	0	0	0
5	137	57	0	0	0	0	16	0
6	4	16	0	1	5	15	0	0
7	43	19	0	0	37	0	18	0

(d)

	0	1	2	3	4	5	6	7
0	0	506	0	0	0	0	38	47
1	113	0	0	0	0	5	2	96
2	42	9	0	0	6	19	1	44
3	2	2	2	0	0	46	39	130
4	0	0	0	0	0	2	2	0
5	25	2	0	42	0	0	15	0
6	0	9	0	0	7	12	0	0
7	16	16	0	0	0	2	3	0

(e)

	0	1	2	3	4	5	6	7
0	0	75	0	59	2	66	21	81
1	40	0	0	5	0	3	25	8
2	50	18	0	124	87	85	0	27
3	45	326	36	0	0	424	46	334
4	0	39	19	19	0	3	129	303
5	51	55	0	13	0	0	20	0
6	39	38	0	66	85	39	0	0
7	51	10	0	0	231	368	230	0

(f)