

FEEDING PATTERNS AND AGGRESSIVE BEHAVIOR IN JUVENILE AND ADULT AMERICAN FLAMINGOS¹

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Abstract. We studied the feeding and aggressive behavior of adult and juvenile American Flamingos (*Phoenicopterus ruber ruber*) at a coastal salina in Venezuela. Most birds fed in large flocks in early morning, roosted at mid-day, and resumed feeding in late afternoon-early evening. Flamingos rarely flew, except when disturbed. Adults in our study stepped at the same rates while feeding as did Chilean Flamingos (*P. chilensis*) feeding in the Chilean and Bolivian Andes. Paired observations of birds within mixed-age flocks revealed that adults stepped more during feeding bouts, but less between bouts, and spent more time overall with their bills in the water filter-feeding, than did juveniles. We calculate that the food-intake rate of juveniles was, at most, 82% that of adults. Both adults and juveniles walk-fed and stamp-fed. Juveniles, but not adults, were twice as likely to be supplanted when stamp-feeding than when walk-feeding. Juveniles were more often involved in aggression, especially as recipients, than were adults. Aggressive encounters significantly affected the amount of time flamingos spent filter feeding.

Key words: Activity patterns; feeding behavior; American Flamingo; *Phoenicopterus ruber ruber*; wetlands; Venezuela.

INTRODUCTION

In many colonial waterbirds juveniles forage less efficiently than do adults (see review in Bildstein 1983). In several species this phenomenon, which is sometimes accompanied by age-related differences in aggression and habitat use (Goss-Custard et al. 1982a, 1982b), has been linked to deferred maturity (Lack 1968, Burger and Gochfeld 1981, Greig et al. 1983, Bildstein 1984, MacLean 1986) and higher juvenile mortality (Recher and Recher 1969, Heppleston 1971).

Previous studies of age-related differences in the foraging behavior of colonial waterbirds have focused on species that stalk and subsequently pursue relatively large and highly mobile prey (Bildstein 1983), and not on species that filter-feed on abundant and relatively immobile small

prey. The presumption has been that individuals feeding on limited and relatively large mobile prey require longer periods of time to develop the suite of foraging skills needed to feed at adult rates than do species that feed on more abundant, smaller, and less mobile prey (cf. Amadon 1964, Ashmole 1971). Recently, however, Giroux and Bedard (1988) have shown that even in herbivorous species such as Snow Geese (*Chen caerulescens*), juveniles forage less efficiently than adults; a circumstance the researchers linked to higher juvenile mortality in the species.

American Flamingos (*Phoenicopterus ruber ruber*) are filter-feeding wading birds that breed in coastal South America, the Caribbean basin, and the Galapagos Islands (Allen 1956, Kear and Duplaix-Hall 1975, Ogilvie and Ogilvie 1986). Researchers have suggested that first-year American Flamingos suffer higher mortality than do older birds (Allen 1956, de Boer 1979). Although it is unclear why this might be so, de Boer (1979) proposed that lower juvenile survivorship could result from an inability on the part of juveniles

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to find sufficient food. Although juvenile flamingos begin to filter feed in their second week (Chapman 1905, Studer-Thiersch 1975), the possibility that first-year birds do not feed as proficiently as adults has not been examined.

Studies of flamingo feeding biology include general and detailed descriptions of the behavioral patterns used (Buffon 1781, Allen 1956, Rooth 1965, Ogilvie and Ogilvie 1986), estimates of prey consumption (Rooth 1965), accounts of their mouth parts (Jenkin 1957), and descriptions of spatial and temporal patterns of feeding activity (Hurlbert and Keith 1979; Hurlbert 1982; Britton et al. 1986; Espino-Barros and Baldassarre 1989a, 1989b). Studies of individual variation in feeding behavior, similar to those that have been reported for other species of water birds (e.g., gulls, Burger and Gochfeld 1981; Maclean 1986; ibises, Bildstein 1983; herons, Recher and Recher 1969), are lacking.

Here, we detail and compare the feeding behavior of adult and juvenile American Flamingos in coastal Venezuela. Specifically, (1) we document age-related differences in the foraging and aggressive behavior of flamingos in this population, and (2) discuss the potential consequences of our findings in terms of the concept of a behavioral bottleneck and its impact on social behavior, habitat use, and conservation in this species.

METHODS

We studied flamingos feeding in a coastal salina (10°58'N, 68°20'W) at the Cuare National Wildlife Refuge, near Chichiriviche, in Falcon State, Venezuela, from 21 April–1 May 1989. The Chichiriviche salinas, which are used as feeding sites by flamingos that breed approximately 90 km away on Bonaire in the Netherlands Antilles (de Boer 1979), support at least several thousand birds each winter and spring (Guzman 1986; M. Lentino, pers. comm.; Bildstein, Frederick, and Spalding, pers. observ. in 1988 and 1989). The number of flamingos feeding at the site declines during the spring as the dry season progresses and water in the salinas evaporates (de Boer 1979; M. Lentino, pers. comm.).

We towed a 1,000-micron mesh, rectangular-mouthed tapering plankton net attached to a benthic sled (two skis 61 cm apart) to capture potential flamingo prey items in the water column. The 61-cm wide net extended from less than 1 cm above the flocculent layer to the sur-

face of the water, a distance of 13 cm. Between 11:30 and 11:50 on 27 April, we towed the sled 0.40–0.55 m/sec over a distance of 23.7 m, twice over undisturbed sediment, and twice with one person stepping about 5 m ahead of the sled to disturb the flocculent and vegetative layers. Samples were placed in 45% alcohol, stained with Rose Bengal, and examined with a 10× microscope. Samples of mud were similarly strained through 1,000-micron mesh and stored in alcohol.

We used binoculars and telescopes to watch flamingos from two 3.5 m cinderbrick towers used by tourists. Almost all of the flamingos whose feeding behavior we studied fed within 300 m of the towers; however, we included flamingos feeding and roosting more than a kilometer from the towers in our activity surveys.

Initial observations indicated that flamingo activity was synchronized within flocks. We recorded the numbers of birds in both roosting flocks (i.e., birds standing in groups, often on one leg) and feeding flocks (i.e., groups of walking and stamping birds that engaged in intermittent filter-feeding) at the site during 16 morning (06:50–08:59), 22 mid-day (09:00–13:00), and 8 late afternoon–early evening (16:00–18:30) scan samples (Altman 1974) on 11 different days. We used scan sampling during 8 morning, 6 mid-day, and 6 late afternoon–early evening surveys to examine temporal variation in walking, walk-feeding, stamp-feeding, standing, preening, and bathing among birds within feeding flocks. During our observations, temperatures ranged from 25–31°C, winds were light, and no precipitation fell.

Flamingos were counted as walking when they stepped with their head up or extended forward without feeding, and as walk-feeding when they walked at a relatively constant pace with the head alternately up or extended forward, and down, either filter feeding in the water column, or repeatedly probing the water column with “forceps movements” of the bill (cf. Rooth 1965). Birds were counted as stamp-feeding when they stamped their toes while rotating their body clockwise or counterclockwise around their partially or fully submerged bill (see also Allen 1956, Rooth 1965). Flocks were defined as groups of flamingos in which the nearest-bird distance averaged <25 m, and where no bird was >50 m from the nearest flock member.

We recorded the ratios of adults and juveniles

in seven flocks on five days and compared those ratios with the age ratios of the nearest neighbors of juveniles within those flocks. Juveniles and adults were determined by plumage (Bent 1926, Allen 1956, Rooth 1965). We counted as juveniles only those individuals with entirely gray-and-white plumage (i.e., clearly young of the year), and as adults individuals with pink or bright red plumage. The few birds that appeared to be molting from juvenal to adult plumage were not included in our observations.

PAIRED FEEDING OBSERVATIONS

We recorded the behavior of 46 "paired" adult and juvenile flamingos feeding together in mixed flocks, as well as the behavior of 70 unpaired birds. Paired 4-min observations were recorded within 10 min of each other, and were limited to birds feeding within 20 m of each other. We recorded (1) the numbers of steps taken (stamping and otherwise), (2) whenever the bird submerged its bill and was feeding, and (3) aggressive interactions with other flamingos. Observations, which were made throughout the day, were dictated into a cassette recorder for later transcription. We defined aggression as threat displaying (Allen 1956, Ogilvie and Ogilvie 1986) and the rapid approach of one bird that resulted in displaying, body contact, or the rapid withdrawal of another individual. Threat displays and approach were assumed to be dominant behavioral patterns; rapid withdrawal was considered a subordinate pattern.

OTHER FEEDING OBSERVATIONS

We also recorded the stepping rates of feeding birds during 200 20-sec observation bouts, and we recorded both the direction and rate of turning (in degrees) of stamp-feeding individuals during 100 30-sec observation bouts. We also monitored the behavior of 17 adults for up to 79 min, to determine average durations of feeding patterns and synchrony in feeding behavior among nearest neighbors.

We used Chi-square tests, *t*-tests and paired *t*-tests, and analysis of variance to analyze our data (Sokal and Rohlf 1969).

RESULTS

The number of flamingos feeding and roosting at the salina declined from approximately 1,100 on 21 April to less than 600 on 1 May. The water level, which we measured with a marked stake

at the edge of the salina, dropped at a rate of 4.5 mm/day. On 27 April, when we towed a plankton sled through a portion of the salina frequently used by feeding birds, the water was 18 cm deep, including a flocculent layer of 5–8 cm.

Flamingos rarely flew, even when disturbed by people discharging firearms and fishing at the site. About half of the birds took flight briefly and circled above the area on the morning of 30 April following the aftershock of a 5.0 Richter-Scale earthquake centered 25 km away earlier in the day.

Roosting flocks averaged 315 ± 247 SD birds ($n = 47$). Aside from one singleton, all of the birds we observed during 4-min observations fed in flocks of between 16 and 923 individuals ($\bar{x} = 591$ birds/flock for juveniles, $n = 47$; $\bar{x} = 419$ birds/flock for adults, $n = 113$; $P = 0.0002$; *t*-test).

POTENTIAL PREY

Flamingos appeared to filter feed both from the water column and along the benthic surface. None of the four mid-day tows, however, produced any obvious prey items, despite our "filtering" an estimated 7,512 liters of salina water. Though most flamingo prey may have been smaller than our mesh size, we expected to find at least a few small items caught on the mesh. We believe that flamingos were not filtering substantial amounts of prey from the water column. We also strained 850 ml of the top 8 cm of sediment collected at five different sites within the salina for potential prey items. Although we found large numbers of widgeon grass (*Ruppia maritima*) seeds in our sample, all of the 56 seeds we examined closely consisted of old hulls from the previous season. We also identified 218 pieces of polychaete worms (family Capitellidae), most of which appeared to represent at least half of a worm (i.e., a total of approximately 109 worms, or 0.14/ml of mud). As the water level dropped, birds feeding along the edge of the salina plucked dead or moribund 3–10 cm fishes from the water surface.

FEEDING BEHAVIOR

Flamingos fed mainly during early morning and late afternoon-early evening, and roosted during the middle of the day (Table 1). Feeding activity appeared to be greater late in the afternoon than earlier in the day (Table 2).

Walk-feeding was more common than was stamp-feeding (Table 2). Individuals walk-fed for

TABLE 1. Relative occurrence of flamingos in roosting versus feeding flocks during morning, mid-day, and late afternoon-early evening surveys.

Time of day ¹	Mean number of birds	Percent in	
		Feeding flocks	Roosting flocks
Morning (<i>n</i> = 16)	869	79	21
Mid-day (<i>n</i> = 22)	726	28	72
Late afternoon-early evening (<i>n</i> = 8)	1,000	73	27

¹ Morning = 06:50-08:59; Mid-day = 09:00-13:00; Late afternoon-early evening = 16:00-18:30.

an average 612 sec ($\pm 1,099$ SD, *n* = 23). Birds stamp-fed for an average of 289 sec (± 266 , *n* = 50), unless disturbed by another bird, in which case they moved on after having stamp-fed for only 160 sec (± 95.2 , *n* = 15). Walk-feeding flamingos usually moved at least 20 m during 4-min observations. Stamping flamingos fed in one location, turning rapidly in place (\bar{x} = $493 \pm 156^\circ$ SD/30-sec observation, *n* = 50 adults).

Although we found the circular plateaus surrounded by shallow depressions that result from stamp-feeding (cf. Gallet 1950) throughout the salina, flamingos appeared to stamp-feed in certain portions of the salina more than in others. Stamping may have been socially facilitated, with its occurrence in one individual increasing the likelihood of its occurrence in neighboring birds. In all four pairs of nearest-neighbor adult flamingos we watched for prolonged periods, both birds frequently switched in unison from walk-feeding to stamp-feeding and back to walk-feeding, and in one instance, two adults even synchronized individual feeding bouts (i.e., submersed and lifted their bills in unison).

Flamingos that both stamp-fed and walk-fed stepped more, both within and between feeding bouts, than did birds that only walk-fed (Table

3). When stamp-feeding, adults stepped at more than three times the pace of walk-feeding birds (50 ± 7.6 steps/20-sec observation versus 15 ± 4.5 steps/20-sec, $P = 0.0001$, *n* = 200). In 27 of our 4-min observations individual flamingos both walk-fed and stamp-fed. During these observations, feeding bouts were longer, and the number of steps per bout greater, when the bird was stamp-feeding than when it was walk-feeding (Table 4).

AGE-RELATED DIFFERENCES IN FLOCKING BEHAVIOR

Although adults often fed together without juveniles, we never saw juveniles feeding without adults. Over five days, seven mixed-age feeding flocks ranged from 153 to 935 birds, with adults comprising 96-99% of all birds counted (\bar{x} = 97% adults). Of 111 juveniles feeding within these flocks, 37% had another juvenile as their nearest neighbor: more than 10 times the number expected based on a random distribution ($P < 0.001$; Chi-square test for goodness-of-fit).

AGE-RELATED DIFFERENCES IN FEEDING BEHAVIOR AND AGGRESSION

Neither the number of individual feeding bouts nor the overall number of steps taken by adult and juvenile flamingos differed during our paired 4-min observations (Table 5). However, adult flamingos stepped more during individual feeding bouts, and less between bouts, and they spent more time with their bills in the water during feeding bouts, than did juvenile flamingos (Table 5). As a result, adult flamingos spent more time filter feeding overall than did juveniles (Table 5).

Both adult and juvenile flamingos regularly engaged in both walk-feeding and stamp-feeding during 4-min observations (Table 6), and there was no indication of an age-related difference in the frequency of use of these two foraging techniques ($\chi^2 = 0.53$, $P = 0.47$).

TABLE 2. Activities of flamingos in feeding flocks during morning, mid-day, and late afternoon-early evening surveys.

Time of day ¹	Percent engaged in					
	Walking	Walk-feeding	Stamp-feeding	Inactive	Preening	Bathing
Morning	10	29	15	38	9	0
Mid-day	5	36	9	45	4	0
Late afternoon-early evening	8	52	12	10	15	2

¹ Morning = 06:50-08:59, eight surveys of a total of 2,593 birds; Mid-day = 09:00-13:00, six surveys of a total of 1,186 birds; Late afternoon-early evening = 16:00-18:30, six surveys of a total of 1,243 birds.

TABLE 3. Behavior of juvenile and adult flamingos during 4-min observations with and without stamp-feeding behavior.

Behavior	Juveniles			Adults		
	Without stamping (n = 24)	With stamping (n = 24)	P ¹	Without stamping (n = 63)	With stamping (n = 49)	P
Number of feeding bouts	\bar{x} = 42.7 SD = 14.7	\bar{x} = 36.0 SD = 15.8	0.14	\bar{x} = 40.3 SD = 12.2	\bar{x} = 37.5 SD = 11.0	0.20
Total number of steps	\bar{x} = 170 SD = 55.4	\bar{x} = 289 SD = 120	0.0001	\bar{x} = 153 SD = 55.7	\bar{x} = 326 SD = 146	0.0001
Number of seconds feeding	\bar{x} = 149 SD = 45.3	\bar{x} = 136 SD = 38.7	0.30	\bar{x} = 170 SD = 34.7	\bar{x} = 167 SD = 27.1	0.66
Number of seconds per feeding bout	\bar{x} = 3.79 SD = 1.69	\bar{x} = 4.20 SD = 1.76	0.42	\bar{x} = 4.63 SD = 1.86	\bar{x} = 4.86 SD = 1.70	0.51
Number of steps per feeding bout	\bar{x} = 2.31 SD = 0.93	\bar{x} = 5.98 SD = 4.05	0.0002	\bar{x} = 2.73 SD = 1.21	\bar{x} = 7.47 SD = 4.69	0.0001
Mean number of steps between feeding bouts	\bar{x} = 2.27 SD = 4.09	\bar{x} = 2.86 SD = 1.99	0.54	\bar{x} = 1.25 SD = 1.19	\bar{x} = 1.96 SD = 1.21	0.003
Number of steps during feeding bouts/number of steps between bouts	\bar{x} = 2.46 SD = 2.37	\bar{x} = 2.84 SD = 2.86	0.61	\bar{x} = 4.31 SD = 4.27	\bar{x} = 4.66 SD = 3.48	0.64

¹ *t*-tests.

Aggressive interactions occurred in 26% of our 4-min feeding observations. Juveniles were more likely to be involved in aggressive encounters ($\chi^2 = 10.8$, $P = 0.001$, Table 7), and were more likely to be the recipient of aggression during these interactions (95% of aggressive encounters versus 32% for adults, $\chi^2 = 17.8$, $P < 0.001$), than were adults. For juveniles, but not adults, aggression was significantly more frequent during 4-min observations when stamp-feeding occurred than in those observations without stamping (for juveniles, $\chi^2 = 4.15$, $P = 0.042$; for adults, $\chi^2 = 1.88$, $P = 0.17$, Table 7). Even so, aggressive interactions were recorded in 24% of the 4-min adult observations in which stamping occurred, and aggressive interactions terminated 23% of the 65 stamp-feeding events we recorded among 17 adult flamingos that we watched for prolonged periods. In many of the instances where stamp-feeding birds were harassed by another flamingo, the second bird began stamping at the site vacated by the first. An analysis of variance of the total time

flamingos spent filter feeding indicates that, when age is held constant, the occurrence of aggressive interactions (2-way ANOVA, $P < 0.01$) significantly affects total time spent filtering. For example, feeding adults interrupted by aggressive encounters spent 7% less time filter feeding, and interrupted juveniles 6% less time feeding, than did individuals whose feeding behavior was not interrupted.

Although a number of additional species, including Olivaceous Cormorants (*Phalacrocorax carbo*), eight species of wading birds, at least three species of shorebirds, Gull-billed Terns (*Sterna nilotica*), and Black Skimmers (*Rynchops niger*) fed within several meters of flamingos, flamingos did not interact aggressively with these birds.

DISCUSSION

ACTIVITY PATTERNS AND FLOCKING BEHAVIOR

The decreasing number of flamingos feeding at the site over the course of our study probably

TABLE 4. Behavior of flamingos during 4-min observations in which both walk-feeding and stamp-feeding occurred.

	Mean time with head down per bout			Mean number of steps per bout		
	Walk feeding	Stamping	P ¹	Walk feeding	Stamping	P
Juveniles (n = 11)	\bar{x} = 2.92 SD = 1.13	\bar{x} = 4.13 SD = 1.96	0.01	\bar{x} = 2.47 SD = 1.09	\bar{x} = 7.57 SD = 3.57	0.0003
Adults (n = 16)	\bar{x} = 3.88 SD = 1.57	\bar{x} = 4.89 SD = 1.88	0.06	\bar{x} = 3.11 SD = 1.63	\bar{x} = 9.83 SD = 4.23	0.0001

¹ Paired *t*-tests.

TABLE 5. Behavior of juvenile and adult flamingos feeding in mixed-age flocks during paired 4-min observations.

Behavior	Juveniles <i>n</i> = 46	Adults <i>n</i> = 46	<i>P</i> ¹
Number of feeding bouts	\bar{x} = 39.5 SD = 15.8 Range = 10–92	\bar{x} = 37.5 SD = 11.4 Range = 11–67	0.45
Total number of steps	\bar{x} = 229 SD = 109 Range = 75–549	\bar{x} = 244 SD = 145 Range = 40–593	0.32
Number of seconds feeding	\bar{x} = 143 SD = 43.1 Range = 31–212	\bar{x} = 175 SD = 33.8 Range = 73–212	0.0007
Number of seconds per feeding bout	\bar{x} = 4.01 SD = 1.75 Range = 1.59–8.77	\bar{x} = 5.13 SD = 2.03 Range = 2.08–11.6	0.001
Number of steps per feeding bout	\bar{x} = 4.12 SD = 3.46 Range = 0.77–16.7	\bar{x} = 5.49 SD = 4.49 Range = 0.42–23.2	0.02
Mean number of steps between feeding bouts	\bar{x} = 2.58 SD = 3.26 Range = 0.19–21.0	\bar{x} = 1.48 SD = 1.17 Range = 0.09–4.26	0.05
Number of steps during feeding bouts/number of steps between bouts	\bar{x} = 2.68 SD = 2.66 Range = 0.05–14.8	\bar{x} = 5.60 SD = 4.60 Range = 0.40–21.8	0.0005

¹ Paired *t*-tests.

reflects the loss of feeding habitat resulting from the evaporation of water in the salina (de Boer 1979, Guzman 1986).

As has been reported for flamingos elsewhere (Rooth 1965, Poulsen 1975, Britton et al. 1986, Espino-Barros and Baldassarre 1989), most of the birds we watched fed principally early in the morning, and again late in the afternoon, after roosting for several hours at mid-day. However, at least some flamingos fed on each of two moonlit nights we scanned the salina looking for birds, and it may be that considerable additional feeding occurred after dark (cf. Rooth 1965).

FEEDING BEHAVIOR

Given the absence of large prey in our samples of the water column, flamingos must have been gathering food from the benthic interface, or from bottom sediments. It seems likely that the birds were getting some nutrition from polychaete worms and, possibly, from *Ruppia*. Nevertheless, we lack firm information concerning what the birds were feeding on at the site.

The American Flamingos we watched averaged 45 steps/min when walk-feeding, considerably more than the two *Phoenicoparrus* species

that Hurlbert (1982) studied at several altiplano lakes in the Chilean and Bolivian Andes (*P. jamesi* = 10–15 steps/min; *P. andinus* = 20–30 steps/min), but similar to the values reported by Hurlbert (1982) for the congeneric Chilean Flamingo (*Phoenicoparrus chilensis*) (40–60 steps/min). American and Chilean flamingos also appear to stamp-feed at similar rates (American Flamingos = 150 steps/min; Chilean Flamingos = 130–200 steps/min). Stamping birds at Chichiriviche circled at rates averaging 20–25 sec/360° circle, considerably faster than what Rooth (1965) reported for stamp-feeding American Flamingos breeding on Bonaire (45–60 sec/circle).

Hurlbert (1982) credited the interspecific differences he reported to differences in prey being

TABLE 6. Relative occurrence of walking and stamping feeding behavior during 4-min observations.

	Percent of observations with		
	Walking only	Stamping only	Both walking and stamping
Juveniles (<i>n</i> = 48)	50	2	48
Adults (<i>n</i> = 114)	43	5	52

TABLE 7. Relative occurrence of aggressive interactions during 4-min observations.

	Percent of observations with aggression		
	Observation		All observations
	With stamping	Without stamping	
Juveniles	58% ($n = 24$)	29% ($n = 24$)	44% ($n = 48$)
Adults	24% ($n = 49$)	14% ($n = 63$)	19% ($n = 112$)
All birds	32% ($n = 73$)	18% ($n = 87$)	26% ($n = 160$)

taken and, possibly, to differences in water depth used by the three sympatric species. American Flamingos are considerably taller and have longer culmens than do Chilean Flamingos (Blake 1977); but bill structure is quite similar in the two species, and both apparently filter-fed in the same manner (Jenkin 1957). Baldassarre (pers. comm.) found *Ruppia* seeds in the stomachs of American Flamingos collected in the Yucatan in 1989, and Hurlbert (1982) reported that Chilean Flamingos were more likely to stamp-feed in areas where *Ruppia* carpeted the benthic surface. The same appears to be true for American Flamingos at Chichiriviche.

AGE-RELATED DIFFERENCES

Although juvenile flamingos comprised only 3% of the birds we watched, most juveniles fed near each other within mixed-aged flocks, and often had other juveniles as nearest neighbors. Based on several individually recognizable juveniles, as well as on the numbers of juveniles seen together in small groups within larger flocks, it was our impression that juvenile-juvenile associations were maintained for at least several days. However, we never saw isolated flocks of juveniles similar to those seen by Baldassarre (pers. comm.) in the Yucatan.

Bildstein (1983) found that juvenile White Ibises (*E. albus*) feeding in mixed-age flocks also tended to feed nearer to other juveniles on the peripheries of flocks, and the same is true for juvenile American Robins (*Turdus migratorius*) (Gochfeld and Burger 1984). Our observations indicate that juvenile flamingos, like juveniles in several other species of flock-feeding birds (cf. Groves 1978; Goss-Custard et al. 1982a, 1982b), are subordinate to adults. We suggest that age-related segregation within mixed-age flocks may result when juveniles attempt to avoid aggression by adults by surrounding themselves with other juveniles (i.e., a "selfish-herd effect," sensu Hamilton 1971). Although researchers have re-

ported sighting all-juvenile flocks of flamingos outside of the breeding season, especially during migration (Scott 1975), and when food is scarce (Espino-Barros and Baldassarre 1989b), such flocks appear to be relatively uncommon (de Boer 1979, Johnson 1989). The small number of juveniles at our site (approximately 3% of the total population), together with limited feeding locations (as suggested by aggressive interactions among feeding birds), may have precluded the formation of all-juvenile flocks at Chichiriviche.

Feeding adults and juveniles stepped at the same rates and engaged in the same number of feeding bouts per unit time (Table 5). However, the feeding bouts of adult flamingos were 28% longer than those of juvenile flamingos, and adults spent 22% more time feeding during paired 4-min observations than did juveniles feeding nearby (Table 5).

Although we were unable to measure the rate at which food was being consumed by adult and juvenile flamingos, we believe that the differences we observed in time spent filter-feeding by members of the two age classes parallel differences in consumption rates. Support for this notion comes from observations of captive flamingos at the St. Louis Zoo in St. Louis, Missouri, and at the Riverbanks Zoo in Columbia, South Carolina (Bildstein, unpubl. data). In these situations, subordinate birds that had shortened their feeding bouts because of aggressive encounters with dominant individuals, compensated by feeding more frequently, so that overall, the times spent feeding by subordinate and dominant individuals were quite similar. Finally, if juvenile flamingos handle "captured" prey less efficiently than do adults (cf. Burger 1980, Henderson 1981, MacLean 1986), differences in adult and juvenile feeding rates may actually have been greater than the difference we recorded in time spent feeding for the two age classes.

If we assume that the juveniles we observed were filtering food at the same rate as the feeding adults we watched, then juvenile flamingos for-

aged at approximately 82% of the foraging efficiency of feeding adults. By comparison, recently fledged White Ibises preying on fiddler crabs (*Uca* spp.) in coastal South Carolina, USA, salt marshes fed at only 40%, and one-year-old birds at only 70%, the rate of >two-year-old breeding adults (Bildstein 1983, 1984). Similarly, the strike efficiencies of both recently fledged and at least 6-month-old Little Blue Herons (*Egretta caerulea*) were considerably less, 60% and 73–80%, respectively, than those of breeding adults (Recher and Recher 1969). The same appears to be true for Gray Herons (*Ardea cinerea*) and Great Blue Herons (*A. herodias*) (Cook 1978, Quinney and Smith 1980). The somewhat greater age-related differences in these species, compared with those we report for flamingos, bolsters the suggestion that birds feeding on relatively large mobile prey require long periods of time to develop foraging skills than do birds feeding on abundant small prey (Amadon 1964, Ashmole 1971).

We were unable to determine whether the lower foraging efficiency of juveniles required them to spend more time feeding each day. Espino-Barros and Baldassarre (1989a, 1989b), who studied American Flamingos at an estuary in the Yucatan in Mexico, reported that during the breeding season, juvenile flamingos spent more time feeding than did adults; but that outside of the breeding season, juveniles actually spent *less* time feeding than did adults. These researchers suggest that juveniles may have fed less than adults because members of this age class rested more often than did adults (Espino-Barros and Baldassarre 1989a, 1989b). Unfortunately, we did not collect data that would allow us to test this possibility. Nor did we collect data on feeding activity after dark, which apparently occurs in this species (cf. Rooth 1965, Britton et al. 1986), and which may have differed considerably from our daytime observations.

Stamp-feeding has been discussed at considerable length in the literature. The behavior appears to enable flamingos to sort and remove prey from refuges within mud and aquatic vegetation (Allen 1956, Rooth 1965 and references therein, Hurlbert 1982). In fact, a common scientific collection technique for polychaete worms consists of swirling mud and water, allowing it to settle briefly, and then pouring the supernatant through a sieve. In undisturbed sediments, polychaetes are often found in the flocculent material above the denser mud. The circling behavior of

flamingos may enable birds to stir worms from the underlying mud and concentrate them in the flocculent layer. As mentioned above, the stamp-feeding birds that we watched appeared to feed similarly to birds employing this method elsewhere, often in a contagious manner at several sites within the salina (cf. Jenkin 1957). Both adult and juvenile flamingos were equally likely to use this feeding behavior (Table 6). However, juveniles were twice as likely to be attacked, usually by adults, when stamp-feeding than when walk-feeding (58% versus 29% of 4-min observations with and without stamp-feeding). Attacking adults typically supplanted the stamp-feeding juveniles they approached, and began stamp-feeding in their place.

Why this occurred is unclear. One possibility is that stamp-feeding is energetically expensive (cf. Pennycuik and Bartholomew 1973), and that adults parasitize juveniles by displacing them after they have dislodged considerable prey from hiding places below the benthic surface or within vegetative mats. Another possibility is that flamingos stamp-feed only in especially dense concentrations of prey and that adults use juveniles to locate these concentrations, even if juveniles themselves are unable to take full advantage of them. Whatever the reason, juveniles were easily outmanoeuvred during these encounters, yielding to adults in all but a few of the instances we observed.

Overall, feeding juveniles were more likely to be engaged in aggressive encounters than were feeding adults, and juveniles were more likely than adults to be the recipients of aggressive behavior. Similar age-related inequalities in aggressive behavior have been reported in Ruddy Turnstones (*Arenaria interpres*) (Groves 1978) and Oystercatchers (*Haematopus ostralegus*) (Goss-Custard et al. 1982a, 1982b); and Goss-Custard et al. (1982a, 1982b) have suggested that the inequality is responsible, at least in part, for the fact that juvenile Oystercatchers leave preferred feeding sites when adults arrive.

POTENTIAL CONSEQUENCES OF AGE-RELATED DIFFERENCES IN FEEDING AND AGGRESSION

Overall, our observations indicate that juvenile American Flamingos do not forage as efficiently as adults. Researchers have suggested that declines in the numbers of flamingos at Chichiriviche and elsewhere along the Venezuelan coast

are linked to decreasing food availability (de Boer 1979, Guzman 1986). Our observations suggest that juveniles might suffer sooner from these shortages because of their lower feeding rates (i.e., less time spent filtering/4-min observ.), which, in at least some instances, would be further reduced because of the overall subordinate status of this age class, and their greater target value to adults attempting to supplant feeding birds. Although the percent of juveniles in the feeding flocks we watched remained at approximately 3% during our study, in other years, higher proportions of juveniles at the site have been reported by other workers earlier in the season when the overall flamingo population is much greater (de Boer 1979). Similarly, Espino-Barros and Baldassarre (1989b) report higher percentages of juveniles at a coastal site in the Yucatan during months in which the total flamingo population was high, and when activity budgets indicated that both juvenile and adult flamingos spent less time feeding per day. As the dry season progresses, and as food availability decreases at Chichiriviche, juveniles may leave the site earlier than do adults because they feed less efficiently than adults, and are interrupted more often (cf. Goss-Custard et al. 1982a, 1982b). If such a behavioral bottleneck exists, it could, in part, explain the suggested lower survivorship of this age class within the population (cf. de Boer 1979). Clearly, further studies are needed to test this hypothesis.

Behavioral studies such as ours can play an important role in determining the extent to which environmental change will affect the population dynamics of wading birds (cf. Goss-Custard et al. 1990). For example, many of Venezuela's coastal wetlands, including several sites that are currently used as feeding grounds by American Flamingos, are seriously threatened by human disturbance and development (Guzman 1986). Our results suggest that the loss of these feeding habitats, and the likelihood of concomitant increases in population densities at remaining sites, will impact juvenile flamingos more severely than adults. We strongly recommend that wildlife managers and researchers involved in protecting this species incorporate the results of studies such as ours into their conservation strategies.

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