RESEARCH ARTICLE

Patterns of Aggression Among Captive American Flamingos (*Phoenicopterus ruber*)

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Many species of flamingo are endangered in the wild but common in zoos, where successful captive breeding programs are a management priority. Unlike their counterparts in the wild, captive flamingo individuals are easy to mark and follow, facilitating longitudinal data collection on social dynamics that may affect reproduction. We studied a captive group of American Flamingos at the Audubon Zoo in New Orleans, LA to document patterns of aggression between individuals during the onset of breeding. We used a social network approach to test whether overall aggression would be higher during courtship or following establishment of pair bonds. Aggression was higher following pair bond establishment than during courtship, suggesting that individuals in our study population may compete more intensely for resources such as nesting sites than for mates. We also found that males were more aggressive than females during all stages of the study period and that there was a positive relationship between age and aggression in males during the pair-bond stage. We discuss these findings in light of management practices for captive populations of flamingos and general patterns of aggression in social animals. Zoo Biol. XX:XX–XX, 2013. © 2013 Wiley Periodicals Inc.

INTRODUCTION

Natural populations of flamingo face a variety of threats (e.g., Cezily et al., 1995; Bechet and Johnson, 2008), and four of six recognized flamingo species are in a state of decline in the wild (Ottenwalder et al., 1990; IUCN, 2011). For this reason, ex situ conservation methods such as captive breeding programs designed to maintain long-term retention of genetic diversity may play an important role in the management of flamingos (Pritchard et al., 2012). Unfortunately, flamingos have been historically difficult to breed in captivity (Farrell et al., 2000). As such, an improved understanding of flamingo reproductive behavior is likely to improve ex situ management of this species (Cezily et al., 1996). Managers often use information on behavior of individuals to inform captive management practices (Wielebnowski, 1998), but wild flocks of flamingos often consist of hundreds or thousands of individuals, complicating detailed study of social behavior due to difficulties in tracking and studying individuals within these groups (Allen, 1959; Bildstein et al., 1993; King, 2000). Because so little is known

about these birds in the wild, it is useful to gather detailed data on the reproductive behavior of captive individuals. Captive flamingos are easy to observe and many potentially confounding variables (e.g., diet and access to carotenoids) can be controlled (King, 2000), leading to informed behavioral studies that may also increase our understanding of wild populations.

Intraspecific aggression among group living animals in captive environments is often associated with stress and reduced reproductive output (Cezily et al., 1996;

Sandell, 1998; Ramos, 2003; Jakubas, 2004; Ellis and Good, 2006; Gonzalez-Voyer et al., 2007). Such aggressive behavior is found in all species of both captive and wild populations of flamingos and is likely associated with large group sizes (Bildstein et al., 1993; Farrell et al., 2000; Perdue et al., 2011). In flamingos, aggression has been found to increase as the breeding season progresses (Farrell et al., 2000) and to negatively affect the foraging success of juveniles in the wild (Cezilly et al., 1996). However, many questions remain about how aggressive behavior is exhibited leading up to and during breeding. In particular, aggression during the onset of breeding may arise from competition over mates, or competition over limiting resources such as nest sites or food. Distinguishing between these two alternatives, as well as identifying any age- or sex-related propensities to engage in aggressive interactions, can help curators to more successfully manage captive populations.

Flamingo breeding has been described as opportunistic (Studer-Thiersch, 2000). Group courtship displays by reproductively active flamingos are induced by favorable environmental conditions (e.g., high nutrient availability and warm temperatures) and onset of reproductive condition (Cezilly et al., 1995, 1996; Farrell et al., 2000). Shortly following these displays, individuals then form pair-bonds for the purposes of nest building, chick rearing, and protection from intraspecific aggressors (Stevens et al., 1992; Shannon, 2000; Perdue et al., 2011). Pair-bonds do not typically persist for more than one season (Cezilly et al., 1997), meaning that courtship display and pair establishment are likely to occur every breeding season. For this reason, patterns of aggression during these periods are likely to have important consequences for breeding success.

Four peer-reviewed studies have been published on the aggressive behavior of captive flamingos; three on Chilean Flamingos (*Phoenicopterus chilensis*), and one on American Flamingos (*P. ruber*). Farrell et al. (2000) observed increased aggression by both male and female Chilean Flamingos in the breeding season compared to the non-breeding season, but no differences were observed in males versus females in either period. In a second study conducted only during the breeding season, Chilean Flamingo adults were more aggressive than juveniles, and bonded individuals (in small groups of two or more) were significantly more aggressive than solitary birds (Perdue et al., 2011). Stevens et al. (1992) suggested that egg losses in Chilean Flamingos were a result of intraspecific aggressive interactions at nesting mounds. Finally, Anderson et al. (2009) determined that preferred neck-resting position predicts aggression in American Flamingos. Beyond these studies, aggressive conspecific interactions among captive flamingos and our understanding of how social interactions shift as individuals transition from nonbreeding to breeding status have gone largely unexplored.

In the present study, we characterize patterns of aggression among captive American flamingos with a focus on how these patterns change as animals transition from courtship to pair establishment. To do so we used Social Network Analysis (SNA), which provides useful tools for describing and analyzing the structure of social interactions in gregarious species (Croft et al., 2008; Wey et al., 2008). SNA is based on modeling a system of nodes (that represent individuals) and the ties (interactions or relationships) that connect those nodes. SNA introduces the possibility of quantifying individual centrality (importance or position) within a group based upon the interactions that occur between individuals. Wey et al. (2008) suggests that SNA may improve our understanding of social structure by examining measures of social interaction directly (as opposed to traditional measures of group size, mating system, and rates of interaction). This allows for both qualitative and quantitative analyses. As opposed to general comparisons of aggression rates, SNA offers the advantage of tracking interactions among specific individuals with known characteristics, providing a more complete understanding of social variation among individuals within the group. For example it can provide insight into patterns in which individuals direct their aggression (e.g., whether males direct aggression more often to other males, females, or randomly).

To date, researchers have utilized network theory to describe social structure in a diverse array of taxa in the wild including mammals, fish, and birds (reviewed in Croft et al., 2008, 2011; Wey et al., 2008). Studies have also applied SNA to captive animal management. McCowan et al. (2008), for instance, used SNA to study aggression in captive rhesus macaques (*Macaca mulatta*). Using event-sampling methodology, they were able to examine metrics for groom reciprocity, subordination, displacement, and aggression. They concluded that aggression and subordination are affected by group composition (i.e., age and sex) and that manipulation might be a useful tool in reducing aggression levels within these captive groups. In a separate study, White et al. (2010) used SNA to experimentally test the possible link between social complexity and reproductive success in captive cowbirds (*Molothrus ater*). They compared individuals conditioned in dynamic social groups in which composition was consistently altered, and stable social groups in which composition remained fixed. Upon mixing dynamic-conditioned and stable-conditioned males, they found that dynamic-conditioned individuals showed greater reproductive success. To date, few studies have utilized SNA to map avian aggressive social structure, but as the above studies evidence SNA can be a powerful tool in behavioral research as well as captive animal management.

In our study, we mapped and analyzed social interactions between individual American Flamingos at the Audubon Zoo in New Orleans, LA. Our first goal was to assess how patterns of aggression vary across contexts, with a particular focus on differences between courtship versus pair-bond establishment in the nest building stage. This question is of importance for managers because it may provide insight into whether animals are competing more intensely for mates (i.e., during courtship), or resources once pair formation has

occurred (i.e., for nesting sites or food). Our second goal was to characterize patterns of aggression in relation to sex and age, a question of importance for managers. Based on findings reported for Chilean flamingos, we predicted that there should be little difference in aggressive behavior between males and females and that age should be associated with increased aggression in both sexes.

METHODS

We studied a group of 34 (16 males and 18 females) individually marked American Flamingos from February 20 to April 12 2012 at the Audubon Zoo. This captive population has bred successfully in past years and exhibited courtship displays as described by Studer-Thiersch (2000). Age and sex data were obtained from zoo records (L. Schoen, unpublished data). We constructed a standardized ethogram based on preliminary observations (5 hr) and recorded individual agonistic encounters using a combination of focal-animal sampling and opportunistic observation (Altmann, 1974). For focal animal samples, we recorded consecutive 5-min sampling periods on randomly selected individuals between 1,100 and 1,600, 2–3 times a week during the study period for a total of 17.17 hr of observation throughout our study. We selected individuals for focal observation using a random number generating procedure, and at least one focal observation was conducted for each individual within the population (5.32 ± 2.81 SD focal observations per individual; range = 1–11). During focal-animal observations, we also made opportunistic observations of aggressive interactions by non-focal animals. We did not start recording opportunistic observations of aggression until March 11 causing our traditional (non-SNA) t-test analysis of overall rate of aggression to incorporate data between March 11 (as opposed to February 23), and April 12; aggression was relatively rare prior to March 11. We noted the initiators and recipients of all agonistic actions including directed pecking/squawking and stand-offs (in which two or more individuals mutually exchanged extended vocalizations and waved their heads in an aggressive display; Studer-Thiersch, 2000). A majority (58%) of our observations of aggressive interactions were opportunistic (i.e., did not involve a focal individual). As such, we are confident that differences in number of observations among individuals did not heavily impact our ability to sufficiently capture levels of aggression for each individual.

We created separate networks for the courtship period (February 20–March 22 2012; Fig. 1a) and the pair-bond period (March 23–April 12; Fig. 1b). As such, our data collection period during the courtship stage was slightly longer than that during the pair-bonding stage (29 days and 9.5 hr of observation vs. 22 days and 7.4 hr of observation, respectively). The cut-off date between courtship and pair-bond was determined by visually assessing the proportion of pair-bonded individuals and the relative frequency of
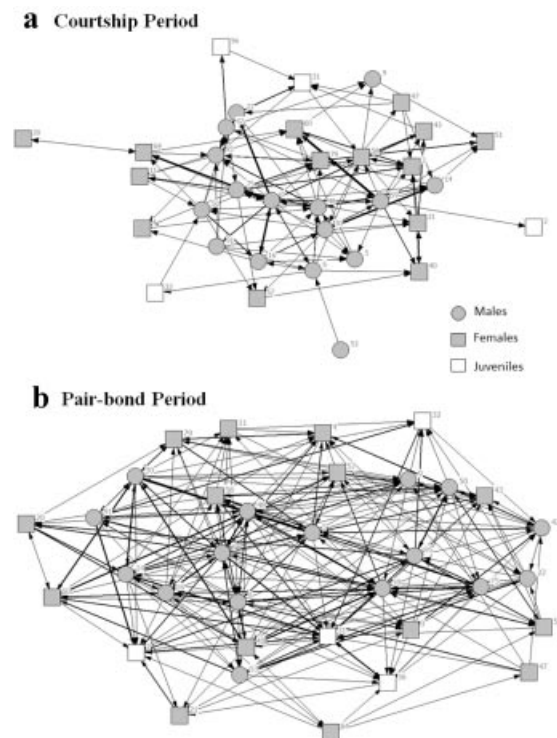

Fig. 1. Graphical depictions of American flamingo social network at Audubon Zoo, based on agonistic interactions. Nodes indicate individuals and ties indicate directed aggressive interactions (ties include arrows signifying the direction of the interaction). The thickness of ties indicate weight of interaction (thinnest lines = 1 interaction; thickest lines = 4 interactions). Panel (**a**) depicts the courtship period network, during which juveniles and females were involved in relatively few agonistic initiations, and a few individual males exhibited relatively large amounts of aggression and were therefore central within the network. Panel (**b**) depicts the pair-bond period network, which was much denser than the courtship period, reflecting higher levels of overall aggression. As in the courtship network, however, juveniles and females remained closer to the outskirts and males tended to be more central due to greater amounts of aggressive initiations. See text for more details.

courtship displays (Fig. 2). Our cut-off date of March 22 corresponds to the time at which courtship displays had halted, a majority of individuals were pair-bonded, and zookeepers created artificial mounds within the exhibit to stimulate nest building. Modest shifts (i.e., ± 7 days) in the cut-off date between these two stages did not change our qualitative results.

We mapped directed, weighted networks (i.e., interactions had an initiator and recipient, and ties between individuals were scored based on the number of interactions between those individuals). Each node (point on the network) represents a specific individual and each tie connecting the nodes represents a directed aggressive interaction. Using UCINET software we were able to quantify and compare aggressive behavior between groups of individuals and between the temporally disparate networks (Borgatti et al., 2002; Hanneman and Riddle, 2005). Creating a
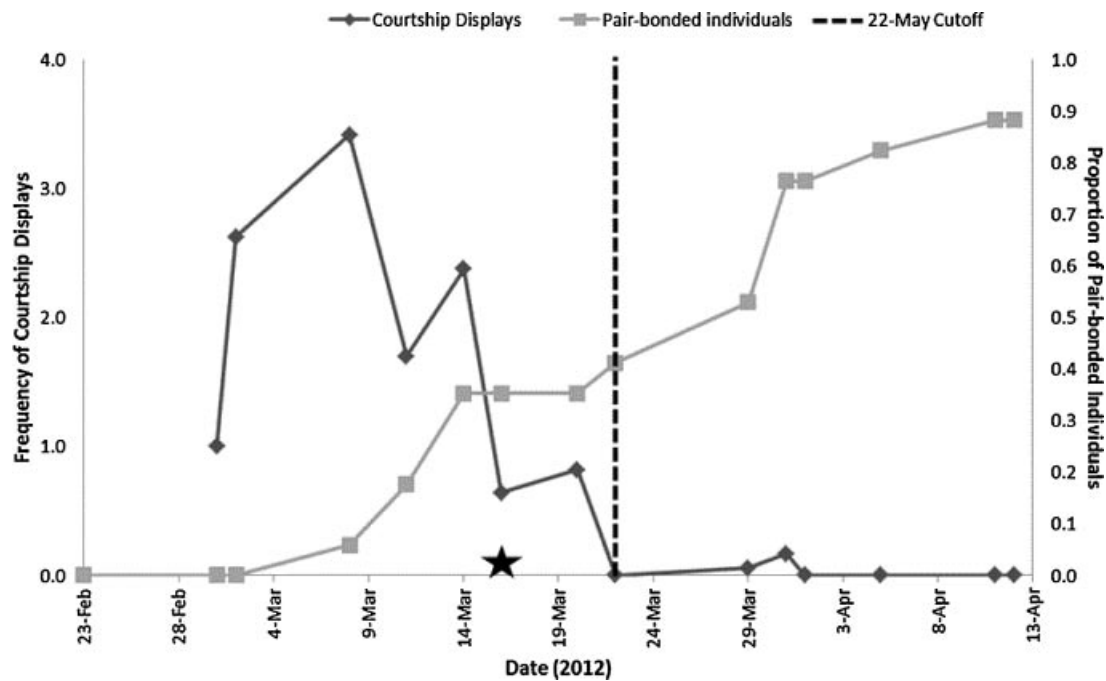
Fig. 2. The proportion of pair-bonds (right axis) increased, and frequency of courtship displays (left axis) decreased during our study of captive American flamingos in the Audubon Zoo. The dotted line at March 22 shows the breakpoint we used to distinguish between the courtship and pair-bond networks analyzed. The star indicates the date at which dirt mounds were created by keepers in order to stimulate nest building (March 16).

directed social network allowed us to analyze which flamingos were initiating and receiving aggression. In addition, we also used a more traditional analysis (we analyzed rates of aggressive interactions defined as a certain number of aggressive interactions observed within an established period of time) to determine the overall trend of aggression as the season progressed and confirm the results achieved using network analysis. Our traditional measure of rates of aggression (i.e., number of aggressive interactions per 5 min) unlike SNA, did not allow for comparisons using extra-focal observations so we only included the aggressive interactions of our focal individuals (this did not lead to different results for overall group levels of aggression).

We quantified aggression using standard network metrics at the individual level (network terminology defined in Table 1). These measures were chosen to capture different aspects of individual social connectedness and network structure. We also calculated network-level versions of individual-level measures (Table 1). One key measure, network degree centralization, provides an index of variance among individuals in the number of ties (the higher the variance, the less equally aggressive interactions are distributed among individuals). Network data generally violates assumptions about independence of data points, so significance is more accurately determined by generating a distribution from the data, rather than using standard significance tests (Croft et al., 2011). For this reason, UCINET evaluates significance via bootstrapping permuta-

tion calculations without test statistics, or degrees of freedom (Hanneman and Riddle, 2005). We also determined differences in aggression between males and females, and between the pre-breeding network and breeding network using permutation t-tests. We square-root transformed our measures of degree centrality (out-degree and in-degree; Table 1) to meet assumptions for normality. In order to statistically test the likelihood that aggressive interactions were not random with respect to sex (whether males or females directed aggression to a particular sex), we utilized an E–I Index (external–internal index) permutation test with males and females as our classes.

RESULTS

We constructed two social networks based on aggressive interactions, one for the courtship period and one for the pair-bond period (Fig. 1). We observed a significant increase in overall aggressive interactions in the (earlier) courtship network versus the (later) pair-bond network (one-tailed t-test; $t = -4.78$, df $= 33$, $P < 0.05$), as measured by density. The pair-bond network also had a significantly higher incidence of aggressive encounters initiated (as measured by mean out-degree; $P < 0.0001$; mean total out-degree $\pm$ SE; courtship: 2.25 ± 0.15 vs. pair-bond: 3.54 ± 0.20), and received (as measured by mean in-degree; $P < 0.0001$; mean total in-degree $\pm$ SE; courtship: 2.33 ± 0.10 vs. pair-bond: 3.59 ± 0.17). A more traditional analysis of differences in

TABLE 1. Social network metrics used to characterize patterns of aggression among captive American Flamingos

Metric	Definition	Application	Results
Individual level metrics			
Out-degree centrality	Number of ties originating from an individual	A metric for determining which individuals initiate aggressive interactions	Males more aggressive than females during pair-bond and courtship
In-degree centrality	Number of ties directed toward an individual	A metric for determining which individuals are receiving the most aggressive interactions	Equal levels of aggression reception among males and females during courtship and pair-bond
Network level metrics			
Density	Number of realized ties divided by the number of possible ties within the network	Used to analyze the overall levels of aggression within our population and compare aggression levels temporally	Pair-bond period exhibited more aggression than courtship period
Homophily	The tendency of ties to exist between similar individuals (of the same sex in the present study)	Used to ascertain which individuals are prime targets for aggression by a specified group of other individuals	Males and females distributed aggression without regard to sex in both courtship and pair-bond periods
Clustering co-efficient	The density of ties among the neighbors (those connected via ties) of the focal individual	A means of determining whether individuals focused aggression on a particular subset of other individuals, without regard to sex of those individuals	Pair-bond period had greater within-group formation than courtship period
Degree centralization	An index of variance in the number of ties among individuals	Provides measures of how evenly aggressive interactions are initiated and received	Relatively low measures throughout the study indicate that aggression was fairly equally distributed

Shown is the name and definition of each metric (following Wey et al., 2008, Hanneman and Riddle, 2005), as well as a short description of the way in which we applied the metric to answer questions about aggression in flamingos, and a summary of results.

rates of aggression between the two stages corroborates an overall increase in aggression during the pair-bond period versus the courtship period (one-tailed t-test; df refer to number of observation days: $t = -2.34$, df $= 11$, $P = 0.019$). The mean clustering co-efficient (defined in Table 1) of the pair-bond network was significantly larger than that of the courtship network ($P = 0.0001$; mean clustering co-efficient $\pm$ SE; pair-bond: 0.43 ± 0.019 vs. courtship: 0.17 ± 0.02), congruent with a higher degree of subgroup formation (formation of groups within the population) after pair-bonds were formed.

Males were more aggressive than females in both stages of the study. During the courtship period, males initiated significantly more aggression (mean out-degree $\pm$ SE; male 2.72 ± 0.24 vs. female 1.84 ± 0.10; $P = 0.0008$; Fig. 3a). During the pair-bond period, when overall aggression was higher, males continued to exhibit higher levels of aggression (mean out-degree $\pm$ SE; male 4.41 ± 0.21 vs. female 2.76 ± 0.19; $P < 0.0001$; Fig. 3b).

Centralization provides measures of how evenly aggressive interactions are initiated and received among individuals in a network, respectively; a higher value indicates greater variance in the distribution of these events across individuals. Network out-degree and in-degree centralization provide insights into finer-grained relationships of how age may interact with sex to affect patterns of aggression during these two time periods. Network out-

degree centralization were similar between the courtship, and pair-bond periods (16.58% vs. 7.87%, respectively), suggesting an intermediate level of variance in the distribution of aggression in both stages. However, the difference between the two is consistent with our finding that during courtship a few individuals initiated many aggressive interactions whereas during the pair-bond period aggressive behavior was more evenly distributed (see Fig. 3).

During the courtship period, there was no relationship between age and aggression in males (Fig. 4a; linear regression; $r^2 = 0.13$; $t = 1.46$, df $= 14$, $P = 0.17$). Similarly, females showed no relationship between age and aggression (Fig. 4a; linear regression; $r^2 = 0.12$; $t = -1.28$, df $= 12$, $P = 0.22$). During the pair-bond period, there was a significant increase in aggression (out-degree) with age among males (Fig. 4b; two-tailed t-test; $r^2 = 0.29$; $t = 2.42$, df $= 14$, $P = 0.03$), but again there was no relationship between age and aggression for females (Fig. 4b; two-tailed t-test; $r^2 = 0.01$; $t = 0.35$, df $= 12$, $P = 0.73$). These findings suggest that although there was no age-based difference in aggression among males and females during the courtship period, as the season progressed a sub-set of relatively old males exhibited increased levels of aggression relative to the females and the rest of the males.

In contrast, there was a more equitable distribution of reception of aggressive interactions across the study period, with no easily discernible outliers during the courtship period
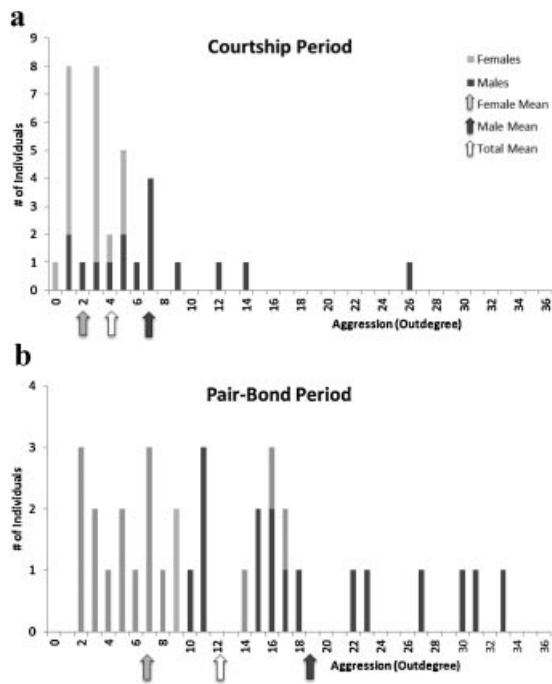

Fig. 3.   Histograms showing the numbers of individuals initiating aggressive initiations (as measured by out-degree; see Table 1). **a**: During the courtship period there was a right skewed distribution with male outliers displaying relatively large amounts of aggressive initiations. **b**: Comparatively there was less skew during the pair-bond period. Refer to Table 1 for a more detailed description of out-degree and its applications within this study.
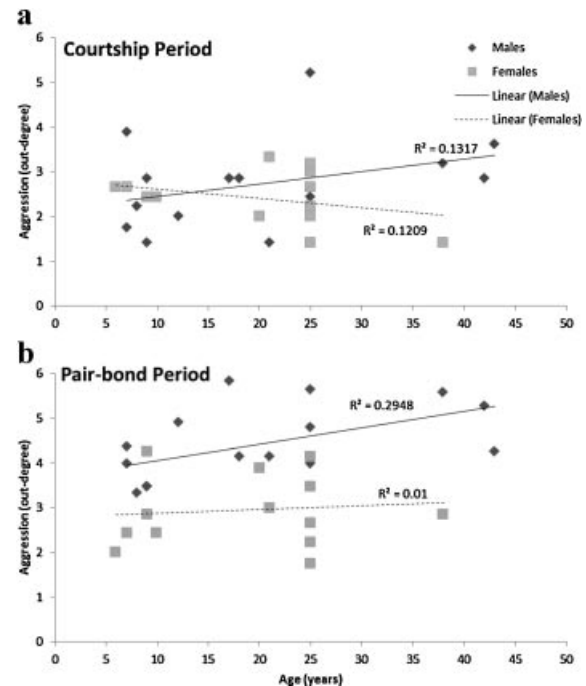
Fig. 4.   Linear regression for out-degree versus age in male and female American flamingos in the Audubon Zoo during (**a**) the courtship period, during which there was no significant relationship among males and females and (**b**) the pair-bond period, during which aggression was positively associated with age among males, but not females.

versus pair-bond period (in-degree centralization 4.09% for the courtship network vs. 8.66% for the pair-bonding network). This result is corroborated in both courtship and pair-bond periods by mean reception of aggressive interaction, and homophily, the later of which we used in this study to assess the propensity for outgoing ties to be directed to members of the same sex. During the courtship stage, there was no difference in reception (mean in-degree $\pm$ SE; male 2.41 ± 0.14 vs. female 2.27 ± 0.14; $P = 0.50$) and individuals directed aggression towards males and females uniformly (mean homophily $\pm$ SE; males $= 0.61 \pm 0.069$, females $= 0.43 \pm 0.083$; E–I Index, $P = 0.118$). This held true during the pair-bond period as there was, again, no difference in reception (mean in-degree $\pm$ SE; male 3.87 ± 0.21 vs. female 3.35 ± 0.25; $P = 0.42$), and no significant deviation from randomness in proportion of same-sex directed outgoing ties (mean homophily $\pm$ SE; males $= 0.47 \pm 0.03$, females $= 0.55 \pm 0.06$; E–I Index, $P = 0.878$). Thus, aggression was directed without regard to sex of the recipient throughout our study period.

DISCUSSION

In the captive population of American flamingos we studied at the Audubon zoo, males were consistently more aggressive than were females throughout our study period, which included the early stages (i.e., courtship display and pair formation) of the breeding season. This was counter to our predictions, and differed from a previous study that found equivalent levels of aggression in male and female Chilean Flamingos (Perdue et al., 2011). Perdue et al. (2011) began their study after pair-bond formation, whereas, our study concluded with pair-bond formation. It is possible that aggression levels between sexes begin to reach a state of equilibrium after pair-bonds are fully formed and nest construction begins; nest protection and chick rearing may become a primary concern for both males and females alike. To our knowledge, no studies have explored sex differences in aggression during incubation and chick rearing. Perdue et al. (2011) also found that pair-bonded Chilean Flamingos were significantly more aggressive than solitary individuals. Pair-bond status, however, was fairly uniform within our study group (32 of 34 flamingos were in a pair-bond).

A second major finding of our study is the documentation of a temporal shift in social structure during the onset of breeding as the study population transitioned from courtship to established pair-bonds. More specifically, we observed significant increases in aggression over time as the onset of the breeding season progressed. This was in agreement with another study in which levels of aggression, during the breeding season of captive Chilean Flamingos, increased as time progressed (Farrell et al., 2000). Additionally, 13% of eggs laid were destroyed due to aggressive interaction between neighbors. Farrell et al. (2000) concluded that the observed increases in aggression were most likely due to an increased demand for nest/chick defense; they suggested that artificial nest mounds at least 1.5 neck lengths apart be built prior to egg deposition in order to alleviate aggression. Though our own study was conducted prior to egg deposition, significant increases in agonistic interaction may too be a defense strategy.

We also documented a significant positive correlation between age and aggression in males during the pair-bond stage. Though a previous study found differences in aggression between juveniles and adults (Bildstein et al., 1991), no other study has looked at patterns of aggression in relation to exact age in flamingos. Our finding suggests that age is associated with a males' tendency to be aggressive. Collis and Borgia (1992) found a relationship between age and aggressive dominance in satin bowerbirds (*Ptilonorhynchus violaceus*), despite androgen supplementation; they suggest that this is consistent with the idea that experience plays a large role in aggression and dominance. It is possible that accumulation of experience in male flamingos influences willingness to invest energy in agonistic encounters. More longitudinal studies, however, could give further insight into the potential relationship between age and aggression.

By assessing these trends in a SNA framework, we were able to gain novel insights into more subtle social dynamics associated with flamingo aggression that traditional approaches to behavior may overlook. At the overall network level, though both the courtship network, and pair-bond network had a low clustering co-efficient, the courtship network had a significantly lower clustering co-efficient than the pair-bond network. Because clustering co-efficient is a measure of the density of interactions between an individual and its neighbors, our results indicate that there were fewer well-connected clusters of individuals in the courtship period. This difference can most easily be explained by pair-bond formation following courtship. Based on qualitative observations, bonded individuals seemed to retaliate to aggression directed toward their partners. We also observed pair-bonded individuals staking claim to artificial nesting mounds, which seemed to lead to increased aggressive interactions with spatially adjacent pairs. Regardless, as the lack of differentiation in reception in both networks suggests, individuals still distributed aggression relatively homogenously, and any potential subgroups that may have formed were most likely due to spatial arrangement, not social position. This, paired with a seemingly indiscriminate distribution of aggressive initiations rather than targeted initiations towards specific individuals, suggests that elevated aggression may result from competition for nesting resources rather than competition for mates.

The social network approach also yielded interesting insights at the individual level. Measures of centrality at the individual level (i.e., comparisons of individual measurements) may not necessarily lend statistically pertinent information (James et al., 2009), but we think it noteworthy to highlight several aspects of this particular system. For

example, though aggression levels increased during the study, most central individuals remained central throughout, suggesting that social structure, in terms of individual positions within the network, remained relatively stable as time progressed. In the courtship network, the individual that initiated the highest amounts of aggressive interactions we recorded was a male whose closest competitors during the courtship season were two other adult males. This same highly aggressive flamingo displayed the second highest level of aggression in the pair-bond network, while the most aggressive individual was a different adult male. Interestingly, the most aggressive male during the courtship period paired with another male during the pair-bond period. Also, during the pair-bond network, a few females displayed levels of aggression nearly equivalent to those of the males in that network. Defending their pair bonded mate may have contributed to this increase in female aggression.

The higher variance in aggressive initiations initiated during courtship, despite constant food availability within the exhibit, demonstrates that certain individuals exhibit higher levels of aggression. Furthermore, highly aggressive individuals could heavily affect overall network structure (Sih and Watters, 2005), though this may be less important once pair-bonds form in our study group. Bildstein et al. (1991) showed that feeding behavior is hindered by aggressive interaction, particularly in younger individuals who received a greater proportion of aggressive displays. Received aggression may negatively affect the foraging activity of breeding individuals, especially females who require a disproportionate amount of energy for reproduction relative to males. This, paired with limited copulation success due to pinioning (King, 1994), may contribute to reproductive failure (Farrell et al., 2000). Forming a better understanding of the differences in aggression levels and social structure between wild and captive flocks might provide more insight into management techniques that would maximize group health.

Spatial structure of the exhibits might impact aggressive behaviors, as increased area seems to reduce competition pressures in captive flamingos (Farrell et al., 2000). Our particular exhibit was approximately $14\,m \times 15\,m$ with a single feeding area, and housed 34 individuals, a density of approximately one animal per $6.2\,m^2$ (the density of individuals in other studies was not reported). Though wild populations of flamingo are typically dense (Tuite, 1979), they are much larger in number than captive populations. Estevez et al. (2003) show that aggression levels decrease with increasing group size in domestic fowl; small captive groups of flamingos may experience larger-than-natural rates of aggression. But rather than manipulation of group sizes, increases in exhibit size, or foraging space could ameliorate aggression by providing more areas for refuge of subordinate individuals, and potentially relieving competitive pressures regarding nesting resources. However, this possibility remains untested, and increasing exhibit size may not be practical in every zoo. We suggest further research to compare the social structure of varying groups inhabiting disparately sized exhibits.

Future studies could also explore the effects of the experimental removal of highly central (i.e., aggressive) individuals on the social structure of the population. Due to flamingos heightened response to disturbance during pre-breeding (courtship and pair establishment), and breeding seasons, any such removal should occur during the non-breeding season while manipulation is not likely to negatively impact breeding. Flack et al. (2006) show significant alterations in primate social structure upon removal of highly central individuals; however, it is difficult to determine whether, the removal of an individual within our flamingo population will elicit significant shifts in social structure in accommodation for the missing individual (another may take the vacant position). Before proceeding with removals, it would be important to assess the reproductive output of these central individuals and the colony as a whole when they are present, in order to have a baseline for comparison. Because individuals differ in their level and consistency of aggression (Réale et al., 2007), investigating individual differences could be an exciting future research direction with management implications, especially in small captive populations with detailed data on individuals. Using SNA, managers may be able to identify highly aggressive or stressed individuals and take appropriate management actions.

There are fundamental differences between captive and wild flocks, especially with regard to flock size and foraging needs. Still, zoo studies remain a useful tool in understanding animal behavior, and flamingos are a prime example of why captive research is necessary and can yield valuable results (King, 2000). Additionally, individual level and network level SNA metrics could prove important in revealing potential causes of animal stress (e.g., by elucidating which individuals display disproportionate amounts of aggression and which individuals receive this aggression), as well as aiding in the development of techniques that might serve to promote population health (e.g., determining sufficiency of exhibits in providing areas for refuge from aggression). The indiscriminate initiation of aggressive interaction along with the increased level of aggression during the pair-bond stage suggests that elevated aggression may be linked to competition for nesting resources, and not competition for mates. Because aggression might not be obligate for successful breeding, efforts to reduce aggressive interactions in captive populations could be useful in promoting individual health and reproduction. Furthermore, keeping in mind that highly central individuals appeared to remain central throughout the onset of the breeding season, we suggest further network theory based research investigate the possible correlations and carry-over effects of aggression and social structure during the non-breeding season on individual reproductive success during the breeding season. Regardless of the cause of aggression, longitudinal studies may be useful in predicting future mating success, as was predicted by SNA of social structure in long-tailed manakins (*Chiroxiphia linearis*)

(McDonald, 2007). Historically, zoos have had trouble with successfully mating flamingos (Farrell et al., 2000); if able to successfully predict or promote reproductive success, network theory and more detailed analyses of social structure and aggression may prove to play a valuable role in husbandry and management which could become increasingly important for conservation if wild populations continue to decline.

ACKNOWLEDGMENTS

REFERENCES

Allen RP. 1959. The flamingos: their life history and survival. New York: National Audubon Society.

Altmann J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.

Anderson MJ, Williams SA, Bono AJ. 2009. Preferred neck-resting position predicts aggression in Caribbean flamingos (*Phoenicopterus ruber*). Laterality 15:629–638.

Bechet A, Johnson AR. 2008. Anthropogenic and environmental determinants of greater flamingo *Phoenicopterus roseus* breeding numbers and productivity in the Camargue (Rhone delta, southern France). Ibis 150:69–79.

Bildstein KL, Frederick PC, Spalding MG. 1991. Feeding patterns and aggressive behavior in juvenile and adult American flamingos. Condor 93:916–925.

Bildstein KL, Golden CB, McCraith BJ, Bohmke BW, Seibels RE. 1993. Feeding behavior, aggression, and the conservation biology of flamingos: integrating studies of captive and free-ranging birds. Am Zool 33:117–125.

Borgatti SP, Everett MG, Freeman LC. 2002. Ucinet for windows: software for social network analysis. Harvard, MA: Analytic Technologies.

Cezilly F, Boy V, Green RE, Hirons GJM, Johnson AR. 1995. Interannual variation in greater flamingo breeding success in relation to water levels. Ecology 76:20–26.

Cezilly F, Viallefont A, Boy V, Johnson AR. 1996. Annual variation in survival and breeding probability in greater flamingos. Ecology 77:1143–1150.

Cezilly F, Boy V, Tourenq C, Johnson AR. 1997. Age-assortative pairing in the Greater Flamingo *Phoenicopterus ruber roseus*. Ibis 139:331–336.

Collis K, Borgia G. 1992. Age-related effects of testosterone, plumage, and experience on aggression and social dominance in juvenile male satin bowerbirds (*Ptilonorhynchus violaceus*). The Auk 109:422–434.

Croft DP, James R, Krause J. 2008. Exploring animal social networks. Princeton, NJ: Princeton University Press.

Croft DP, Madden JR, Franks DW, James R. 2011. Hypothesis testing in animal social networks. Trends Ecol Evol 26:502–507.

Ellis JC, Good TP. 2006. Nest attributes, aggression, and breeding success of gulls in single and mixed species subcolonies. Condor 108:211–219.

Estevez I, Keeling LJ, Newberry RC. 2003. Decreasing aggression with increasing group size in young domestic fowl. Appl Anim Behav Sci 3:213–218.

Farrell MA, Barry E, Marples N. 2000. Breeding behavior in a flock of Chilean flamingos (*Phoenicopterus chilensis*) at Dublin zoo. Zoo Biol 19:227–237.

Flack JC, Girvan M, Waal FBM, Krakauer DC. 2006. Policing stabilizes construction of social niches in primates. Nature 439:426–429.

Gonzalez-Voyer A, Sxekely T, Drummond H. 2007. Why do some siblings attack each other? Comparative analysis of aggression in avian broods. Evolutionary 61:1946–1955.

Hanneman RA, Riddle M. 2005. Introduction to social network methods. Riverside, CA: University of California, Riverside Available online at: http://faculty.ucr.edu/hanneman/.

IUCN. 2011. IUCN Red list of threatened speciesVersion 2011.2. Available online at: www.iucnredlist.org.

Jakubas D. 2004. Sibling aggression and breeding success in the Grey Heron. J Waterbird Biol 27:297–303.

James R, Croft DP, Krause J. 2009. Potential banana skins in animal social network analysis. Behav Ecol Sociobiol 63:989–997.

King C. 1994. Management and research implications of selected behaviors in a mixed colony of flamingos at Rotterdam Zoo. Int Zoo Yearb 33:103–113.

King C. 2000. Captive flamingo populations and opportunities for research in zoos. J Waterbird Biol 23:142–149.

McDonald DB. 2007. Predicting fate from early connectivity in a social network. PNAS 104:10910–10914.

McCowan B, Anderson K, Heagarty A, Cameron A. 2008. Utility of social network analysis for primate behavioral management and well-being. Appl Anim Behav Sci 109:396–405.

Ottenwalder JA, Woods CA, Rathburn GB, Thorbjarnarson JB. 1990. Status of the greater flamingo in Haiti. Colon Waterbird 13:115–123.

Perdue B, Gaalema DE, Martin AL, Dampier SM, Maple TL. 2011. Factors affecting aggression in a captive flock of Chilean flamingos (*Phoenicopterus chilensis*). Zoo Biol 30:59–64.

Pritchard DJ, Fa JE, Oldfield S, Harrop SR. 2012. Bring the captive closer to the wild: redefining the role of ex situ conservation. Oryx 46:18–23.

Ramos JA. 2003. Intraspecific aggression by Roseate Tern adults on chicks in a tropical colony. J Waterbird Biol 26:160–165.

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007. Integrating animal temperament within ecology and evolution. Biol Rev 82:291–318.

Sandell M. 1998. Female aggression and the maintenance of monogamy: female behaviour predicts male mating status in European Starlings. Proc Biol Sci 265:1307–1311.

Shannon PW. 2000. Social and reproductive relationships of captive Caribbean flamingos. J Waterbird Biol 23:173–178.

Sih A, Watters JV. 2005. The mix matters: behavioural types and group dynamics in water striders. Behaviour 142:1417–1431.

Stevens EF, Beaumont JH, Cusson EW, Fowler J. 1992. Nesting-behavior in a flock of Chilean Flamingos. Zoo Biol 11:209–214.

Studer-Thiersch A. 2000. What 19 years of observation on captive greater flamingos suggests about adaptations to breeding under irregular conditions. J Waterbird Biol 23:150–159.

Tuite CH. 1979. Population size, distribution, and biomass density of the lesser flamingo in the eastern rift valley. J Appl Ecol 16:765–775.

Wey T, Blumstein DT, Shen W, Jordan F. 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. Anim Behav 75:333–344.

White DJ, Gersick AS, Freed-Brown G, Snyder-Mackler N. 2010. The ontogeny of social skills: experimental increases in social complexity enhance reproductive success in adult cowbirds. Anim Behav 79:385–390.

Wielebnowski N. 1998. Behavioral ecology and conservation biology. New York: Oxford University Press, Inc. p 130–162.