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Research article

Social associations in captive Caribbean flamingos *Phoenicopterus ruber* and their implications for flock management

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Abstract
Studying the flamingo's preferential associations provides information on welfare indicators such as aggression and reproduction. This study investigated associations within the Caribbean flamingo *Phoenicopterus ruber* flock at Zoo de Granby, Québec, using an association index (AI) to measure the strength of associations. Based on previous literature, it was predicted that (1) pairs would remain stable throughout the study, (2) younger individuals would be more likely to change partners than older individuals, and (3) pairs with a large age difference would be more likely to switch partners. Contrary to the prediction, only 58% of pairs were maintained throughout the study; however, the strength of the associations increased in 2016. No relationship was found between the age of an individual and their likelihood to change partners, nor between the age difference between partners and their likelihood to split. This research demonstrates that captive flamingos can have strong associations. Regarding the management of the flock, the flamingos appear to demonstrate free mate choice and further research would be needed to assess whether there is stability in pairings between multiple years.

Introduction

Flamingos (Phoenicopteridae) are long-lived, gregarious birds that form associations within their colonies (King and Bračko 2014; Rose et al. 2014). Wild greater flamingos form pairs but do not tend to maintain the same pairing through multiple breeding seasons (King 2008a; Johnson and Cézilly 2009). However, it has been reported that captive flamingos form lasting partnerships and exhibit mate fidelity (Pickering 1992a; Shannon 2000; Studer-Thiersch 2000; King 2008a; Rose et al. 2014; Rose and Croft 2017). Researchers have suggested mate fidelity in captivity is due to limited numbers of individuals from which to choose a mate (Studer-Thiersch 2000; Rose et al. 2014). The limited options for mates, and an often male-biased sex ratio, could lead to increased mate guarding during the breeding season in an attempt to assure paternity (Weir et al. 2011). Based on this information, it was predicted that the Zoo de Granby (Granby, Québec, Canada) flock would exhibit stable pairings.

Another factor in flamingo socialisation is the age of the flamingos (Cézilly et al. 1997; Pradel et al. 2012). Studies have found that the probability of breeding was dependent on the breeding experience of the individuals (Pradel et al. 2012) and that flamingos showed a preference towards older individuals (Cézilly et al. 1997). The researchers conducting these studies hypothesised it was due to the increased experience of the older flamingos rendering them better at obtaining resources such as food, mates and nesting sites (Cézilly et al. 1997; Schmaltz et al. 2011; Pradel et al. 2012). Young flamingos are hypothesised to be inexperienced and inefficient at foraging, which means that while they are physically able to reproduce, it would be costly, thus making them a less than ideal partner

(Pradel et al. 2012). Age plays a role in the likelihood of changing partners; younger individuals are thought to change partners more often than older ones due to their inexperience (Ens et al. 1993; Choudhury 1995). Inexperienced individuals are more likely to choose an incompatible mate and would therefore gain more from a pair change (Ens et al. 1993; Choudhury 1995). Based on this literature, it was predicted that younger individuals would be more likely to change partners than older individuals, and pairs with a large age difference would be more likely to switch partners.

Through studying the associations of the Zoo de Granby flamingo flock, it is possible to gain insights into possible causes of aggression and reproductive issues within the flock, which in turn allow the assessment of welfare (Shannon 2000; Melfi 2009). This information can also be used for flock management to ensure strongly bonded pairs are kept together since social bonds are important for their welfare and the separation of bonded pairs could lead to stress and decreased welfare (Rose and Croft 2015a). For the purpose of this study, associations were quantified using an association index (AI), to analyse the relative strengths of the associations. The generated data were used to assess the predictions that (1) pairs would remain stable throughout the study, (2) younger individuals would be more likely to change partners than older individuals, and (3) pairs with a large age difference would be more likely to switch partners.

Methods

Establishment and history of the Zoo de Granby flock

The Zoo de Granby flamingo flock was established in 1979 and consisted of 18 flamingos from Cuba. Between 1983 and 1988, the zoo received an additional 20 flamingos from Cuba. Since then, the flock has consisted of a combination of captive born flamingos and flamingos from Cuba, although no wild flamingos have been received since 2010.

Through the years, several changes were made to stimulate reproduction, including the addition of mirrors, the introduction of a higher protein diet during the breeding season, lights on timers installed, and nests built by keepers to encourage the flamingos to nest. In June 1990, an egg was laid but was infertile. Later that year, another egg was laid that did not hatch, but was proven to be fertile. In 1992, four eggs were laid, and one successfully hatched. In 1993, six females laid an egg and three of them laid twice after losing an egg during incubation. Only one of these eggs successfully hatched while others were infertile. Another egg successfully hatched in 1994. Contrary to the theory that full-winged males have a higher success rate, the proven breeder male at Zoo de Granby was one of the males with a partially amputated wing (Pickering 1992a; Lanthier 1995).

Study area and subjects

A flock of 28 Caribbean flamingos *Phoenicopterus ruber* consisting of 15 males and 13 females was studied at Zoo de Granby. Observations were conducted at both the indoor and outdoor enclosures. Outdoor enclosure observations were conducted from the public viewing areas, and indoor enclosure observations were conducted from inside the enclosure using a blind to remain hidden from the flock. The open-topped outdoor enclosure consists of ~286 m^2 of accessible ground cover (grass) and a large pond (~686 m^2) covering approximately 71% of the enclosure. Twice a year, the flamingos are caught by keepers and relocated to the opposite enclosure. The indoor enclosure is about 66 m^2 consisting of a substantial portion featuring mud for nesting building and shallow water basin. The enclosure features mirrored half-walls in an attempt to make flock appear larger to the flamingos, which can encourage breeding (O'Connell-Rodwell et al. 2004). The indoor enclosure is shared by the flamingo flock and six cattle egrets *Bubulcus ibis*. The flock ranges in age from 7 to 38 years old (mean=20.2). Individual flamingos can be identified using leg bands with unique numbers and colour combinations. Through individual identification, information can be obtained from zoo records to determine age, sex and Zoological Information Management System (ZIMS) database number. Mentions of individual flamingos will include an M or F to reference their sex, followed by their band number (ex: M27) or ZIMS number for those with no band number (ex: F-B03020). The flamingos were fed a regular diet of Mazuri Flamingo Complete (#5644) and Mazuri Breeder Reproduction (#5645) during the breeding season (December–May). They were fed at various times; usually between 1030 and 1330. When the flamingos were indoors from October to April, the food trays were placed in the enclosure away from the nesting area to prevent nest disturbance and trays were placed with space between them prevent feeding aggression within the flock. The outdoor feeders included a large trough at the water's edge, a standing duck-proof feeder near the shoreline, and seven bowls hidden in fake nests on the shore.

Data collection

Focal animal behavioural sampling was conducted to collect individual's behaviour and social affiliations (see Ethogram in Appendix 1). Focal animals were chosen based on the visibility of their leg bands for identification, without a determined order from one day to the next. On a given day, an individual would be selected for a focal once. Each sampling period lasted for 10 min with the behaviour of the focal animal recorded every 15 sec. A cellphone application called Interval Timer AD (halmi.sk 2015) was used as a notification of when to record a behaviour.

Social interactions were estimated using frequency of proximity of an individual to another one; individuals could be actively feeding with another flamingo or resting side by side and both would be considered a social interaction. If the flamingos were near each other prior to the start of the focal and continued with their behaviours during the focal, they were considered as interacting. If the individuals approached within one neck length of each other during a focal, they were recorded as interacting if they were doing the same behaviour consistently for more than three recordings (45 sec). This method follows that used by Rose and Croft (2017) to determine social bonds based on a paper by Rose and Croft (2017) wherein flamingos would be considered within a group or pairing when they would perform regular behaviours (resting, foraging, preening, locomotion) within one neck length of another flamingo without demonstrating aggressive behaviours towards the other flamingo.

Data were collected between July 2015 and June 2016. Sampling during various seasons differed based on weather and availability. The flamingos were in their outdoor enclosure between July and September 2015, and again between May and June 2016. Between July and September 2015, data were collected daily. While the flamingos were indoors from October to December 2015, data were collected almost every Friday, and between January and April 2016, data were collected on two consecutive days each week, usually on Tuesdays and Wednesdays. Once the flamingos were returned outdoors, data were collected daily between May and June 2016.

There was a sudden change in pairings in late December 2015 or early January 2016. Due to this change in mate pairs, the study was split into two time periods, named 2015 (July–December 2015) and 2016 (January–June 2016). Group displays during the breeding season are most frequent between January and May, so it was assumed that the 2016 period aligns with the breeding season (Shannon 2000).

From the focal sampling data, a list of the pairings was created, detailing how often each individual was seen within that pairing,

how often each individual was seen alone, and if the individual maintained the pairing throughout the study or changed partners. Zoo records provided the age and sex of the individuals to better examine their social preferences.

Data analysis

Data were compiled, and the social interactions were analysed using an association index (AI) (Martin and Bateson 2007). The AI used the number of times each individual (a, b) was each seen separately (Na, Nb), and the number of times the individuals were seen together (Nab). When an individual was interacting with two other individuals (forming a triad), it was considered that this individual was interacting with each one independently. Using the AI equation (Nab / Na + Nb + Nab), it was possible to calculate a value between 0 and 1 representing the ratio of time individuals spend together versus time spent apart. This equation corresponds to the simple ratio index (Croft et al. 2008) given that the number of times two individuals are observed but in different groups is equal to 0 due to the focal technique. An AI value of 0 demonstrates no affiliation between individuals, and a value of 1 suggests a full affiliation. An AI value of 0.5 would mean individuals spend equal time together and apart; it is for this reason that affiliated pairs will be considered those with AI values of 0.5 or greater. A pair will be considered strongly associated when it has an AI value of 0.8 or higher and fully associated with an AI value of 1.0 (Bräger et al. 1994). It was considered that there was no association when none or a single co-occurrence of the two individuals was recorded, and a weak association for AI<0.5.

Results

Out of 1,032 total focals, 964 focals were unique per individual and day (i.e., at 34 instances, an individual had two focals in a given day). An average of 11.0 focals were performed a day (sd=2.55; min=4; max=16), with no major difference across the different periods. In 2015, each individual was the object of 22.0 focals on average (sd=5.86; min=12; max=32), while it was 14.8 focals on average in 2016 (sd=2.89; min=10; max=21) due to a shorter number of days of surveys (52 in 2015 versus 42 in 2016).

In 2015, the association index (AI) values ranged from 0 to 0.87 with an average value of 0.036+/-0.14 demonstrating a large range of association strengths (Figure 1). Out of the 378 possible pairs, the individuals of 298 pairs were never observed interacting together, 47 only once, 20 pairs had a weak association (AI<0.5), 10 were associated (AI 0.5–0.8), and only three had a strong association (AI>0.8). In 2016, the AI values ranged from 0 to 1 with an average value of 0.034+/-0.17. Individuals of 352 pairs were never observed interacting together; six only once, seven pairs had a weak association (AI<0.5), three were associated (AI 0.5–0.8), and 10 had a strong association. If only paired individuals are considered (AI≥0.5), the AI is 0.73+/-0.09 in 2015 but significantly increases to 0.88+/-0.16 in 2016 (P=0.006).

Combining the two periods, 19 associated pairs were identified. Out of the 12 male-female pairs associated in 2015, seven (58%) remained associated in 2016 (Table 1). All but two (M6 and F38) in 2015, and all individuals but one (M50) in 2016 were associated with at least one other individual. M50 spent the vast majority

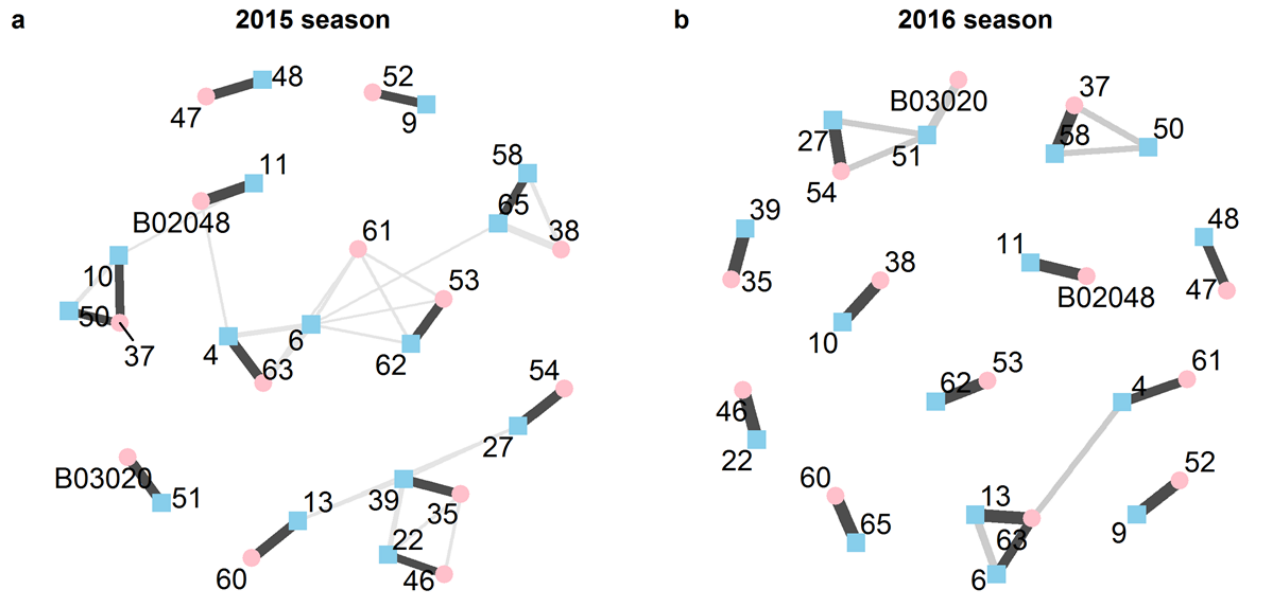

Figure 1. Social networks of the 2015 (a) and 2016 (b) social associations. Each flamingo is represented by their band number or Zoological Information Management System (ZIMS) number in the case of B03020 and B02048 who do not have band numbers. The strength of the associations is represented by the thickness of the lines. The thin lines represent weaker associations while the thick lines represent stronger associations.

Table 1. Associated pairs in either 2015, 2016, or both periods, ordered by the sum of the association index. Strong association (AI>0.8) are shown with [a], and association (AI 0.5–0.8) with [b]. Index letters [c] and [d] highlight connected triples (i.e., triads). The * IDs display the only non male-female pair. The bottom of the table presents individuals that were not associated in the given year.

Pair						2015	2016
Oldest individual			Youngest individual				
ID	Sex	Age	ID	Sex	Age	AI	AI
54	F	38	27	M	18	0.825[a]	0.968[a]
35	F	15	39	M	15	0.733[b]	1.000[a]
11	M	38	B02048	F	14	0.872[a]	0.857[a]
53	F	14	62	M	7	0.739[b]	0.971[a]
09	M	38	52	F	14	0.688[b]	0.970[a]
22	M	20	46	F	15	0.587[b]	1.000[a]
47	F	38	48	M	14	0.783[b]	0.606
51	M	14	B03020	F	13	0.750[b]	0.467
63	F	24	06	M	16	0.380	0.625[b,c]
63	F	24	13	M	16	0	1.000[a,c]
37	F	15	58	M	14	0	1.000[a]
65	M	33	60	F	16	0	1.000[a]
38	F	38	10	M	16	0	0.933[a]
04	M	31	63	F	24	0.778[b]	0.074
13	M	16	60	F	16	0.805[a]	0
37	F	15	50	M	14	0.633[b,d]	0.138
10	M	16	37	F	15	0.667[b,d]	0
65*	M*	33*	58*	M*	14*	0.612[b]	0
04	M	31	61	F	8	0.023	0.567[b]
06	M	16				alone	-
38	F	38				alone	
50	M	14				-	alone

of his time in 2016 alone in the water basin or at the edge of the flock where he rarely interacted with other individuals. Triads were detected: female 37 was associated with two individuals in 2015 (M10 and M50), and in 2016 (M50 and M58), and the female 63 was associated with two individuals in 2016 (M6 and M13). Interestingly, individuals from three pairs were never seen together in 2015 (AI=0) while they were always seen together in 2016 (AI=1).

Of the pairs formed in 2015, all but one (male-male) were male-female pairs. Of the pairs formed in 2016, all were male-female pairs. There is a significant relation between the AI in 2015 and 2016, even after taking into account male-female pairs only (AI2016=0.02+0.73*AI2015; P<0.001) but it only explains a fraction of the variability (r^2=0.35). Indeed, 96% of male-female pairs that had no association in 2015 (183) kept no association (177), while only 58% of male-female pairs that were associated in 2015 (12) remained associated in 2016 (7).

The study also looked at the age of individuals within pairings (Figure 2). No significant relationship was found between the age of an individual and its likelihood to change partners (linear binomial model, P=0.45, n=26). No significant relationship was found between the absolute difference in age of partners and the likelihood the pairs to split (linear binomial model, P=0.07, n=13).

Discussion

Some studies of wild greater flamingos suggest they do not maintain pair bonds between breeding seasons, but studies have shown captive populations of flamingos to have high levels of mate fidelity (Pickering 1992a; Farrell et al. 2000; Shannon 2000; Studer-Thiersch 2000; Rose and Croft 2017). Accordingly, it was predicted that associations would remain stable throughout this study. The results demonstrated strong association of pairings within each year with increased mate fidelity in 2016. Between 2015 and 2016, a moderate level of mate fidelity was observed (58%). These findings support other studies which have seen mate fidelity in captivity (Pickering 1992a; Shannon 2000; Studer-Thiersch 2000; King 2008a; Rose et al. 2014; Rose and Croft 2017). While smaller flocks have been suggested to have higher levels of mate fidelity due to limited mate choices, this study revealed moderate levels of mate fidelity suggesting a small flock may not necessarily limit mate choice (Pickering 1992a; Farrell et al. 2000; Shannon 2000; Studer-Thiersch 2000; Rose et al. 2014). Unfortunately, it was not possible, even by the flamingo keepers, to identify the cause of the pair changes. There are several possible reasons for pair separations including failure to reproduce in the current or previous breeding season, availability of unpaired individuals and age (Ens et al. 1993; Choudhury 1995). Failure to reproduce is a

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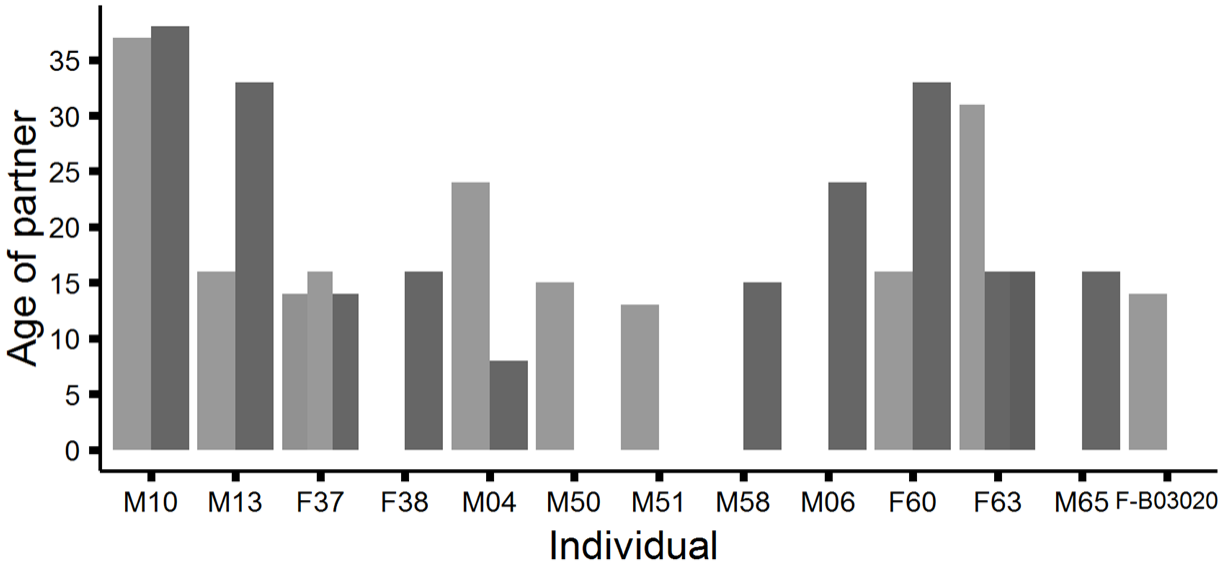

Figure 2. Distribution of the change in partner age from 2015 to 2016. On the x-axis is a list of individuals who changed partners in 2016. The y-axis shows age of the partner in years. The light gray bars show the data from the 2015 associations, and the dark gray bars show the data from the 2016 associations.

likely reason behind pair changes in the Zoo de Granby flock as they have not successfully reproduced in 10 years.

The pair changes are also likely to be related to the prior unavailability of unpaired individuals. According to the better option hypothesis by Ens et al. (1993), for an individual to leave its partner, the chance of finding a better partner must outweigh the risk of being unpaired. If unpaired flamingos are not available within the population, it is unlikely for pairs to risk separating (Ens et al. 1993). When the triads in the study flock split, there were suddenly three unpaired individuals available. These newly available individuals may have been the stimulus for other pairs to switch partners to potentially increase future reproductive success (Ens et al. 1993; Choudhury 1995). In contrast, a study found that when new individuals were added to a captive flock, no pairings were formed between the established and new individuals even though they had not successfully reproduced the previous breeding season (Frumkin et al. 2016). Their finding is consistent with most research on captive flamingo populations where mate fidelity is common (Pickering 1992a; Shannon 2000; King 2008a). Further research on the Zoo de Granby flock would need to be conducted to determine if the switch was a coincidence or if there are consistent pair changes between breeding seasons as there are in wild populations of flamingos. A study by Cézilly and Johnson (1995) showed that greater flamingos in southern France changed mates between consecutive breeding seasons 98.3% of the time. Another study by Pickering (1992b) demonstrated 89% mate fidelity in captive Caribbean flamingos. Comparatively, only 58% of the flamingos at Zoo de Granby maintained pairings between the two years.

The second prediction was that younger individuals would be more likely than older individuals to change partners. Research has suggested that younger birds would change pairs more frequently than older birds because the younger, more inexperienced individuals are more likely to pick an incompatible mate and therefore have the most to gain in terms of future reproductive success by changing mates (Ens et al. 1993; Choudhury 1995). Mate changes in older individuals are still possible because, should a high-quality individual become available, it would be advantageous to leave the current partner for the higher quality unpaired individual (Choudhury 1995). The present results did not show a difference in terms of age and likelihood of changing partners.

The final prediction was that pairs with a large age difference would be more likely to switch partners. Research shows that breeding with individuals of a similar age is common in greater flamingos (Cézilly et al. 1997) and barnacle geese *Branta leucopsis* (Black and Owen 1995); however, long-lived species generally show a preference for older individuals because they are more experienced and generally have better breeding success (Schmaltz et al. 2011; Pradel et al. 2012). This study found no relationship between the age difference between partners and the likelihood of the pair splitting. Possible explanations are the limited mate options within the flock due to small flock size, younger age distribution of the flock, lack of previous breeding experience, and the lack of consideration of sexual display complexity (SDC) during this study. While age was considered, this study did not consider the SDC, which has been shown to be more accurate indicator of quality than age in greater flamingos (Perrot et al. 2016). There is also a quadratic relationship between age and SDC for greater flamingos suggesting that SDC increases until flamingos are approximately 20 years old then begins to decrease (Perrot et al. 2016). Individuals with more complex and versatile displays, and therefore a higher SDC value, are more likely to become breeding individuals (Perrot et al. 2016). Further study of the flock should include group display complexity to have a better understanding of the mate choices within the flock.

Future research on the Zoo de Granby flock should include SDC, the participation of individuals in group displays, and the effects of a Canadian climate on the behaviour of a tropical species of bird. Small flock size seems to be the most limiting factor for the Zoo de Granby flock. The recommended flock size for breeding is 40 or more flamingos while Zoo de Granby only has 28 flamingos (Pickering et al. 1992). The Zoo de Granby flock is also housed in an open-topped enclosure, meaning the flamingos are either wing-clipped or pinioned, which further reduces likelihood of successful reproduction (King 2008b). The arising recommendations for Zoo de Granby are to increase flock size while creating an even sex ratio, consider adding a net to the enclosure to avoid the necessity of wing-clipping the flamingos, and conduct further research to see if there is mate fidelity between multiple years.

Conclusions

1) Contrary to the prediction and previous studies, only 58% of the 2015 pairings were maintained in 2016. However, an increase in association strengths was observed in 2016 compared to those in 2015.
2) No relationship was found between the age of an individual and their likelihood to change partners, nor between the age difference between partners and their likelihood to split.
3) The study's findings identify areas that require future research, including participation in group displays, sexual display complexity, and the suitability and possible effects of a Canadian climate on the behaviour of a tropical species of bird.
4) Regarding the management of the flock, the flamingos appear to demonstrate free mate choice and further research would be needed to demonstrate if there is stability in pairings between multiple years.

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