

CONTEST ASYMMETRY AND MULTIPLE BIRD CONFLICTS DURING FORAGING AMONG NONBREEDING AMERICAN FLAMINGOS IN YUCATAN, MEXICO¹

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Abstract. Aggressive behavior of feeding American Flamingos (*Phoenicopterus ruber ruber*) was observed to determine asymmetries associated with contest outcomes. The size difference between male and female flamingos appeared to be the primary determinant of contest roles in two-bird interactions, but contest intensity increased with a reduction in the relative difference in size of the contestants. Multiple bird interactions (i.e., >2) were never initiated by more than two birds, and all identifiable age and sex classes were represented among birds winning and initiating interactions. The large number of adult male-adult female groups involved in multiple bird interactions suggests that some degree of pair bonding had occurred and that mate competition may also be occurring in aggressive interactions in foraging aggregations.

Key words: Aggression; American Flamingo; flock; foraging; Mexico; nonbreeding.

INTRODUCTION

Game theory, through the use of evolutionary stable strategy models, allows an evaluation of the evolution of animal conflict on an individual level (Maynard Smith and Price 1973). Games may be viewed as either discrete (e.g., hawk and dove games), or continuous (e.g., wars of attrition; Parker 1984). In either case, the choice of strategy depends on asymmetries in the value of a resource to opponents, the resource holding potential (fighting ability) of individuals, or in some condition such as ownership, that is not correlated with resource value or fighting ability (uncorrelated asymmetries) (Parker 1974, Maynard Smith and Parker 1976). Individuals often lack complete information on asymmetries, which can only be obtained during a contest and at a cost to the contestants (Parker and Rubenstein 1981, Enquist and Leimar 1983).

Among American Flamingos (*Phoenicopterus ruber ruber*), aggressive behavior is highly ritualized (Rooth 1965) and frequently involves more than two individuals. Although the aggressive behavior of this species has been described (Allen 1956, Rooth 1965, Kahl 1975), there are few studies on the behavioral ecology of aggression associated with this highly gregarious species (Bildstein et al. 1991). Our objective was to doc-

ument aggressive interactions occurring among feeding American Flamingos during the nonbreeding period and assess these interactions relative to the potential function of some asymmetries.

STUDY AREA AND METHODS

The Celestun Estuary on the northern coast of the Yucatan Peninsula is the principal nonbreeding site for the Yucatan population of American Flamingos. Espino-Barros and Baldassarre (1989) provided a map and description of the study area, which before Hurricane Gilbert was primarily a brackish estuary with extensive submergent beds of widgeongrass (*Ruppia maritima*) and muskgrass (*Chara* spp.). Hurricane Gilbert struck Yucatan in September 1988, however, and nearly all of this vegetation was destroyed due to a tidal surge that increased water turbidity and salinity. Salinity ranged from 8–24 ppt before the storm (Espino-Barros and Baldassarre 1989) to 18–34 ppt that we recorded in February 1989.

Flamingos were observed from January to March 1989 from observational blinds in the northern third of the Celestun Estuary, where most feeding occurred, and aggressive encounters were documented using the ad libitum sampling procedure (Altmann 1974). Aggression was monitored only in aggregations of feeding flamingos because aggressive interactions were not frequent among resting groups of birds. All observations were made with a 15 × 60× power

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spotting scope during diurnal hours and were concurrent with observations for an investigation of temporal and spatial characteristics of feeding aggregations. Sampling proceeded from one edge of an aggregation to the middle, by moving the spotting scope progressively in the same direction to prevent sampling the same individuals twice. The limited field of view of the spotting scope and the number of birds within that view served as a random sample. The flamingos in the field of view then were observed until the first aggressive interaction occurred. Intraspecific aggressive encounters were described by recording the level of intensity of the encounter, outcome of the encounter, order of involvement, sex and age of the individuals in the encounter, and activity prior to the encounter.

Encounter intensity was described using three criteria. The highest level of intensity was actual contact, which generally involved "bill-fighting," and less frequently, pecking at the back, sides, and tail feathers of the opponent (Rooth 1965). The second level was threat, which occurred when a flamingo displayed an outstretched neck, usually with back and shoulder feathers raised (Rooth 1965). The third and lowest level of intensity was no display. This level was indicative of flamingos that either continued to feed regardless of a direct advance from another individual or promptly left a feeding site. Displacement occurred when another flamingo, exhibiting one of the higher levels of intensity, advanced towards the retreating individual and occupied the same foraging site. Flamingos often were observed walking within a feeding aggregation; however, when actually feeding, they were stationary and would tread the mud bottom with their feet utilizing the "stamping-marking time" method of feeding (Rooth 1965). Therefore, displacement was easily observed regardless of the level of intensity.

An encounter began when one or more flamingos made contact or exhibited a threat display, but contact usually was preceded by threat posturing. Although preening, courtship, and flight were observed before encounters, they collectively represented less than 1% of the observations and were not included in the analysis. Outcome of encounters was tallied as either win or lose, with winning status assigned to birds that either were able to supplant or resist displacement from foraging locations.

Although ritualized group courtship activity (Rooth 1965) had begun by mid-January, pair

status was not readily observable through behavior or proximity of individuals in feeding groups. Male American Flamingos are larger (162.6–172.7 cm) than their female counterparts (132.1–160.0 cm; Allen 1956) and this character of sex identification is readily observed in the field (Rooth 1965). Juveniles were classified as any birds with light pink, white, or grey feathers, whereas birds with entirely orange-red body feathers were classified as adults (Rooth 1965). All frequency data for aggressive encounters were analyzed by the chi-square procedure (Zar 1984).

RESULTS

We observed 371 aggressive interactions of which 38% ($n = 141$) involved more than two birds (Table 1). The relative frequencies of interactions were: 62% ($n = 230$) for two birds; 19% ($n = 70$) for three birds; 18% ($n = 65$) for four birds; 1% ($n = 4$) for five birds; and <1% ($n = 2$) for six birds. Aggressive encounters occurred among individuals of all age classes and both sexes (Table 2). No injuries occurred from aggressive encounters, which concurs with earlier reports (Rooth 1965).

TWO-BIRD AGGRESSIVE INTERACTIONS

Comparison by sex and age. We summarized aggressive encounters among American Flamingos where both sex and age were known among contestants (Table 2) and found that for males, adults initiated more aggressive encounters than expected (74%; $P < 0.05$), whereas juvenile males responded more (40%; $P < 0.05$). Females contrasted with males in that adults responded to more encounters than expected (89%; $P < 0.001$) while juveniles initiated more encounters than expected (34%; $P < 0.001$). When data were pooled by sex, more males initiated aggressive encounters than responded to attacks (69%; $n = 241$; $P < 0.001$), whereas females responded to more encounters (83%; $n = 123$; $P < 0.001$) than they initiated (Table 3). When data were pooled by age, there was no difference ($n = 418$; $P = 0.30$) between flamingos initiating or responding to aggressive encounters, nor was there any difference ($n = 418$; $P = 0.12$) between ages in the incidence of winning or losing encounters. We note here that sample sizes associated with pooling data by sex or age are larger than the combined sample sizes in Table 2 because only one classification criterion (i.e., sex or age) needed to be known for these comparisons.

TABLE 1. Frequency and outcome of multiple bird aggressive interactions of wintering American Flamingos ($n = 141$).

Age-sex class of losers (respond)	Age-sex class of winners (initiate)										
	AM*	AF	JM	JF	AM AM	AF AF	AM AF	AM JM	AM JF	JM JM	JM JF
AM					2 (3)		22 (13)	1		3 (5)	(1)
AF					1		6 (5)			5 (2)	1 (1)
JM					1		7 (8)				2
JF					1		1 (1)			2 (1)	
AM AM	3 (2)	(1)	(1)	(1)	1 (1)		3 (5)	(1)		1 (1)	
AM AF	4 (12)	(1)			3 (1)		31 (32)				
AM JM	(1)	1			2		(1)				
AM JF			(1)				1 (1)				
AF AF								1		1	
AF JM	(1)										
AF JF				(1)							
JM JM	6 (4)	(3)			2 (2)	(1)	5 (5)			1 (1)	1
JF JF	2 (2)	1			1 (1)						
JM JF	3 (1)		(3)				3 (3)				1 (1)
AM AM AF					1 (1)						
AM AM JM	(1)						1 (1)				
AM AF AF	1				(1)						
AM JM JF					1						
JM JM JF			(1)								
AF AF AF					1					(1)	
JF JF JF										1	
AM AM AF AF							2 (2)				
AM AM JM JF	(1)										

* AM = adult male; JM = juvenile male; AF = adult female; JF = juvenile female.

Where sex-age class was known, males initiated and won most encounters with other sex-age classes, and as size became more equal (e.g., adult males versus adult males), the initiator won most of the encounters (Table 3). Both adult and juvenile females did not initiate nor win many aggressive encounters. Combining data by sex, males won more encounters than they lost (67%; $n = 368$; $P < 0.001$), whereas females lost more than they won (88%; $n = 123$; $P < 0.001$). Adults won about equally as often as they lost (54%; $n = 255$; $P > 0.05$), whereas juveniles lost more (62%; $n = 163$; $P < 0.001$). Again, sample sizes for sex or age comparisons are greater than com-

bined sample sizes in Table 3 because only one criterion needed to be known.

Level of intensity. During two-bird encounters, individuals that did not display threats lost more encounters than they won (88%; $P < 0.001$), whereas birds that threatened won more than they lost (66%; $P < 0.001$). Birds that exhibited contact won and lost about equally ($P = 0.94$; Table 4). During two-bird interactions involving individuals within the same age and sex class, the frequency of individuals using contact was higher (60%; $n = 113$) than during interactions involving individuals from different sex and age classes (43%; $n = 348$).

TABLE 2. Relative frequency (%) of prior activity, level of intensity, and order of involvement in two-bird aggressive encounters ($n = 174$) between wintering American Flamingos by age and sex class.

Age-sex class	Relative frequency (n)						
	Activity prior		Order of involvement		Level of intensity		
	Feeding	Locomotion	Initiation	Response	Contact	Threat	No display
Adult male	33 (44)	67 (91)	74 (101)	26 (36)	50 (69)	40 (55)	10 (13)
Juvenile male	53 (51)	47 (45)	61 (58)	40 (38)	51 (49)	38 (36)	12 (11)
Adult female	92 (76)	8 (7)	11 (9)	89 (74)	28 (23)	16 (13)	57 (47)
Juvenile female	66 (21)	34 (11)	34 (11)	66 (21)	28 (9)	41 (13)	31 (10)

TABLE 3. Frequency of outcome and order of involvement of two-bird aggressive encounters ($n = 174$) between wintering American Flamingos by age and sex classes.

Age-sex class of losers (respond)	Age-sex class of winners (initiate)			
	Adult male	Juvenile male	Adult female	Juvenile female
Adult male	23 (23)	5 (0)	0 (0)	3 (0)
Juvenile male	22 (27)	19 (19)	2 (0)	3 (0)
Adult female	49 (49)	20 (22)	4 (4)	1 (0)
Juvenile female	12 (15)	6 (9)	3 (4)	2 (2)

Order of involvement and activity prior to interaction. Regardless of intensity, individual flamingos won 70% of encounters they initiated versus 22% of those in which they responded to the initiator (Table 5). The majority of initiators were walking when the encounter began (78%; $n = 456$; $P < 0.001$); 73% of the flamingos that were walking prior to interactions won these encounters.

THREE-BIRD OR LARGER AGGRESSIVE INTERACTIONS

Aggressive interactions among more than two flamingos were characterized by a variety of age and sex groups that won or initiated interactions. The number of flamingos initiating or winning encounters never exceeded two individuals (Table 1). Although most interactions were won (58%; $n = 141$) and initiated (52%; $n = 141$) by adult male/adult female "pairs," groups of all age and sex classes initiated and won encounters. When two birds initiated an encounter, they were generally observed simultaneously approaching the other individual(s) from the same direction. There often was a sequential response to such approaches, with other individuals joining a contest after it had already begun.

INTERSPECIFIC AGGRESSIVE INTERACTIONS

Interspecific interactions were observed on only two occasions during the study period as other species were rarely observed within foraging groups of flamingos. These interactions involved an American White Pelican (*Pelecanus erythrorhynchos*) and an American Coot (*Fulica americana*). In both instances, a foraging flamingo initiated and won the encounters when approached by the other species. In Venezuela, Bildstein et al. (1991) also noted that feeding American Flamingos did not interact aggressively with other waterbirds.

TABLE 4. Relative frequency (%) and frequency of outcome of two-bird aggressive interactions compared with level of intensity, order of involvement, and prior activity for wintering American Flamingos.

	Relative frequency (frequency) of interaction outcome		χ^2	P
	Win	Lose		
Level of intensity				
Contact	50 (108)	50 (109)	0.005	ns
Threat	66 (96)	34 (49)	15.2	<0.001
No display	12 (12)	88 (85)	54.9	<0.001
Order of involvement				
Initiation	70 (169)	30 (72)	39.4	<0.001
Response	22 (47)	78 (171)	70.5	<0.001
Prior activity				
Feeding	27 (71)	73 (189)	53.5	<0.001
Walking	73 (142)	27 (53)	40.6	<0.001

DISCUSSION

TWO-BIRD AGGRESSIVE INTERACTIONS

Contest asymmetries. Because males average 13.7 cm taller than females (Allen 1956), we believe that body size is the primary determinant of contest outcome in feeding American Flamingos. Females did not initiate encounters with males and rarely won when challenged by males (Tables 1, 3). This is consistent with a "common sense" evolutionary stable strategy as proposed by Maynard Smith and Parker (1976), and such differences in contest outcome due to size are commonly reported in the literature (Parker 1984). When data were compared for encounters among flamingos of the same age and sex class only, those birds initiating aggressive encounters generally won ($P = 0.01$). This would suggest that American Flamingos do not exhibit uncorrelated asymmetry based on prior occupancy for role

TABLE 5. Relative frequency (%) and frequency of order of involvement of two-bird aggressive interactions compared with level of intensity for wintering American Flamingos.

	Relative frequency (frequency) of order of involvement		χ^2	P
	Initiation	Response		
Level of intensity				
Contact	58 (127)	42 (91)	5.9	0.02
Threat	70 (101)	30 (44)	22.4	<0.001
No display	13 (13)	87 (85)	52.9	<0.001

assessment in conflicts (Maynard Smith 1974, Hyatt and Salmon 1978, Hammerstein 1981).

Although an asymmetry in fighting ability appears to exist due to size, differences in resource value may exist that are not readily assessed by contestants. For example, we did not measure the value of the food resource. However, resource value and fighting ability may often be contradictory (Parker and Rubenstein 1981), whereby a small individual in a contest with a larger individual places a higher value on the resource, and will thus fight harder. Specifically, the value of the food resource may be higher for female flamingos because they probably need to search longer before finding another individual of lower fighting ability. Indeed, females did win eight encounters that were initiated by males (Table 1), thus assuming a role that would not appear to be consistent with assessment based on size differences alone. Therefore, although the cost of competing with an individual of greater size may be high, the smaller individual may have more to gain by displacing the larger for access to the food resource.

Level of intensity. If size is used by flamingos as a cue to settle contests with a minimum of energy expenditure, then one would predict that encounters involving two individuals of similar size would result in lack of information about apparent fighting ability (Selton 1980) and result in conflicts of higher intensity (Maynard Smith and Parker 1976). We found this the case for American Flamingos in that the highest level of intensity (contact) was used more often by male flamingos than females and also occurred more during encounters where individuals were of equal sizes.

In ritualized contests, the individual contestants do not incur injury costs and only accrue energetic costs that are in direct proportion to the level of the tactic used in the contest. Parker and Rubenstein (1981) argue that in most ritualized contests, the winner will always be the individual that displays with the highest intensity, regardless of fighting ability. Therefore, one would predict that if there were no potential costs, then females should choose to escalate the conflict when challenged by males. However, we did not observe this; female flamingos generally withdrew from contests without making contact with the opponent, presumably because of the risk of physical injury.

Overall, we believe that large asymmetries in

American Flamingo fighting ability appear to be readily determined, with roles having been assessed with a minimum of escalation. However, flamingo contests among individuals of the same sex and age reached a higher level of intensity than contests among individuals of different sex and age classes. This supports the notion that in the absence of good cues of relative differences in fighting ability, there is ambiguity in the assessment of contest roles. This leads to higher intensity contests of longer duration (Parker and Rubenstein 1981).

THREE-BIRD OR LARGER AGGRESSIVE INTERACTIONS

The majority of multiple bird interactions were initiated together by an adult male and adult female. Throughout the study, flamingos exhibited synchronized courtship behavior (Allen 1956) in larger groups separate from feeding aggregations and, less commonly, in small groups within feeding aggregations. Therefore, the high incidence of adult male and adult female associations suggests that some degree of pair bonding had already occurred.

Individual flamingos may be able to increase relative fighting ability through cooperation in aggressive encounters. Although there is no evidence that flamingos maintain family units through the nonbreeding season, parent-offspring and sibling-sibling cooperation could be a mechanism for increasing both personal and inclusive fitness by gaining preferential access to food. However, if flamingos do not remain in family groups during the nonbreeding season, the variety in age and sex of the flamingo groups initiating or responding to aggressive advances would suggest that cooperation is largely opportunistic.

The observed occupancy of the feeding site where the encounter occurred, and the high incidence of feeding immediately after the encounter, suggest that the feeding site, and presumably the food therein (Jenkin 1957), was the payoff for the winning individuals. Bildstein et al. (1991) also reported that in aggressive interactions where stamp-feeding flamingos were harassed, the second bird often occupied the site vacated by the first. However, this would not explain the encounters among adult male-adult female pairs and among adult male-adult female pairs with individual adult males. However, the high level of courtship activity that occurred

among flamingos suggests that competition for mates may be occurring concurrently with competition for food.

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