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SOCIAL GROUPING BEHAVIORS OF CAPTIVE FEMALE *HIPPOPOTAMUS AMPHIBIUS*

by

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B.S. Northwest Missouri State University, 1996

A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science
in the Department of Biology
in the College of Sciences
at the University of Central Florida
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ABSTRACT

Levels of sociality vary depending on the costs and benefits associated with grouping behavior. Grouping species form either ephemeral aggregations due to resource availability, or structured groups based on familiarity of individuals. Because there are different costs and benefits associated with different types of groups, it is important to understand more about group structure before making predictions about specific behaviors. Female *Hippopotamus amphibius* are known to aggregate in the wild but the true nature of their grouping behavior is still not understood. My objective was to determine if captive female hippos form either ephemeral aggregations or social groups. Behavioral data, using continuous focal animal sampling and scan sampling, were collected on a group of nine captive female hippos housed at Disney's Animal Kingdom[®] Theme Park. The behavioral data were used to analyze interactions between hippos, association patterns for kin and non-kin as well as familiarity, dominance hierarchy, and habitat preferences. My results support the hypothesis that hippos are forming social groups due to the attraction to particular individuals. There were more associations between kin than non-kin and also between individuals that have been together longer. Captive female hippos were also found to exhibit dominance patterns within the group. The results from this study may aid in the general understanding of hippopotamus behavior and aid in the captive management of hippos. Using my results as a starting point, research can begin looking at grouping patterns and its costs and benefits of sociality in wild hippopotamus populations.

To mom and daddy

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INTRODUCTION

Living in groups has both benefits and costs for individuals within the groups (Krebs and Davies 1993). Grouping may increase foraging efficiency and access to food resources (Molvar and Bowyer 1994; Lenihan and Van Vuren 1996; McGuire et al. 2002; Blundell et al. 2004; Gompper 1996), reduce risk of predation (Lenihan and Van Vuren 1996; McGuire et al. 2002; Blundell et al. 2004; Gompper 1996), lower energetic costs in thermoregulation and daily activities (Lenihan and Van Vuren 1996; McGuire et al. 2002), and help with care and raising of young (McGuire et al. 2002). On the other hand, grouping may increase transmission of diseases or parasites (McGuire et al. 2002; Blundell et al. 2004; Gompper 1996), increase competition for food resources and mates (Molvar and Bowyer 1994; McGuire et al. 2002; Blundell et al. 2004; Gompper 1996), and increase visual cues for predators (McGuire et al. 2002).

Individuals can form groups that are either ephemeral aggregations or groups that are highly structured (social groups). Brown (1975) defines aggregations as groups that form by chance due to an attraction to a specific location (e.g. migration routes) or to a common resource (e.g. food or water). In the sharing of these locations or resources, members within these aggregations potentially benefit from increased foraging efficiency or predator avoidance (Morse 1980; Stensland et al. 2003; Utami et al. 1997; Sugardjito et al. 1987 and FitzGibbon 1990). Individuals within an aggregation will passively come together due to an attraction to the location or resources and not due to specific individuals within the group, therefore, lacking any social structure within the group.

Unlike an aggregation, social groups contain structure that enables individuals to gain benefits from other individuals within the group (Morse 1980). Individuals within a social group

actively seek out specific individuals to interact or group with. The structure of social groups can be based on kin, age, sex, mating systems and/or the formation of dominance hierarchies. Social groups composed of closely related individuals form a kin-based group, which can include either parents and their offspring or all or some extended family members (Brown 1975). Individuals in a kin-based group gain benefits by aiding in the survival and reproduction of kin which increases their own inclusive fitness (Krebs and Davies 1993). Grouping behavior may also be influenced by familiarity as well. Individuals may group with specific individuals they are more familiar with in order to reduce aggressive interactions within the group (Griffiths et al. 2004).

Often interactions between individuals within one of these group types are used to determine dominance status within the group. Individual dominance rank is often determined from repeated aggressive interactions among individuals within the group and may be based on age or size of individuals (Drews 1993). Higher ranked individuals will have priority to first matings or with the best mate choice, gain increased protection from predators, and/or access to the best resources or preferred habitat (Wirtu et al. 2004; Fournier and Festa-Bianchet 1995).

Determining whether a group is an aggregation or a social group is critical in order to understand the evolution of grouping and the possible costs and benefits. However, there are species in which their grouping behaviors are unknown. The grouping of these species, whether as an aggregation or a social group, must be determined before any predictions about that species' costs and benefits of grouping can be made and analyzed.

The hippopotamus, *Hippopotamus amphibius*, is a species of ungulate where females have been observed to live in groups during the day in a shared water source. At night the group

breaks up and individuals move alone onto the shore to forage (Klingel 1991). Hippopotami (hippos) often form rafts during the daytime which consists of the hippos lying together, with some individuals allowing others to rest their heads on their backs. In the wild, female hippos are found in groups with their calves and sometimes adult males within a shared water source. Within these groups, usually one territorial male hippopotamus is present (Karstad and Hudson 1986). Often bachelor males form groups in separate water sources. The bachelor males are subordinate to territorial male hippos and must fight and overcome territorial males in order to gain access to a territory (Eltringham 1999). Although the basic grouping behavior of male hippos is understood, almost nothing is known about the grouping of female hippos as long term identification and individual relatedness is extremely difficult to obtain in the wild. It is uncertain if female hippos group due to the attraction to the water resource, to males or to other specific females.

The nocturnal lifestyle of the hippopotamus coupled with its diurnal aquatic habitat make it difficult to study hippos in a natural, wild setting. The usual methods of identifying individual animals using ear tags, paint spots or radio collars, are ineffective on hippos (Eltringham 1999). Ear tags tend to break through the ear when the hippopotamus flicks its ears upon resurfacing, paint spots tend to fade away quickly due to the hippos' aquatic life and hippos' necks are similar in size to their head so radio collars slip off (Eltringham 1999). In addition, anesthetizing hippos is problematic as doses are difficult to assess and animals can easily be overdosed or only partially immobilized (Eltringham 1999). In order to anesthetize them, the hippos must be darted which leads to even more problems. Hippos must be darted on land so this limits any darting activity to the night when hippos are on land foraging. If the

hippos are darted, then they must be kept from running into the water due to possibilities of drowning once anesthetized (Eltringham 1999). These constraints have made it difficult to study hippopotamus' grouping behavior in the wild as well as in captivity; therefore, there is limited behavioral data available. Being able to study a captive group of hippos using individual natural markings (scars, bumps, colorations, etc.) to identify individuals may give insight into their natural grouping behavior.

The objective of my study was to determine if captive female hippos form either ephemeral aggregations due to an attraction to a resource, or social groups due to an attraction to specific individuals. Gaining knowledge of grouping behavior in captive female hippos can lead to the understanding of their behavior in the wild and provide the much needed first step in understanding hippopotamus grouping behavior.

If female hippos form ephemeral aggregations due to the attraction to a resource, then a) they will exhibit random interactions between individuals; or b) they will group in shallow waters (less than 1.5 meters in depth) of the river where the hippos can lay or stand while sleeping to increase energy conservation while resting (Eltringham 1999).

If female hippos form social groups due to the attraction to specific individuals, then a) they will exhibit patterns of non-random interactions between individuals; b) they will associate more with individuals that are kin; and/or c) they will associate more with individuals they are more familiar with.

If female hippos establish a dominance hierarchy among the individuals within the group, then a) older individuals will hold a higher rank within the hierarchy; or b) larger sized individuals will hold a higher rank within the hierarchy.

METHODS

Biology of study animal

The hippopotamus is a nocturnal, amphibious ungulate found throughout sub-Saharan Africa. They require open waters to lie in during the day surrounded by sufficient grasses to feed on during the night (Eltringham 1999). Hippos prefer shallow, slow moving waters in rivers and lakes but use mud pits when water sources are scarce (Eltringham 1999). During the day, hippos either remain in the water or can be found along the shores basking in the sun. To keep from overheating or having their skin dry out and crack, they will not venture too far from a water source during the day and spend the majority of their time in the water (Eltringham 1999). Hippos cannot float, so they require water shallow enough they can stand in and keep their heads above water when resting. In deeper water, they either walk along or make leaps across the bottom. They are able to remain under water and hold their breath for approximately 4-6 minutes (Eltringham 1999).

At sunset, hippos will leave the water to feed on land. They usually follow a regular path from the water source to feed on grasses at grazing sites that may be several kilometers away (Eltringham 1999). Due to their inactivity during the day and low metabolic rate, they do not require a large intake of food on a nightly basis (Eltringham 1999). Hippos do not defend territories on land while grazing at night and typically graze alone; except for instances of a mother and calf (Eltringham 1999).

Male hippos are larger in body mass than females, but no significant difference exists in length and girth between the sexes (Marshall and Sayer 1976; Laws 1963). Males weigh an average of 1490-1546 kilograms while females weigh an average of 1277-1385 kilograms

(Ledger 1968; Pienaar et al. 1966). The recorded highest age reached in captivity is 61 years and maximum age is thought to be approximately 40 years in the wild (Eltringham 1999). Males reach sexual maturity at approximately 7.5 years of age (Laws and Clough 1966) while females are sexually mature at approximately 9 years of age (Laws and Clough 1966). Sexual maturity has been found to be reached at younger ages in captivity (Wheaton et al. 2006). Females mate with the males in the water and, after an approximately 8 month gestation period, will give birth in the water as well. After the birth of the calf, females separate themselves from the group for a couple of weeks before returning to the water with the calf (Laws and Clough 1966).

Females aggressively protect their calves from infanticide by male hippos and from predators. Predators of young hippos include lions, hyenas and sometimes crocodiles. Adult hippos have little concern for predators, but rare prides of lions have been known to kill adult hippos (Ruggiero 1991; Guggisberg 1961).

Study area and animals

I collected behavioral data on nine captive adult female hippos housed at Disney's Animal Kingdom[®] Theme Park in Lake Buena Vista, Florida (Table 1). This population is larger than any other captive population of hippos in North America (Davis 2005) and similar to wild population group sizes. In the wild, the average number of hippos per group has been documented as 10, with group size increasing up into the hundreds during times of drought (Laws and Clough 1966). Therefore, a captive population of nine hippos should provide good insight into the behaviors of wild populations of hippos. Since hippos spend the majority of their daylight time in the water, I focused on markings located on the heads of the captive hippos to

identify individuals. Different markings I used as identifiers included bumps, ridges, coloration patterns, and neck grooves.

At night, all hippos are housed individually in separate stalls inside a barn, and released into the exhibit in the early morning. The exhibit consists of both land and water portions which simulate a natural hippopotamus habitat. The exhibit is part of the Kilimanjaro Safari[®] ride at Disney's Animal Kingdom[®] Theme Park with trucks traveling along a path adjacent to the exhibit throughout park operating hours.

In the barn, eight of the stalls are 4.6 meters wide by 7.6 meters long; with one stall that is 9.1 meters wide by 7.6 meters long. In the morning, hippos are given approximately 25% of their daily hay portions and 50% of their daily produce and grain before being let out into the exhibit. Some of this produce is placed directly within the exhibit. Every morning the hippos are released haphazardly one-by-one into the exhibit at sunrise, which places all nine hippos into the exhibit approximately 45 minutes after sunrise. The exhibit measures approximately 121.9 meters long by 24.4 meters wide; approximately 18.3 meters of this width is water and 6.1 meters is land (Figure 1). The hippos remain in the exhibit throughout the day. At approximately 30 minutes before sunset, all the hippos are brought back into the barn for the night and are placed haphazardly into separate stalls. On return to their stalls, they are fed the remaining 75% of their daily hay portions and 50% of their daily produce and grain.

All nine hippos have been housed under these conditions since 2003, with no males or offspring in the group since this time. Prior to 2003, the group was split and the compositions varied from year to year. With the exception of one mother-daughter pair and two half-sisters,

who share the same father, all hippos are unrelated. The hippos ranged in age from 9-35 years of age with average body mass ranging from 1379-1846 kilograms (Table 1).

One hippopotamus (G) spent the first 31 years of her life solitarily housed before being transferred to Disney's Animal Kingdom® in 2003 to become part of the current group of female hippos. The lack of opportunity to interact with other hippos for the majority of her life may affect her behaviors within the group. The other eight hippos have spent some part of their lives with other hippos; therefore they have been able to exhibit social behaviors for more time in their lives. I considered this aspect of this hippopotamus (G) during my data analysis as her unique social history may affect the results.

Behavioral observations

I observed all nine individual hippos using continuous focal animal sampling (Altmann 1974). Each focal observation was 10 minutes in duration and observations were conducted between approximately 6:30 am and 9:00 am (before visitors were present and trucks began driving on the ride path) six days each week. Observations began on June 18, 2007 and ended December 20, 2007 for a total of 100.5 hours of focal observations. I used a randomization table to determine the order of focal animal observations on each day. I observed animals from the path adjacent to the exhibit using 10 X 50 wide angle binoculars and the naked eye.

Observations began once all nine female hippos were in the exhibit to ensure that each individual had the opportunity to interact with all other individuals in the group. During each observation, I recorded individual behavior, all interactions that occurred between the focal animal and other individuals in the group and which hippos the focal animal came into contact with during the observation. Behaviors that were recorded during the focal animal observations are listed in

Table 2. During the focal animal observations, I also made note of any interactions that occurred between known individuals other than the focal animal.

Following each 10 minute observation, I used scan sampling to record the location of each hippopotamus within the exhibit and position of each hippopotamus relative to the other hippos. The positions recorded included which animals were next to each other, which animals were head resting and which animals were receiving head resting. For each hippopotamus, I noted the location and positions relative to other hippos on a diagram of the exhibit.

Habitat measurements

An aerial image of the exhibit was imported into the ArcView 9.2 program (ESRI 2006) and divided into 3 meter by 3 meter cells (Figure 1). Because the exhibit, including the river bottom, is constructed of gunnite, the water levels in the exhibit did not change over time; therefore depth measurements were recorded once at the completion of the study. Water depth was measured using a 3 meter length of PVC pipe marked with intervals in centimeters. Depths were determined by conducting measurements along 16 transects, 6 meters apart, in the exhibit. Depth measurements were taken at 0.3 meter intervals along the transect line beginning at the shore line down to the maximum water depth. The depths were then recorded in the ArcView 9.2 program (ESRI 2006) for each cell of the river within the exhibit.

Data analysis

Due to the unique social history of one hippopotamus (G), all of the following data analyses were conducted twice. The first analysis included all nine hippos in the study (n = 9)

and the second analysis included only eight hippos with the removal of one hippopotamus (G) ($n = 8$).

To test my two predictions of female hippos exhibiting patterns of random or non-random interactions, G-tests for goodness-of-fit were used to test the null hypothesis that hippos interact randomly with other hippos. The total, affiliative and aggressive interactions from the focal observations were all examined. Individual G-tests were run for each hippopotamus, and to correct for multiple tests ($n = 9$ or $n = 8$ (without G)), a Bonferroni adjustment was performed, which resulted in a rejection criteria of $p = 0.005$.

To test the prediction that female hippos will group in shallow areas (less than 1.5 meters in depth) of the river where the hippos can lie or stand to increase energy conservation while resting, I used the location data and ArcView 9.2 (ESRI 2006). The data from the scan sampling of the hippo locations within the exhibit were placed into the exhibit image in ArcView 9.2 (ESRI 2006). The cells within the exhibit image were of 22 different depths and were divided into five depth categories (0.0 – 0.5 m, 0.6 – 1.0 m, 1.1 – 1.5 m, 1.6 – 2.0 m, 2.0 – 2.5 m)

For each depth category, I determined individual and total number of hippos. Within ArcView 9.2 (ESRI 2006), I generated random points within the exhibit image that was equal to the total number of hippopotamus points (5204 and 4622 (without G)) as well as individual hippopotamus points (point numbers varied) and determined the number of random points per depth category. To determine if hippos are distributing themselves in the exhibit in relation to a specific depth rather than randomly, I compared actual data to the randomly generated data using a G-test for goodness of fit. Individual G-tests were run for each hippopotamus, and to correct

for multiple tests ($n = 9$ or $n = 8$ (without G)), a Bonferroni adjustment was performed, which resulted in a rejection criteria of $p = 0.005$.

To test the predictions that female hippos will associate more frequently with kin or familiar individuals (total number of years individual hippos have been together), I used a twice-weight association index (TWI) to quantify social interactions (Lehner 1996):

$$\text{TWI} = \frac{N_{AB}}{(N_A + N_B + N_{AB})}$$

where N_{AB} is the total number of times individuals A and B are observed together (defined as being in physical contact with one another or interacting together); N_A the number of times individual A is observed without individual B; N_B the number of times individual B is observed without individual A. This index is based on how often individuals are seen together or are not together and not just that a particular individual had been seen during the observation. A twice-weight association index value was calculated from the scan sampling data for rafting behavior for every possible pairing of individuals based on which individual each was next to in the raft. Also, values were calculated from the focal animal observations for total, affiliative and aggressive interactions for every possible combination of hippos and were used to construct an association matrix for each behavior (total interactions, affiliative interactions and aggressive interactions). The twice-weight association index values matrices were then used to determine if individuals associated more with kin than non kin or if they associated based on familiarity. To determine if the twice-weight association index value differed between kin and non-kin, I used a Mann-Whitney U test for each matrix (rafting, total interactions, affiliative interactions, and aggressive interactions). To determine if a correlation existed between the twice-weight

association index value and familiarity, I used a Spearman's rho correlation coefficient for each matrix (rafting, total interactions, affiliative interactions, and aggressive interactions).

To test if female hippos have established a dominance hierarchy, I constructed a dyadic interaction matrix following the procedures outlined in Oliveira and Almada (1996) using all aggressive interactions recorded from the focal animal observations. The "winner" performed an aggressive interaction (dung showering, head shaking/thrusting, vocalization, open mouth (scoop), charging, side/rear turn, jaw clashing, tusk slashing) that caused the "loser" to perform submissive action (move away or crouch). I used the MatMan 1.1 (Noldus, Inc. 2003) program to determine if the hierarchy was linear. Due to having unknown relationships in the dyadic matrix, I used the linearity index h' to determine the linearity of the hierarchy (de Vries 1995). I used Spearman's rho correlation coefficient to determine if the rank of individual hippos was correlated with age or size.

RESULTS

Time budget

All of the social behaviors, except crouch and tusk slashing, were observed in the hippos. In 100.5 hours of observations, hippos were found to spend $68.7 \pm 3.9\%$ of the time in social behaviors, $24.7 \pm 4.6\%$ of the time in solitary behaviors and $6.5 \pm 1.2\%$ of the time out of view. Of the time spent in social behaviors (excluding approach (contact), other and not visible behaviors), hippos spend $67.7 \pm 4.0\%$ of the time participating in affiliative interactions, while only $0.34 \pm 0.07\%$ of the time in aggressive interactions.

Social interactions among hippos

The G-tests for total interactions ($n = 8$, for the number of social partners per individual per G-test) indicated seven hippos interacted significantly different from random, while two hippopotamus interactions were not significantly different from random (Table 3). The G-tests for affiliative interactions ($n = 8$, for the number of social partners per individual per G-test) indicated all nine hippos interacted significantly different from random (Table 3). The G-tests for aggressive interactions ($n = 8$, for the number of social partners per individual per G-test) indicated only one hippopotamus (G) interacted significantly different from random, while eight hippos were not significantly different from random (Table 3). The removal of the one hippopotamus (G) from this analysis did not alter these results.

Habitat use

The total of all hippopotamus locations within the exhibit was significantly different from a random distribution ($G = 12422.18$, d.f. = 4, $n = 5$, $p < 0.0001$) (Figure 2). Individual hippopotamus locations within the exhibit were also significantly different from a random distribution (G range: 108 – 1692, d.f. = 4, $n = 5$, $p < 0.0001$). The greatest proportion of hippopotamus exhibit use was within category 2 (0.6 – 1.0 m) depth of the exhibit, with the smallest proportion found in category 4 (1.6 – 2.0 m) (Figure 3). The removal of the one hippopotamus (G) from this analysis did not alter these results.

Twice-weight association indices analysis

Hippos that were kin engaged in significantly more rafting (Mann-Whitney $U = 5$, $p = 0.038$, $n_1 = 34$, $n_2 = 2$), total interactions (Mann-Whitney $U = 5$, $p = 0.038$, $n_1 = 34$, $n_2 = 2$), and affiliative interactions (Mann-Whitney $U = 3$, $p = 0.019$, $n_1 = 34$, $n_2 = 2$) than non-kin (Figure 4). While there was no difference between kin and non-kin for aggressive interactions (Mann-Whitney $U = 16$, $p = 0.257$, $n_1 = 34$, $n_2 = 2$) (Figure 4). With the removal of hippopotamus G, hippos that were kin engaged in significantly more total interactions (Mann-Whitney $U = 4$, $p = 0.048$, $n_1 = 26$, $n_2 = 2$) and affiliative interactions (Mann-Whitney $U = 3$, $p = 0.032$, $n_1 = 26$, $n_2 = 2$). While there was no difference between kin and non-kin with the removal of hippopotamus G for rafting (Mann-Whitney $U = 5$, $p = 0.063$, $n_1 = 26$, $n_2 = 2$) and aggressive interactions (Mann-Whitney $U = 13$, $p = 0.296$, $n_1 = 26$, $n_2 = 2$).

Familiarity (number of years together) was positively correlated with rafting behavior (Spearman's $\rho = 0.445$, $p = 0.003$, $n = 36$) (Figure 5) and negatively correlated with aggressive interactions (Spearman's $\rho = -0.300$, $p = 0.038$, $n = 36$) (Figure 6). While there was no

correlation between familiarity with total interactions (Spearman's rho = 0.068, p = 0.347, n = 36) and affiliative interactions (Spearman's rho = 0.263, p = 0.061, n = 36). With the removal of hippopotamus G, familiarity (number of years together) was not correlated with rafting behavior (Spearman's rho = 0.193, p = 0.162, n = 28), total interactions (Spearman's rho = 0.028, p = 0.443, n = 28), affiliative interactions (Spearman's rho = 0.064, p = 0.372, n = 28), or aggressive interactions (Spearman's rho = -0.272, p = 0.081, n = 28).

Dominance hierarchy

Captive female hippos were found to spend $0.34 \pm 0.07\%$ of their time performing aggressive interactions (dung showering, head shaking/thrusting, vocalization, open mouth (scoop), charging, side/rear turn, jaw clashing, tusk slashing) and $0.084 \pm 0.02\%$ of their time performing submissive actions (move away or crouch). By examining these behaviors, the structure of the dominance hierarchy in captive female hippos was found to be non-linear ($h' = 0.558$, p = 0.098). Using the dyadic interaction matrix and ranks, I was able to construct the dominance patterns among the female hippos (Figure 7). No correlation existed between hippopotamus rank and age (Spearman's rho = -0.523, p = 0.148, n = 9) or between hippopotamus rank and weight (Spearman's rho = -0.033, p = 0.932, n = 9). The removal of hippopotamus G from the analysis did not alter the results except by removing G from the top of the dominance pattern.

DISCUSSION

I found that female hippos were attracted to a particular micro-habitat within the exhibit, showing a preference for shallow waters. However, their interactions were non-random in that they associated more with kin and more familiar individuals when rafting and interacting. These results support the hypothesis that hippos are forming social groups due to the attraction to specific individuals. A dominance pattern was found among the hippos, although it was not a linear hierarchy and individual ranks did not correlate with age or weight.

Hippos appear to be selecting what type of micro-habitat to dwell in by exhibiting a non-random distribution within the exhibit and a preference for particular depths. In general, species have a preference for specific habitats for a variety of reasons, such as for mating grounds (e.g. amphibians), feeding grounds (e.g. orangutans, Utami et al. 1997), or resting (e.g. manatees, Horikoshi-Beckett and Schulte 2006) though all may depend on the presence of predators. Here, I identified that hippos indicated a preference for shallow water depths (< 1 meter). The average height of the female hippos is 1.19 meters, therefore choosing water depths that are less than 1 meter allows for the hippos to stand in the water and keep their heads above or close to the surface for breathing (Eltringham 1999). Hippos are also able to reduce the use of their legs in holding them up while they are resting if they are able to stand in the shallower waters. Therefore, by resting in shallower waters, hippos may increase energy conservation. Manatees are also known to prefer particular habitats, choosing areas of the water that are shallow and calm while resting. These particular habitat choices allow the manatees to rest near the surface

so they too can lift their heads up to breath and conserve energy while resting (Horikoshi-Beckett and Schulte 2006).

Captive female hippos are attracted to shallow water and at the same time actively seeking out other individuals to interact/group with therefore providing evidence of social groups. The examination of total interactions between hippos resulted in seven of the nine hippos exhibiting patterns of non-random behavioral interactions with other hippos. For affiliative behaviors, all nine hippos exhibited patterns of non-random interactions; therefore the hippos appear to be selecting their social partners. Captive female giraffe (Bashaw et al. 2007) and captive female ring-tailed coatis (Romero and Aureli 2007) have also been found to exhibit non-random interactions between individuals within a group; therefore exhibiting social structure in their groups.

These patterns of non-random interactions in affiliative behaviors have led to association patterns between individual hippos. In dolphins (Möller et al. 2006), elephants (Archie et al. 2005) and lions (Packer et al. 1991), association patterns between individuals are based on kin. The association patterns in hippos suggests a greater association among kin than non-kin, however as my study only included 2 possible pairings of kin a larger sample size is warranted. In many fishes, shoaling behaviors tend to be based on familiarity of individuals within the shoal (Griffiths et al. 2004). I found that the familiarity amongst hippos was important when they were rafting. Hippos were found to raft near individuals with which they were most familiar (had been housed with the longest). By associating with specific individuals based on kin or familiarity, the hippos were exhibiting patterns of non-random interactions, therefore providing evidence for social grouping.

When species come together in groups, individuals often form some sort of dominance structure in order to determine access to mates, habitat space or food resources (Wirtu et al. 2004; Fournier and Festa-Bianchet 1995). For this captive group of hippos, a dominance structure would not be based on mating rights because there are no males present within the group. Also, they are fed individually in their stalls so they do not need to gain access to food resources. This group's dominance rank may determine habitat space use, position in the raft or decrease the number of aggressive interactions within the group in order to reduce the cost of physical conflicts (Fournier and Festa-Bianchet 1995).

The dominance structure of a group is often determined from the aggressive interactions among individuals. Among the group of hippos, there was a very small percentage of time (0.34%) being spent in aggressive behaviors. For these aggressive behaviors, eight of the nine hippos exhibited patterns of random interactions. Therefore, the females are not actively seeking out individuals to be aggressive toward. The lack of a strong linear dominance hierarchy may be explained by these random interactions in hippos. My results revealed aggressive interactions decreased between individuals as the number of years the hippos have been together increased. Familiarity within a group has been found to lower the amount of aggression among group members (Griffiths et al. 2004). The lack of aggressive interactions between individual hippos could be due to already established dominance patterns among the hippos as a result of the amount of time they have been together (Frafjord 1993; Poisbleau 2006). Also, the lack of mates or limited resources in which to fight over may contribute to the small amount of aggressive interactions.

One hippopotamus (G) that exhibited non-random interactions for aggressive behaviors is the individual that was positioned at the top of the dominance structure and has been housed with the group for the fewest years. Before coming to become part of the current group of female hippos at Disney's Animal Kingdom[®], she spent the previous 31 years of her life housed solitary. Being solitary for the majority of her life could explain her aggressive behaviors. This hippopotamus (G) may be the most dominant because she is being more aggressive while trying to establish her position in the group or possibly because she does not know proper social behaviors.

Due to the low sample size and single captive population, it remains unclear if these social patterns would exist in other captive groups or in the wild. Whether these results are indicative of grouping behaviors of wild hippos is also uncertain, but does provide the much needed first step in understanding hippopotamus grouping behavior. Wild hippopotamus behaviors could vary from these results due to the presence of males or offspring. Female hippopotamus may become more aggressive in defense of the young offspring from the males or from possible predators (Eltringham 1999). Future studies can build from my captive findings to help in the understanding of wild hippopotamus behaviors.

My results may also aid in the management of captive hippos. Documenting the basic behavior of hippos will aid in the care and management of animals and understanding the structure and interactions of hippos will aid in the possible introductions of new hippos into an already existing captive group. Captive facilities may want to consider keeping kin together and keeping the composition of hippopotamus groups consistent over many years to reduce aggression within the group. Also, as female hippos are forming social groups, it may be in the

best interest of the hippos to be housed in groups rather than solitarily. Understanding more about grouping in hippos may also help in the management of wild hippopotamus populations. Many hippos are being relocated to reduce human interactions. As kin and familiarity care may be important factors in group formation and persistence, managers should consider moving the entire group, possibly keeping kin and more familiar individuals together to reduce stress and aggression in the groups.

FIGURES AND TABLES



Figure 1. Aerial view of exhibit at Disney's Animal Kingdom[®] Theme Park in which the female hippos are kept during the day. The exhibit was divided into 3 X 3 meter cells for depth analysis.



Figure 2. Aerial view of the exhibit with all hippopotamus locations within the exhibit represented by the yellow dots.

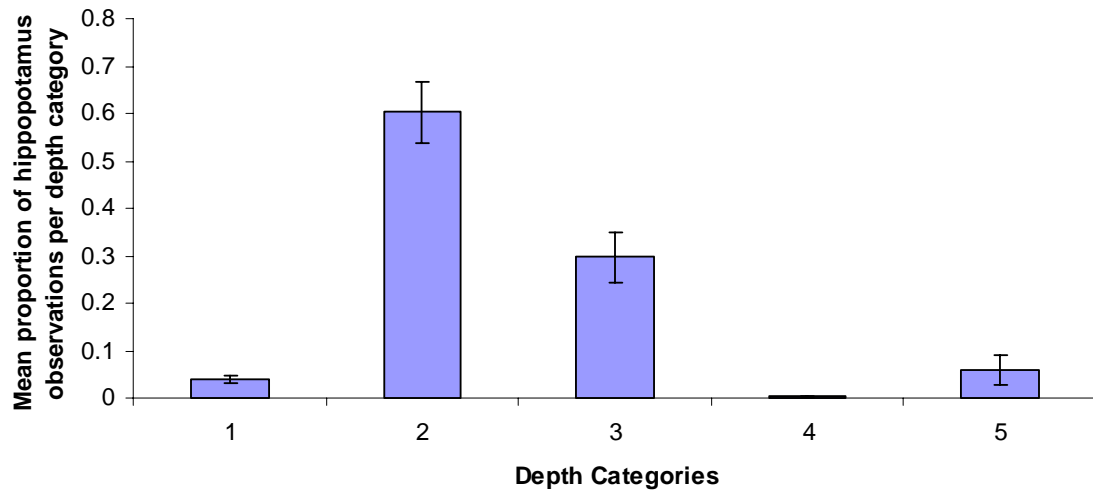


Figure 3. Average proportion of hippopotamus observations within each depth category of the exhibit. Category 1 = 0.0 - 0.5 m; 2 = 0.6 - 1.0 m; 3 = 1.1 - 1.5 m; 4 = 1.6 - 2.0 m; 5 = 2.1 - 2.5 m.

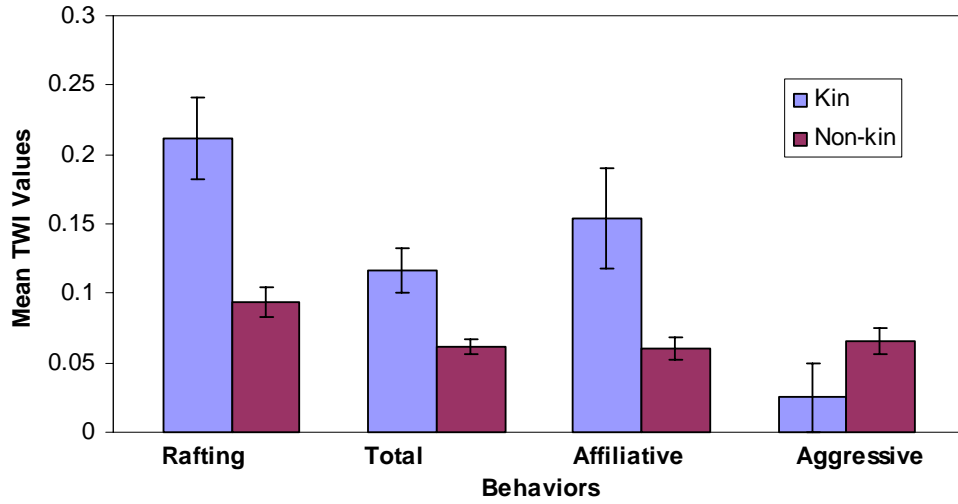


Figure 4. Mean twice-weight index (TWI) values for rafting, total interactions, affiliative interactions, and aggressive interactions for kin and non-kin hippos with standard error bars.

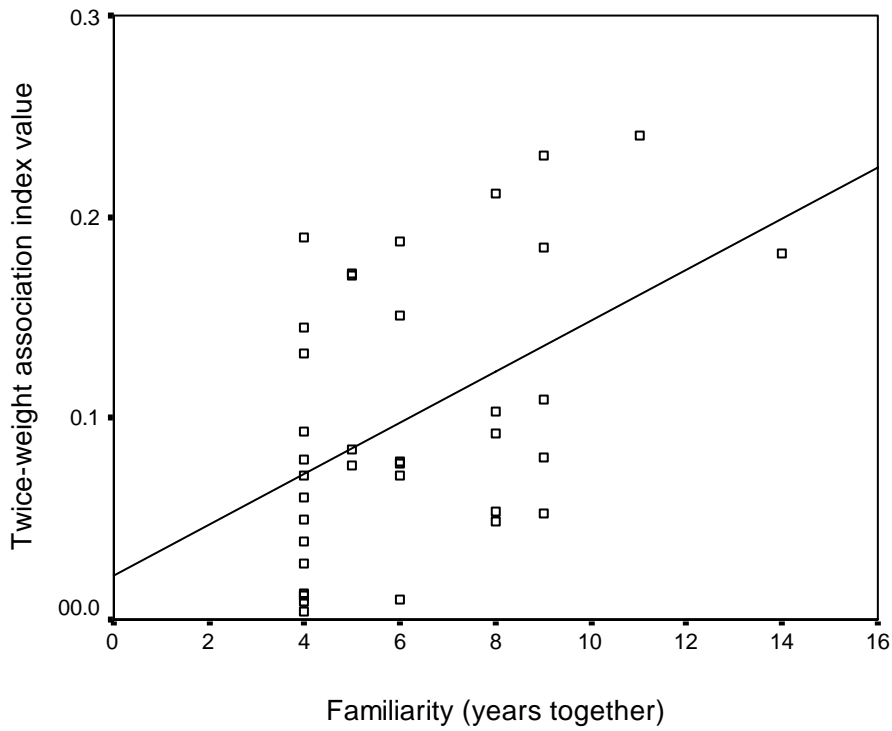


Figure 5. Spearman's rho correlation between the twice-weight association index value for rafting behavior and the number of years the hippos have been together (Spearman's rho = 0.445, $p = 0.003$, $n = 36$).

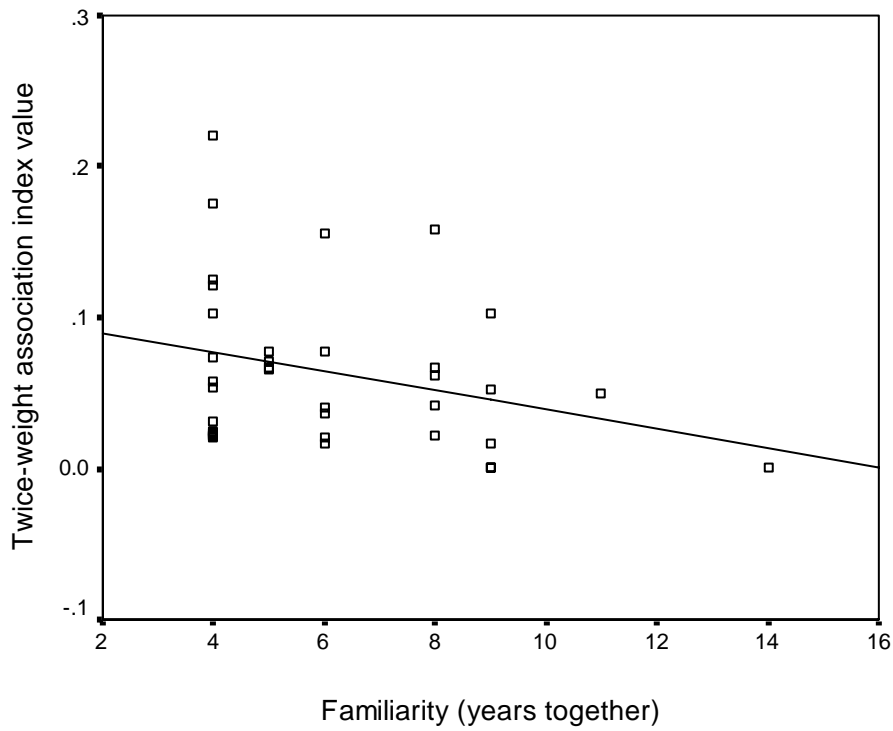


Figure 6. Spearman's rho correlation between the twice-weight association index value for aggressive behavior and the number of years the hippos have been together (Spearman's rho = 0.300, $p = 0.038$, $n = 36$).

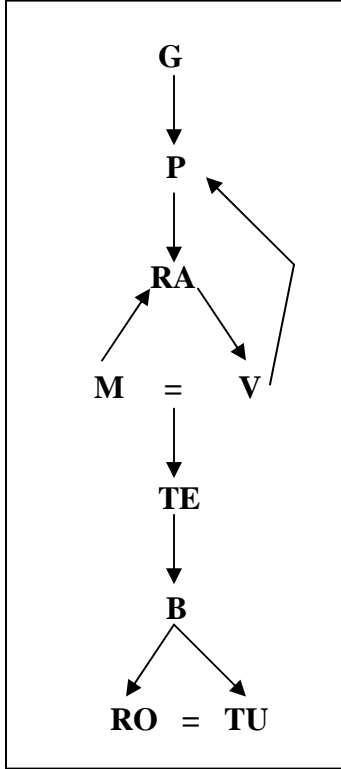


Figure 7. Dominance pattern of captive female hippos.

Table 1. Female hippos at Disney's Animal Kingdom[®] Theme Park observed for focal animal sampling during June - December 2007.

Hippopotamus Name	Age at start of study (June 2007)	Average Mass during study (kg)	Number of years in current group (Barn 6)	Relatedness
P	13	1765	4	Daughter of RA
G	35	1598	4	
V	35	1826	4	
RA	18	1685	6	Mother of P
B	9	1714	8	
TU	11	1846	9	
M	14	1673	9	Half sister of TE
TE	14	1456	9	Half sister of M
RO	17	1379	9	

Table 2. Ethogram for female hippopotamus behaviors at Disney's Animal Kingdom[®] Theme Park used for focal animal observations.

Focal Behavior	Description
Feeding	Animal consuming produce, plant material, or hay
Inactive	Animal not moving
Locomotion	Animal is walking around in or out of water or is porpoising in the water
Open mouth ^{1,3}	Animal opens its mouth and exposes the tusks
Open mouth scoop ^{1,3}	Animal opens its mouth and exposes tusks and then scoops down and back out of the water
Tail paddling ^{1,3}	The movement of the tail up and down at the surface of the water
Snorting ^{1,3}	Animal will snort (blow air out of nostrils)
Underwater bubbles ^{1,3}	Animal releases air underwater
Wheeze-honk ^{1,3}	As implied
Other vocalizations ^{1,3}	Any vocals other than snorting, underwater bubbles or wheeze-honk
Rafting, no head resting ^{1,2}	Animals are together in bundle with no head resting activity (note which animal the focal animal is next to)
Rafting, head resting ^{1,2}	One animal will have chin propped onto the back or rear of another animal (note the identity of head rester and identity of animal rested on)
Dung showering ^{1,3}	Animal will tail paddle while defecating (note which animal it is directed toward)
Head shaking ^{1,3}	One animal shakes head vigorously from side to side (note which animal it is directed toward)
Head thrusting ^{1,3}	One animal thrusts head upward toward another animal (note which animal it is directed toward)
Approach (and contact) ¹	One animal moves toward another animal within one body length away (note if physical contact is made between animals)
Charging ^{1,3}	One animal will lunge toward or run at another animal (note which animal it is directed toward)
Move away ^{1,4}	One animal moves away from another animal
Head rest avoid ^{1,3}	One animal will move to not allow another animal to rest their head on them (note which animal was denied access to head rest)
Side turn ^{1,3}	One animal will turn its side toward approaching animal
Rear turn ^{1,3}	One animal will turn its rear toward approaching animal
Crouch ^{1,4}	One animal will lower the legs placing its body on the ground in response to another animal

Face to face ^{1,2}	Two animals are face to face with each other with no other movement
Jaw clashing (sparring) ^{1,3}	Jaw-to-jaw striking while moving the head from side to side or forward and backward with physical contact between two animals (note which animal retreats from sparring first)
Tusk slashing ^{1,3}	One animal slashes at the body of another animal with its tusks
Other behavior ¹	Any other behavior not listed
Out of view	Animal is physically out of viewing sight
Not visible behavior ¹	Animal can physically be seen but behavior of animal is not visible

¹Behaviors used for G-test for total interactions.

²Behaviors used for G-test for affiliative interactions.

³Aggressive, dominant behaviors that were used in analysis of dominance hierarchy and G-test for aggressive interactions.

⁴Submissive behaviors that were used in analysis of dominance hierarchy.

Table 3. G-test results for total interactions, affiliative interactions and aggressive interactions for each individual female hippopotamus (d.f. = 7, α = 0.005, *significantly different from random).

Hippo	Total Interactions		Affiliative Interactions		Aggressive Interactions	
	G value	p value	G value	p value	G value	p value
B	81.643	< 0.0001*	73.302	<0.0001*	2.013	0.9590
G	14.100	0.0490	36.623	<0.0001*	25.510	0.0006*
M	50.565	<0.0001*	95.255	<0.0001*	11.515	0.1180
P	55.829	<0.0001*	93.343	<0.0001*	5.545	0.5940
RA	8.948	0.2560	26.312	0.0004*	9.651	0.2090
RO	70.535	<0.0001*	70.667	<0.0001*	7.831	0.3480
TE	32.522	<0.0001*	31.960	<0.0001*	19.811	0.0060
TU	27.252	<0.0001*	29.645	<0.0001*	13.863	0.0540
V	36.843	<0.0001*	37.131	<0.0001*	15.035	0.0360

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