

# SEXUAL SIZE DIMORPHISM AND PARENTAL CARE PATTERNS IN A MONOMORPHIC AND A DIMORPHIC LARID

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**ABSTRACT.**—I examined parental care patterns of the Black Skimmer (*Rynchops niger*) and the Caspian Tern (*Sterna caspia*) to determine correlates of sexual size dimorphism and parental care. In both species, the sexes had quantitatively different parental roles, particularly during the chick-feeding period. Females were generally more involved in parental activities at the nest site than males. Caspian Tern males provided greater numbers and total mass of prey than their mates. Black Skimmer males fed chicks less frequently than did their mates (especially when the broods were very young), but males delivered substantially larger prey and thus contributed greater prey-mass, particularly as broods aged. The sexually dimorphic skimmer pattern of parental roles may have increased the feeding efficiency and reduced predation risks to the young. No overt behavioral manifestations of sexual conflict were observed between paired Caspian Terns or Black Skimmers. *Received 1 March 1988, accepted 25 September 1989.*

IN MONOGAMOUS species, pair members typically share genetic interest in their young, and parenting can be viewed as a cooperative venture. Male and female parental roles that are related to any morphological or other nonbehavioral (e.g. physiological) difference between parents may promote the production of surviving offspring.

One general aim of animal mating-system research is to identify and assess the relative importance of ecology, morphology, and phylogeny in diverse parental roles. Among the elements studied are territory quality (Verner and Willson 1966), dispersion of females or breeding sites in time and space (Emlen and Oring 1977), differential costs of gamete and offspring production (Bateman 1948, Trivers 1972), and sexual size dimorphism (Selander 1972, Andersson and Norberg 1981). Body size asymmetry between the sexes could exist either as a cause or an effect of variable parental roles. For instance, large body size of at least one parent may enhance defense of offspring against predators (Storer 1966, Snyder and Wiley 1976, Andersson and Norberg 1981). Alternatively, sexual size dimorphism may cause significant differences in the relative energetic costs of various parental duties and thus constrain the contributions of each sex. For example, sexual di-

morphism might reduce the foraging efficiency of the larger parent (Reynolds 1972, Andersson and Norberg 1981). Young chicks' gape limitations may further influence parental feeding roles. If prey size correlates with adult body size, then early feedings may be performed by the smaller parent and later feedings by its mate (Hagen 1942 *cited in* Amadon 1959, Lack 1968). Finally, parental roles might even be influenced by sexual "despotism" if the larger mate can force its partner to undertake relatively costly parenting duties. For example, Cade (1960) proposed that size superiority and dominance of female raptors may force males to serve as the sole providers during incubation and early chick rearing.

Cause and effect must be separated when considering parental roles linked to sexual size dimorphism. The first step is to determine correlations between parental roles and the participants' relative body sizes. Descriptions of parental role divisions that may confer reproductive advantages feature prominently in discussions of size dimorphism evolution (Storer 1966, Reynolds 1972, Snyder and Wiley 1976, Andersson and Norberg 1981). But a causal relationship cannot be inferred from such correlations (e.g. Williams 1966, Gould and Lewontin 1979). Beneficial divisions of parental labor may have evolved after the size dimorphism arose for other reasons (e.g. as a response to sexual selection or to selection for reduced intersexual competition for food).

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TABLE 1. Locations and numbers of clutch initiations at colonies of Black Skimmers and Caspian Terns nesting on dredge material islands in Lavaca Bay, Texas.

Year	Species	Colony name	Clutches initiated ( <i>n</i> )	Colony location
1982	Caspian Tern	Island 76	74	Island nearest channel marker 76*
1982	Black Skimmer	Island 76	134	Island nearest channel marker 76
1983	Caspian Tern	Island 70	62	Island nearest channel marker 70
1983	Caspian Tern	Island 58	53	Island nearest channel marker 58
1983	Black Skimmer	Ugly Island	33	Island nearest channel marker 56
1983	Black Skimmer	Island 66	71	Island nearest channel marker 66

\* Even-numbered channel markers are ¼ mile apart.

I attempted to correlate sexual size dimorphism and parental care patterns in Black Skimmers (*Rynchops niger*) and compared them with a monomorphic relative, the Caspian Tern (*Sterna caspia*). Both species are piscivorous larids that nest colonially in open areas on the same Texas coastal islands. In both species, males and females incubate, brood, attend, and feed the young (Bergman 1953, Wolk 1959, Erwin 1977). I found differences in the degree of dimorphism between the two species and provided quantitative data on their parental care patterns. I used these data to examine the hypothesis that parental care patterns correlate with sexual size dimorphism through parental cooperation. The hypothesis predicts that, in sexually dimorphic species, the smaller parent will play a greater role in food delivery when the young are small and gape limited, whereas the larger parent will protect the offspring during periods of vulnerability to predators.

#### METHODS

I studied Black Skimmers and Caspian Terns on dredge material islands in Lavaca Bay, Texas (28°39'N, 96°34'W), during the spring and summer (1982-1984). Both species nested on open areas of oyster shell sparsely vegetated with one or more of prickly poppy (*Argemone sanguinea*), Carolina wolfberry (*Lycium carolinianum*), sea purslane (*Sesuvium portulacastrum*), and glasswort (*Salicornia spp.*). Colonies were of single species with the exception of 1983 when skimmer colonies included one to four pairs of Gull-billed Terns (*Sterna nilotica*). Colony sizes studied ranged from 33 to 134 initiated clutches (Table 1).

Nests were checked every fourth day, weather permitting. Typically, nests were marked with painted wooden stakes upon discovery of the first egg. Hatchlings were marked on their heads, necks, or backs with feather dye (picric acid or nyanzol-D). Some were color-banded to facilitate individual recognition within and between broods. Color assignments by

laying order were changed between years and randomized among broods in some colonies. To prevent chick dispersal during nest checks, 50-cm high fences (of 0.6-cm mesh hardware cloth) were erected around study colonies (see Erwin 1977, Nisbet and Drury 1972). Fences and dye marks had no obvious effects on chicks 0-15 days of age or their parents, although older chicks may have been impeded by the fences.

Adult Caspian Terns were captured with a cannon net or nest trap (Giles 1971) just before the hatching period. The birds were laparotomized and sexed by gonadal inspection, dyed on the neck, color-banded, measured, and released. I studied only Caspian Tern families in which one or both adults were marked and of known sex. Because the sexes of Black Skimmers are easily discerned visually (Burger 1981), it was unnecessary to capture individuals for sexual identification. To band and measure Black Skimmer parents, however, I captured them with nest traps and (twice) with cannon nets. I recorded body mass and various linear measurements for both species. Cranium structures differ between the species (see Zusi 1962). I measured depth at base of bill, gonys to tip of lower bill, and relaxed gape (the horizontal measurement between the commissural points; Pettingill 1985: 13) only in skimmers. I measured depth at gonys, commissure, or both in terns only.

Parental activities were monitored from a blind within 20 m of the colony edge. Observers entered the blind during the birds' relatively inactive midday periods and remained inside overnight to minimize disturbance. Shifts were typically 22-24 h and each colony was observed for at least part of each day. Observation periods were 1-7 h, with brief interruptions for nest-attendance scan sampling. Observation times did not differ systematically between species.

Nest attendance was determined by hourly scan samples (Altmann 1974) of nests selected for ease of sampling. We recorded the presence and sex of the incubating or brooding parent, and the sex of parent(s) standing within 1.5 m of the nest. Because the terns' sexes were unknown before laparotomy (approximately when the colony's first egg hatched), fewer early nest-attendance records were obtained for this species.

TABLE 2. Stepwise discriminant analysis of Black Skimmers found dead and sexed by gonadal inspection.

Character	F-value to enter	Order of entry	Discriminant function coefficient <sup>a</sup>	Classification function <sup>b</sup>	
				Male (n = 24)	Female (n = 26)
Culmen	1.2	4	0.0889	1.51	0.85
Depth at base <sup>c</sup>	3.2	2	0.3554	15.86	13.19
Head to tip <sup>d</sup>	566.3	1	0.1810	7.85	6.49
Wing chord	3.8	3	0.0316	3.64	3.41
Gape <sup>e</sup>	1.2	5	-0.1151	-3.88	-3.02
Constant				-1,464.52	-1,117.90

<sup>a</sup> Coefficients for canonical variables.

<sup>b</sup> Add products of measurements and corresponding function values to constant; classify as male or female depending on which results in the higher value for classification function.

<sup>c</sup> Bill depth at base of bill.

<sup>d</sup> Length from back of cranium to tip of upper bill.

<sup>e</sup> Relaxed gape, measured laterally from the commissural points.

Chick-feeding data were collected by event sampling (Lehner 1979). We recorded a total of 3,170 brood-hours for skimmers and 1,920 brood-hours for terns. Brood ages were grouped into four arbitrary categories: 0-3, 4-7, 8-11, and 12-15 days post-hatch. Adults that arrived at the colony with fish in their bills were noted while in approach flight, and those at nests were observed further. We recorded (1) sex of parent; (2) nest number; (3) size of fish; (4) species of fish; (5) whether food was ingested (and, when possible, the hatching order of chick fed); (6) location of the feeding (in the nest, outside the nest but within 1 m, or beyond); and (7) whether one or both parents departed after the feeding.

Feeding rates were analyzed both as number of items and grams delivered per hour. Prey were identified to species in most cases (78.5% of fish delivered by skimmers; 87.1% of fish delivered by terns). Each item was assigned a length as a proportion of the parent's culmen to the nearest ¼ culmen length (see Recher and Recher 1969, Nisbet 1973, Mock 1985), which was subsequently converted to metric units by multiplying that proportion by the appropriate mean culmen length of the parent's species and sex. Prey lengths were converted to approximate fresh mass according to a length-mass regression for each prey

species (S. Holt unpubl. data). For a few prey items (2% of total items recorded for both species), mass was determined using the length-mass relationship of a similarly shaped species (Quinn 1988). If the prey length was noted but the species unidentified, I estimated mass from a composite regression for all species measured (Quinn 1988; 19.4% of total fish delivered by skimmers, 9.4% of total fish delivered by terns). If neither was reported, prey-mass was assumed to equal the mean mass of prey delivered to broods of the same age by the same sex in the same colony (see Mueller et al. 1981). This was necessary for only 2.1% of the fish delivered by skimmers, and 3.4% of fish delivered by terns.

I used the SAS statistical package (SAS 1985), the BIOM statistical package (Rohlf 1983), or the BMDP statistical package (Dixon 1983) for data analysis. Means ( $\bar{x}$ ) are presented with standard errors (SE). I compared means for samples with unequal variances with a *t*-test approximation, using Satterthwaite's approximation for degrees of freedom (df) (SAS 1985). To facilitate generalizations from two or three different samples without violating assumptions necessary for pooling of samples, I combined probabilities from independent tests of significance (Sokal and Rohlf 1981: 780). The calculated value ( $-2 \sum \ln P$ , subse-

TABLE 3. Stepwise discriminant analysis of Caspian Terns sexed by laparotomy on living birds.

Character	F-value to enter	Order of entry	Discriminant function coefficient	Classification function	
				Male (n = 23)	Female (n = 12)
Culmen	7.9	1	0.4408	22.87	22.05
Depth at gonys <sup>a</sup>	4.0	2	0.9360	61.25	59.52
Wing chord	3.9	3	0.0513	4.68	4.58
Commissure <sup>b</sup>	2.0	5	-0.1152	-0.08	-0.59
Tarsus length	2.6	4	0.1435	7.53	7.27
Constant				-2,410.05	-2,295.24

<sup>a</sup> Bill depth at the lowermost ridge of the lower mandible.

<sup>b</sup> Length from the commissural point to the tip of the lower bill.

TABLE 4. Morphological measurements of male (M) and female (F) Black Skimmers captured alive and sexed by discriminant function. All linear measurements in mm; mass in g. Statistical comparisons are by sex.

Character	Sex	$\bar{x} \pm SE (n)$	Range	<i>t</i>	<i>P</i>
Culmen length	M	72.0 $\pm$ 0.44 (57)	62.6–78.4	24.2	0.01
	F	58.7 $\pm$ 0.34 (73)	49.3–64.6		
Head to tip <sup>a</sup>	M	132.3 $\pm$ 0.55 (57)	121.4–138.9	31.7	0.01
	F	111.3 $\pm$ 0.36 (73)	103.3–118.1		
Depth at base <sup>b</sup>	M	28.9 $\pm$ 0.28 (40)	26.4–36.9	17.6	0.01
	F	23.3 $\pm$ 0.12 (71)	21.1–26.4		
Gonys to lower tip	M	102.2 $\pm$ 0.94 (16)	96.3–108.4	15.8	0.01
	F	81.9 $\pm$ 0.83 (13)	77.9–87.1		
Gape <sup>c</sup>	M	26.2 $\pm$ 0.38 (40)	21.0–32.0	8.6	0.01
	F	22.1 $\pm$ 0.28 (39)	19.2–27.7		
Tarsus length	M	33.5 $\pm$ 0.44 (57)	26.3–43.5	8.7	0.01
	F	28.9 $\pm$ 0.29 (72)	23.4–36.9		
Wing chord	M	388.8 $\pm$ 1.46 (57)	355.8–410.0	16.5	0.01
	F	354.7 $\pm$ 1.35 (87)	330.0–400.3		
Mass	M	348.7 $\pm$ 3.44 (56)	260.0–392.0	23.5	0.01
	F	254.0 $\pm$ 2.10 (73)	212.0–292.0		

<sup>a</sup> Length from back of cranium to tip of upper bill.

<sup>b</sup> Depth at the base of the bill.

<sup>c</sup> Relaxed gape, measured laterally from the commissural points.

quently denoted  $-2 \sum \ln P^*$ ) is distributed as a Chi-square value with  $2k$  degrees of freedom (where  $k$  = the number of separate tests and probabilities; Sokal and Rohlf 1981).

## RESULTS

A stepwise discriminant function analysis (Dixon 1983) clearly separated adult male and female Black Skimmers (Table 2). A similar anal-

ysis, requiring a higher *F*-value for inclusion in the discriminant function model (*F*-value to enter = 4.0), separated skimmer sexes with a single measurement (distance from back of cranium to tip of upper bill). Sex was assigned correctly based on classification functions (Table 2) with or without pseudojackknifed procedures (Dixon 1983). The pseudojackknifed procedure adjusts the discriminant function so that the individual being tested is removed from the

TABLE 5. Morphological measurements of male (M) and female (F) Caspian Terns sexed by gonadal inspection (laparotomy,  $n = 72$ ) or observation of position during successful copulation (with cloacal contact,  $n = 15$ ). Measured mates of known-sex birds were included. Statistical comparisons are by sex.

Character	Sex	$\bar{x} \pm SE (n)$	Range	<i>t</i>	<i>P</i>
Culmen	M	70.2 $\pm$ 0.42 (35)	63.0–75.2	3.6	0.01
	F	68.2 $\pm$ 0.35 (32)	64.0–73.0		
Head to tip	M	136.6 $\pm$ 0.63 (36)	129.0–147.0	2.2	0.03
	F	134.8 $\pm$ 0.51 (32)	127.8–140.0		
Depth at gonys <sup>a</sup>	M	15.7 $\pm$ 0.12 (37)	14.0–17.0	2.4	0.02
	F	15.1 $\pm$ 0.15 (32)	13.7–17.0		
Commissure <sup>b</sup>	M	99.5 $\pm$ 0.78 (33)	93.0–113.0	1.5	0.14
	F	97.9 $\pm$ 0.63 (25)	93.0–106.0		
Tarsus length	M	46.3 $\pm$ 0.63 (34)	40.0–55.7	1.4	0.15
	F	45.0 $\pm$ 0.58 (25)	39.0–50.0		
Wing chord	M	418.0 $\pm$ 2.25 (28)	382.0–433.0	0.8	0.41
	F	415.5 $\pm$ 1.92 (25)	393.0–433.0		
Mass	M	649.2 $\pm$ 5.52 (48)	574.0–739.0	-1.3	0.20
	F	661.8 $\pm$ 8.35 (36)	575.0–782.0		

<sup>a</sup> Bill depth at the lowermost ridge of the lower mandible.

<sup>b</sup> Length from the commissural point to the tip of the lower bill.

TABLE 6. G-tests of hourly scan samples of attendance by male and female Black Skimmers during the nest-specific egg (E) and chick (C) periods (expected = 1:1). *P* = probability levels for the null hypothesis are presented.

Year	Colony	Period <sup>a</sup>	Pooled distribution		Scan samples	Pooled G	<i>P</i>	Heterogeneity		
			Male <sup>b</sup>	Female <sup>b</sup>				G	df	<i>P</i>
1982	76	E	1,852	1,984	2,417	4.5	0.03	12.1	57	NS
1983	Ugly <sup>c</sup>	E	351	460	692	14.7	0.01	29.5	20	NS
1983	66	E	611	737	950	11.8	0.01	11.8	12	NS
1982	76	C	997	1,101	1,859	5.2	0.02	58.3	68	NS
1983	Ugly	C	698	696	1,424	0.0	1.00	66.4	20	0.01
1983	66	C	565	572	936	0.0	0.84	4.2	11	NS

<sup>a</sup> E = before the first egg hatched; C = after the first egg hatched.

<sup>b</sup> Number of scan samples in which males or females were in attendance at the nest.

<sup>c</sup> Ugly Island.

function used in its classification. Such analyses of living male and female Caspian Terns were ambiguous (Table 3). Only 18 of 23 (78%) males and 11 of 12 (92%) females were assigned correctly. By the pseudojackknifed procedure, 17 of 23 (74%) males and 10 of 12 (83%) females were assigned correctly. Thus, Caspian Terns overlap in size, and the sexes cannot be distinguished reliably, even by external measurement.

At a mean mass of  $348.7 \pm 3.4$  g, male Black Skimmers were substantially larger than the females ( $\bar{x} = 254.0 \pm 2.1$  g; Table 4). Bill measurements showed little or no overlap between skimmer sexes (Table 4). Male Caspian Terns ( $\bar{x} = 649.2 \pm 5.5$  g) were slightly, but not significantly, lighter than females ( $\bar{x} = 661.8 \pm 8.3$  g). In all linear measurements, male terns were slightly larger than females but overlapped substantially. Only the bill measurements differed significantly (Table 5).

Black Skimmer females generally exceeded or matched their mates' nest attendance (Table 6). Overall, female Black Skimmers attended the nest significantly more than males during the egg period ( $-2 \sum \ln P^* = 39.59$ ,  $df = 6$ ,  $P <$

0.0001), but not thereafter (excluding one sample with significant heterogeneity among nests;  $-2 \sum \ln P^* = 7.93$ ,  $df = 4$ ,  $0.1 > P > 0.05$ ).

Male skimmers brooded sometimes after physically pushing their mates from the nest. Instances of forced brooding exchanges were infrequent and not always recorded. Females also pushed their mates but appeared to be unsuccessful at forcing males off the nests.

Female Caspian Terns typically attended the nest more than males, although two samples revealed significant among-nest heterogeneity (Table 7). Overall, females attended the nest more than males during the egg period (excluding one sample with significant among-nest heterogeneity;  $-2 \sum \ln P^* = 9.93$ ,  $df = 4$ ,  $P < 0.05$ ). After the first egg in the clutch hatched, attendance differences were highly significant (excluding one sample with significant among-nest heterogeneity;  $-2 \sum \ln P^* = 28.34$ ,  $df = 4$ ,  $P < 0.0001$ ).

Female Black Skimmers fed their broods more items than their partners did at Ugly Island (1983, Wilcoxon signed-ranks test,  $T_s = 247.0$ ,  $P = 0.002$ ), Island 66 (1983,  $T_s = 283.5$ ,  $P = 0.008$ )

TABLE 7. G-tests of scan samples of attendance by male and female Caspian Terns during the egg (E) and chick (C) periods (expected = 1:1).

Year	Colony	Period	Pooled distribution		Scan samples	Pooled G	<i>P</i>	Heterogeneity		
			Male	Female				G	df	<i>P</i>
1982	76	E	228	287	528	6.8	0.01	33.2	26	NS
1982	58	E	128	144	288	0.9	0.32	44.4	17	0.01
1983	70	E	52	49	108	0.1	0.76	4.9	5	NS
1982	76	C	558	730	1,160	23.0	0.01	28.3	27	NS
1982	58	C	444	468	1,004	0.6	0.44	17.8	18	NS
1983	70	C	238	320	618	12.1	0.01	18.9	9	0.05

and overall (Fig. 1;  $-2 \sum \ln P^* = 25.6$ ,  $df = 6$ ,  $P < 0.001$ ), particularly when chicks were young. The difference was not significant at Island 76 (1982,  $T_s = 1133.0$ ,  $P = 0.170$ ). Feeding rate differences between the sexes were significant at age classes 0-3 days (Island 76,  $T_s = 72.5$ ,  $P = 0.005$ ; Ugly Island,  $T_s = 10.0$ ,  $P = 0.041$ ; Island 66,  $T_s = 21.0$ ,  $P = 0.001$ ; and overall,  $-2 \sum \ln P^* = 30.8$ ,  $df = 6$ ,  $P < 0.001$ ). At ages 4-7 days, these rates differed at Ugly Island ( $T_s = 16.0$ ,  $P = 0.022$ ), and overall ( $-2 \sum \ln P^* = 15.8$ ,  $df = 6$ ,  $P < 0.025$ ), but not at Island 76 ( $T_s = 68.0$ ,  $P = 0.277$ ) or Island 66 ( $T_s = 12.0$ ,  $P = 0.062$ ). Intersexual feeding rate differences were not significant at any colony for age classes 8-11 or 12-15 ( $P > 0.3$ ). Male skimmers' feeding performances relative to those of females increased with brood-age at Island 66 (Kruskal Wallis  $H = 9.66$ ,  $df = 3$ ,  $P = 0.022$ ), and overall ( $-2 \sum \ln P^* = 15.3$ ,  $df = 6$ ,  $P < 0.025$ ; Fig. 1), but not at Island 76 ( $H = 7.77$ ,  $df = 3$ ,  $P = 0.051$ ) or Ugly Island ( $H = 2.76$ ,  $df = 3$ ,  $P = 0.431$ ). Higher feeding rates were observed during morning and evening peaks (Table 8).

By contrast, male Caspian Terns fed more frequently than females at Island 76 (1982,  $T_s = 546.5$ ,  $P = 0.017$ ), Island 70 (1983,  $T_s = 57.0$ ,  $P = 0.0003$ ) and overall ( $-2 \sum \ln P^* = 24.4$ ,  $df = 4$ ,  $P < 0.001$ ; Fig. 2). Feeding rate differences between the sexes were significant for brood ages 0-3 days at Island 76 ( $T_s = 81.0$ ,  $P = 0.009$ ) and overall ( $-2 \sum \ln P^* = 10.1$ ,  $df = 4$ ,  $P < 0.05$ ), 4-7 days at Island 70 ( $T_s = 3.0$ ,  $P = 0.036$ ), 8-11 days at Island 70 ( $T_s = 1.0$ ,  $P = 0.017$ ), and overall ( $-2 \sum \ln P^* = 9.8$ ,  $df = 4$ ,  $P < 0.05$ ). These differences were not significant for 0-3 days at Island 70 ( $T_s = 6.0$ ,  $P = 0.686$ ), 4-7 days at Island 76 ( $T_s = 60.0$ ,  $P = 0.435$ ) or overall ( $-2 \sum \ln P^* = 8.3$ ,  $df = 4$ ,  $P > 0.05$ ), 8-11 days at

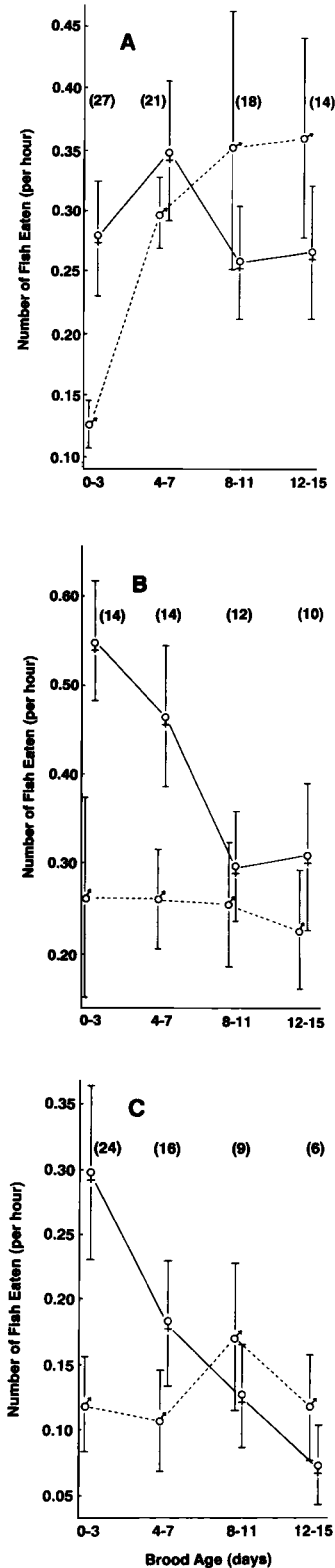


Fig. 1. Feeding rates (by number of separate food items) by male (♂) and female (♀) Black Skimmers as a function of brood age. Brood ages are grouped into four age classes based on days after first hatching. Means and standard error bars are shown with number of broods in parentheses. Fig. 1A is based on 1,060 brood-hours of observation at Island 76 in 1982, Fig. 1B on 750 brood-hours of observation at Ugly Island in 1983, and Fig. 1C on 1,360 brood-hours of observation at Island 66 in 1983.

TABLE 8. Prey delivery rates to broods <16 days of age by adult Black Skimmers and Caspian Terns according to hour of day. Number of broods observed is in parentheses after year and colony.

Hour	Caspian Terns																							
	Black Skimmers				1982 Island 76 (33)				1983 Ugly Island (14)				1983 Island 66 (24)				1982 Island 76 (45)				1983 Island 70 (22)			
	Prey per hour	SE	Brood hours	Prey per hour	SE	Brood hours	Prey per hour	SE	Brood hours	Prey per hour	SE	Brood hours	Prey per hour	SE	Brood hours	Prey per hour	SE	Brood hours	Prey per hour	SE	Brood hours			
0600	1.02	0.27	95	1.05	0.25	44	1.01	0.26	89	2.35	1.25	25	0.70	0.17	40	0.70	0.17	40	0.70	0.17	40			
0700	1.44	0.24	55	1.17	0.25	78	0.82	0.25	121	1.10	0.36	105	0.72	0.14	100	0.72	0.14	100	0.72	0.14	100			
0800	0.99	0.15	73	1.08	0.11	66	0.55	0.19	83	0.67	0.11	125	1.22	0.18	81	1.22	0.18	81	1.22	0.18	81			
0900	1.19	0.34	33	1.18	0.33	65	0.70	0.22	100	0.48	0.12	73	0.89	0.14	80	0.89	0.14	80	0.89	0.14	80			
1000	0.75	0.15	89	0.90	0.22	71	0.55	0.23	104	0.74	0.12	107	0.68	0.12	62	0.68	0.12	62	0.68	0.12	62			
1100	0.68	0.13	68	0.67	0.19	49	0.44	0.14	101	0.62	0.15	70	0.67	0.11	100	0.67	0.11	100	0.67	0.11	100			
1200	0.76	0.54	106	0.96	0.22	48	0.59	0.28	87	1.27	0.34	68	0.53	0.09	102	0.53	0.09	102	0.53	0.09	102			
1300	0.66	0.13	51	0.55	0.20	18	0.59	0.25	40	0.64	0.20	31	0.49	0.10	50	0.49	0.10	50	0.49	0.10	50			
1400	0.25	0.15	12	0.00	0.00	11	0.35	0.14	63	0.77	0.26	10	0.00	0.00	1	0.00	0.00	1	0.00	0.00	1			
1500	0.52	0.17	66	0.41	0.11	29	0.66	0.16	115	1.27	0.34	32	1.20	0.51	7	1.20	0.51	7	1.20	0.51	7			
1600	0.48	0.11	122	1.05	0.28	40	0.60	0.19	111	0.57	0.13	92	0.76	0.15	56	0.76	0.15	56	0.76	0.15	56			
1700	0.55	0.11	86	1.04	0.28	64	0.90	0.24	90	0.90	0.18	94	1.00	0.16	79	1.00	0.16	79	1.00	0.16	79			
1800	0.79	0.16	86	1.41	0.38	85	1.24	0.39	106	0.88	0.20	102	0.60	0.11	95	0.60	0.11	95	0.60	0.11	95			
1900	1.20	0.31	107	2.05	0.63	78	1.87	0.72	103	1.52	0.48	44	0.46	0.08	107	0.46	0.08	107	0.46	0.08	107			
2000	0.68	0.12	86	2.78	1.65	28	1.14	0.34	61	0.70	0.35	13	0.59	0.13	28	0.59	0.13	28	0.59	0.13	28			

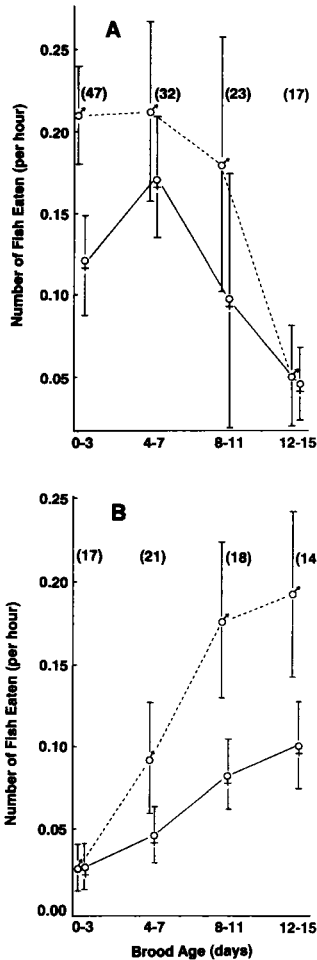


Fig. 2. Feeding rates (by number of separate food items) by male and female Caspian Terns as a function of brood age (symbols as in Fig. 1). (A) Based on 980 brood-hours of observation at Island 76 in 1982. (B) Based on 940 brood-hours of observation at Island 70 in 1983.

Island 76 ( $T_s = 16.0, P = 0.441$ ), 12-15 days at Island 76 ( $T_s = 5.0, P = 0.5$ ), Island 70 ( $T_s = 6.0, P = 0.051$ ), or overall ( $-2 \sum \ln P^* = 7.3, df = 4, P > 0.05$ ). Feeding performances of males relative to those of females did not vary with brood age at Island 76 ( $H = 4.17, df = 3, P = 0.243$ ) or Island 70 ( $H = 5.03, df = 3, P = 0.169$ ). Caspian Tern feeding rates also varied with the time of day (Table 8), though peaks were less discrete.

As skimmer young aged, parents tended to bring larger prey to the nest site. Prey-mass correlated significantly with brood age (Island

TABLE 9. Multiple regression analysis of the effect of brood age, date, and sex of feeding parent Black Skimmer on the estimated mass of prey delivered to the nest site.

Variable	Partial $r^2$	P	Prey items (n)
<b>1982 Island 76</b>			
Brood age	0.14 <sup>a</sup>	0.01	628
Parent's sex	0.08 <sup>b</sup>	0.01	
Date	0.06 <sup>c</sup>	0.01	
Total $r^2$	0.28 <sup>d</sup>	0.01	
<b>1983 Ugly Island</b>			
Brood age	0.07 <sup>a</sup>	0.01	652
Parent's sex	0.06 <sup>b</sup>	0.01	
Date	0.00 <sup>c</sup>	0.29	
Total $r^2$	0.13 <sup>e</sup>	0.01	
<b>1983 Island 66</b>			
Brood age	0.06 <sup>a</sup>	0.01	769
Parent's sex	0.03 <sup>b</sup>	0.01	
Date	0.00 <sup>c</sup>	0.11	
Total $r^2$	0.08 <sup>e</sup>	0.01	

<sup>a</sup> Partial  $r^2$  explained by brood age alone.  
<sup>b</sup> Partial  $r^2$  beyond the variance already explained by brood age.  
<sup>c</sup> Partial  $r^2$  beyond the variance already explained by brood age and parent's sex.  
<sup>d</sup> Total  $r^2$  explained by all three variables.  
<sup>e</sup> Total  $r^2$  explained by brood age and parent's sex (the significant variables).

76, 1982: Spearman  $r_s = 0.50, n = 628, P < 0.01$ ; Ugly Island, 1983:  $r_s = 0.30, n = 652, P < 0.01$ ; Island 66, 1983:  $r_s = 0.27, n = 769, P < 0.01$ ). Brood age was the primary factor explaining differences in prey-mass, though the sex of the parent feeding and the date (at one colony) also accounted for significant degrees of prey-mass variation (Table 9).

Caspian Tern prey-mass also correlated positively with brood age (Island 76, 1982:  $r_s = 0.27, n = 359, P < 0.01$ ; Island 70, 1983:  $r_s = 0.16, n = 238, P < 0.025$ ). Multiple regression analyses revealed that brood age (independent of date) was the most important factor explaining the variance in prey-mass (Table 10).

In all skimmer study colonies, males brought prey much larger (generally averaging two to four times heavier [Table 11]) than prey females brought. In contrast, prey delivered by Caspian Tern sexes did not differ significantly in estimated mass (Table 12).

Young Black Skimmer chicks ate prey of almost all sizes delivered. Chicks aged 0-1 day ingested fish that weighed up to 62 g, and they were apparently capable of eating 2,002 (99%) of the 2,023 prey items delivered to all broods



TABLE 10. Multiple regression analysis of the effect of brood age, date, and sex of feeding parent Caspian Terns on the estimated mass of prey delivered to the nest site. The number of prey items is presented ( $n$ ).

Variable	Partial $r^2$	$P$	Prey items ( $n$ )
<b>1982 Island 76</b>			
Brood age	0.06 <sup>a</sup>	0.01	359
Parent's sex	0.01 <sup>b</sup>	0.09	
Date	0.00 <sup>c</sup>	0.83	
Total $r^2$	0.06 <sup>d</sup>	0.01	
<b>1983 Island 70</b>			
Brood age	0.03 <sup>a</sup>	0.01	238
Parent's sex	0.01 <sup>b</sup>	0.19	
Date	0.00 <sup>c</sup>	0.49	
Total $r^2$	0.03 <sup>d</sup>	0.01	

<sup>a</sup> Partial  $r^2$  explained by brood age alone.

<sup>b</sup> Partial  $r^2$  beyond the variance already explained by brood age.

<sup>c</sup> Partial  $r^2$  beyond the variance already explained by brood age and parent's sex.

<sup>d</sup> Total  $r^2$  explained by the only significant variable (brood age).

aged 0 to 15 days (all samples; see Quinn 1988: appendices I-K). Prey eaten by young skimmer chicks (brood age class 0-3 days) were similar in size to prey offered but not ingested. This was true overall ( $-2 \sum \ln P^* = 9.47$ ,  $df = 6$ ,  $P > 0.1$ ) and for each skimmer colony studied (Island 76, 1982:  $t = 0.52$ ,  $df = 156$ ,  $P > 0.6$ ; Ugly Island, 1983:  $t$  approximation for unequal variances = 1.42,  $df = 31.4$ ,  $P > 0.1$ ; Island 66, 1983:  $t$  approximation for unequal variances = -1.83,  $df = 15.2$ ,  $0.1 > P > 0.05$ ). In general, the youngest chicks were seldom offered prey too large for them to ingest.

Similarly, Caspian Tern young could ingest most prey delivered to the nest site. Even chicks aged 0-1 days ate fish weighing up to 68 g and were able to eat 569 of 594 (96%) prey items delivered to broods aged 0-15 days (both samples; see Quinn 1988: appendices L and M). Large prey seemed to pose swallowing problems for very young Caspian Tern broods on Island 76 (1982). Fish delivered but uneaten in broods aged 0-3 days at that colony were significantly heavier than fish ingested ( $t$  approximation for unequal variances = 2.5,  $df = 7.1$ ,  $P < 0.05$ ). However, this difference did not hold for the other colony (Island 70, 1983:  $t = -1.13$ ,  $df = 21$ ,  $P > 0.25$ ) and was not significant overall ( $-2 \sum \ln P^* = 9.06$ ,  $df = 4$ ,  $0.05 < P < 0.1$ ).

Male Black Skimmer parents fed their broods more by mass than did females at Island 76 ( $T_s$

= 954.0,  $P = 0.0002$ ), Ugly Island ( $T_s = 314.0$ ,  $P = 0.008$ ), and overall ( $-2 \sum \ln P^* = 26.5$ ,  $df = 6$ ,  $P < 0.001$ ; Fig. 3) but not at Island 66 ( $T_s = 471.0$ ,  $P = 0.108$ ). This difference was mainly due to differences in prey-mass delivered to broods aged 8-11 days ( $-2 \sum \ln P^* = 18.3$ ,  $df = 6$ ,  $P < 0.01$ ) and 12-15 days ( $-2 \sum \ln P^* = 13.1$ ,  $df = 6$ ,  $P < 0.05$ ). Prey-mass delivery differed significantly for broods aged 8-11 days at Island 76 ( $T_s = 32.0$ ,  $P = 0.020$ ) but not at Ugly Island ( $T_s = 13.0$ ,  $P = 0.075$ ) or Island 66 ( $T_s = 5.0$ ,  $P = 0.069$ ), and for broods aged 12-15 days at Island 76 ( $T_s = 21.0$ ,  $P = 0.048$ ) but not at Ugly Island ( $T_s = 14.0$ ,  $P = 0.169$ ) or Island 66 ( $T_s = 4.0$ ,  $P = 0.173$ ). Differences between sexes did not vary significantly with brood age overall ( $-2 \sum \ln P^* = 12.5$ ,  $df = 6$ ,  $0.1 > P > 0.05$ ) or for any colony (Island 76,  $H = 6.49$ ,  $df = 3$ ,  $P = 0.090$ ; Ugly Island,  $H = 2.98$ ,  $df = 3$ ,  $P = 0.395$ ; Island 66,  $H = 7.62$ ,  $df = 3$ ,  $P = 0.055$ ).

Male Caspian Terns also were responsible for more of the feeding by prey-mass than females were at Island 76 ( $T_s = 659.0$ ,  $P = 0.001$ ), Island 70 ( $T_s = 72.0$ ,  $P = 0.0003$ ), and overall ( $-2 \sum \ln P^* = 30.0$ ,  $df = 4$ ,  $P < 0.001$ ; Fig. 4). Rates by the tern sexes differed significantly for ages 0-3 days at Island 76 ( $T_s = 88.0$ ,  $P = 0.0006$ ) and overall ( $-2 \sum \ln P^* = 16.2$ ,  $df = 4$ ,  $P < 0.005$ ), but not at Island 70 ( $T_s = 5.0$ ,  $P = 0.502$ ). At ages 4-7 days, rates between sexes were similar at Island 70 ( $T_s = 6.0$ ,  $P = 0.051$ ) and Island 76 ( $T_s = 75.0$ ,  $P = 0.263$ ). Differences at ages 8-11 days were significant at Island 70 ( $T_s = 0.0$ ,  $P = 0.007$ ) and overall ( $-2 \sum \ln P^* = 13.9$ ,  $df = 4$ ,  $P < 0.01$ ), but not at Island 76 ( $T_s = 13.0$ ,  $P = 0.139$ ). At ages 12-15 days, rates were higher for males at Island 70 ( $T_s = 4.0$ ,  $P = 0.028$ ), but rates were not different at Island 76 ( $T_s = 10.0$ ,  $P = 0.916$ ) or overall ( $-2 \sum \ln P^* = 7.3$ ,  $df = 4$ ,  $P > 0.1$ ). Mass delivery rate differences between the sexes varied significantly with brood age at Island 70 ( $H = 10.1$ ,  $df = 3$ ,  $P = 0.018$ ), and overall ( $-2 \sum \ln P^* = 11.0$ ,  $df = 4$ ,  $P < 0.05$ ) but not at Island 76 ( $H = 4.44$ ,  $df = 3$ ,  $P = 0.223$ ).

## DISCUSSION

Black Skimmers have dramatic sexual size dimorphism, whereas Caspian Tern sexes are only slightly different in size. Black Skimmer sexes can be distinguished, even in the field, by human observers (Erwin 1977, Burger 1981), but

TABLE 11. Estimated fish mass (g) delivered to the nest site by male versus female Black Skimmers at different brood ages (days). Prey-mass delivered by the sexes compared with *t*-tests.

Brood age	Male mass ( $\bar{x}$ )	<i>n</i> <sup>a</sup>	Female mass ( $\bar{x}$ )	<i>n</i> <sup>a</sup>	<i>t</i> <sup>b</sup>	df <sup>c</sup>	<i>P</i>
<b>1982 Island 76</b>							
0-3	5.4	54	1.3	115	3.0	56.8	0.01
4-7	7.6	61	3.3	76	2.7	110.9	0.01
8-11	11.8	100	4.2	66	5.0	143.0	0.01
12-15	17.9	100	7.6	56	5.6	143.6	0.01
<b>1983 Ugly Island</b>							
0-3	3.6	74	1.9	158	1.6	106.2	0.11
4-7	9.6	79	3.0	121	4.0	86.2	0.01
8-11	10.1	66	5.1	77	2.0	75.4	0.04
12-15	21.5	27	5.5	50	1.9	36.2	0.06
<b>1983 Island 66</b>							
0-3	3.4	153	1.8	316	4.1	206.6	0.01
4-7	8.4	72	3.8	117	2.2	100.3	0.03
8-11	8.9	52	6.1	40	1.1	79.4	0.01
12-15	9.8	12	3.9	7	1.8	16.1	0.09

<sup>a</sup> Sample size: number of fish delivered by males and by females.

<sup>b</sup> Approximate *t* for samples of unequal variance (male > female).

<sup>c</sup> Satterthwaite's approximation for the degrees of freedom for samples of unequal variance (SAS 1985).

Caspian Tern sexes may be indistinguishable (*sensu* Burley 1981). Sexual dimorphism in size may have influenced skimmer parental care patterns.

The energetic costs associated with incubation may be quite low (Grant 1984), especially at relatively warm temperatures. The risks of nest attendance are difficult to assess. I found 65 (29 males and 36 females) dead adult skimmers, and only 3 dead adult Caspian Terns (Quinn 1988). The ratio of dead adult skimmers to terns (22:1) is substantially greater than the ratio of breeding Black Skimmers to pairs of

Caspian Terns in early June of 1981-1984 in Lavaca Bay (5.3:1; Texas Colonial Waterbird Census Data for Lavaca Bay). Caspian Terns were underrepresented because they breed earlier, and the difference between the ratios of dead adults and breeding pairs is conservative. Most dead birds were on or near a colony, which suggests potentially high risks associated with skimmer nest attendance or other parental duties. Furthermore, the reduced foraging time during nest attendance may be an important cost, particularly for skimmers, which do not feed mates that are incubating (Quinn 1988).

TABLE 12. Estimated fish mass (g) delivered to the nest site by male versus female Caspian Terns at different brood ages (days). Prey-mass delivered by the sexes compared by *t*-tests.

Brood age	Male mass ( $\bar{x}$ )	<i>n</i> <sup>a</sup>	Female mass ( $\bar{x}$ )	<i>n</i> <sup>a</sup>	<i>t</i> <sup>b</sup>	df <sup>c</sup>	<i>P</i>
<b>1982 Island 76</b>							
0-3	11.9	122	8.9	58	1.4 <sup>b</sup>	142.2 <sup>c</sup>	0.16
4-7	22.6	59	13.9	37	1.7	94.0	0.10
8-11	23.8	36	19.2	19	0.7 <sup>b</sup>	52.9 <sup>c</sup>	0.49
12-15	29.2	14	23.5	14	0.6	26.0	0.55
<b>1983 Island 70</b>							
0-3	19.6	18	20.0	14	0.1	30.0	0.95
4-7	23.8	33	15.9	16	1.8	47.0	0.08
8-11	29.0	52	23.1	30	1.0 <sup>b</sup>	78.1 <sup>c</sup>	0.30
12-15	27.8	47	27.9	28	0.0 <sup>b</sup>	43.7 <sup>c</sup>	0.99

<sup>a</sup> Sample size: number of fish delivered by males and by females.

<sup>b</sup> Approximate *t* for samples of unequal variance (SAS 1985).

<sup>c</sup> Satterthwaite's approximation for the degrees of freedom for samples of unequal variance (SAS 1985).

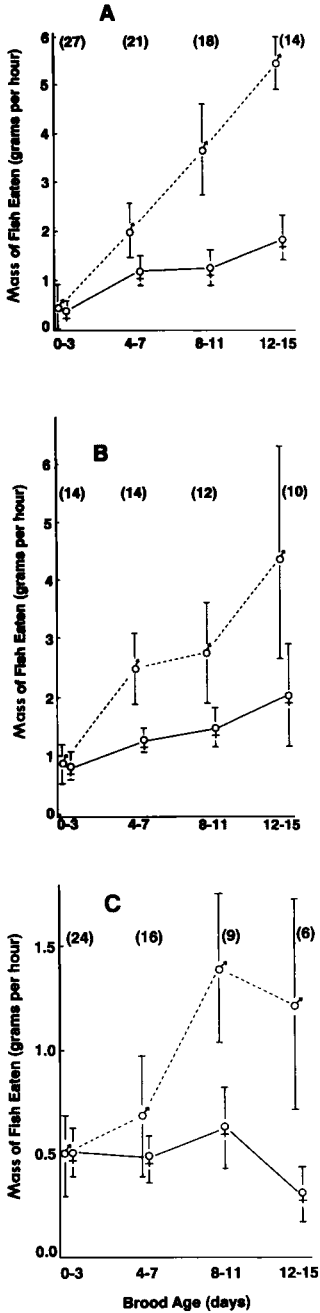


Fig. 3. Feeding rates (by mass) by male and female Black Skimmers as a function of brood age (symbols as in Fig. 1). (A) Based on 1,060 brood-hours of observation at Island 76 in 1982. (B) Based on 750 brood-hours of observation at Ugly Island in 1983. (C) Based on 1,360 brood-hours of observation at Island 66 in 1983.

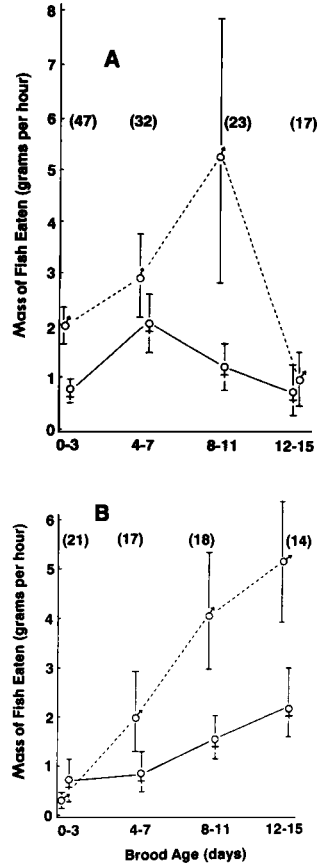


Fig. 4. Feeding rates (by mass) by male and female Caspian Terns as a function of brood age (symbols as in Fig. 1). (A) Based on 980 brood-hours of observation at Island 76 in 1982. (B) Based on 940 brood-hours of observation at Island 70 in 1983.

Burger (1981) found that male skimmers on Long Island, New York, incubated more than females, and attended the nest and brooded significantly more than females during the chick phase. No predation on eggs or chicks was mentioned (Burger 1981). Differences in prey sizes available, food availability (e.g. Pierotti 1981), or predation risk (Quinn 1989) may have been responsible for differences between this and Burger's study.

Skimmer nestling predation risk varied among colonies. The two skimmer colonies in which males had especially high nest attendance were located near nesting groups of Laughing Gulls (*Larus atricilla*), which prey on skimmer nestlings. Predation attempts at nests attended by lone parents were significantly less

frequent when the brooding parent was male (Quinn 1989). The observed increase in male attendance (especially lone brooding of young skimmer chicks) may reduce chick losses to gulls and may be facultative. I observed predation by Laughing Gulls at all colonies except one. This was a colony with no nesting gulls and was the only site at which female skimmers attended the nest significantly more than males.

Larid chicks do not attain thermoregulatory independence until 3–7 days (LeCroy and Collins 1972, Ricklefs 1974), and parental brooding is necessary. During this period, one parent broods while the other forages and delivers food to the nest. At this stage, conflicts of interest between pair members may affect parental roles (see Parker 1979). Because of the size difference between skimmer sexes, males could push their mates off the young and take over brooding (Burger 1981). Though such forceful incidences were uncommon and probably had little influence on parental care patterns during the early chick period, I cannot dismiss sexual conflict as a factor that contributes to early chick-feeding patterns.

In skimmers, providing suitably small prey items to very young chicks was accomplished through accelerated delivery of small prey by females. Burger (1981) also reported more chick feedings by female skimmers, although the sample size was quite small (104 fish). A shift toward larger prey by both sexes occurred as the broods aged. Chick gape size increased with growth, allowing more efficient swallowing of larger prey (see Hulsman 1981). Skimmer chicks' abilities to swallow or digest large prey did not rigidly restrict the prey size fed to chicks, although larger items may have required greater handling times for very young chicks. Because the actual moment of feeding chicks is observably one of predation risk to the chicks (Quinn 1989), the presentation of large prey may increase chick susceptibility to Laughing Gulls.

Black Skimmers fed chicks most actively in the early morning and late evening periods. I was able to collect feeding data only until shortly after sunset. Skimmers are known to engage in crepuscular and nocturnal foraging (Arthur 1921, Pettingill 1937, Robert et al. 1989). I cannot discount the possibility that parental roles shift after dark. The early morning and late evening feeding rates did not suggest a shift in feeding responsibilities between the sexes with the approach or retreat of darkness. Until noc-

turnal data are available, this will remain uncertain.

Chick-feeding delivery rate (items per hour) represents a useful index of parental costs of chick-feeding. Caspian Tern females attended the nest more than males, but males were more heavily involved in the energetically expensive activities of chick-feeding and associated foraging (Ricklefs 1974, Drent and Daan 1980). Males contributed most of the total prey-mass and number of prey to their young. The amount of food per delivery correlated significantly with brood age but not with the sex of the delivering parent nor with the date. This implies size-selective capture or delivery of prey by the parents.

Combined Caspian Tern feeding rates (by both sexes) increased with brood age in 1983, but rates decreased in 1982 after brood age of 4–7 days. A severe storm in 1982 resulted in numerous chick deaths from exposure, disrupted nesting territories, and may have reduced food availability. The storm and the reduced brood sizes are reflected most strongly in feeding rates to broods aged 8–11 and 12–15 days because post-storm observations included mostly broods in these categories. The occurrence of these post-storm broods (mostly one-chick broods), combined with possibly reduced food availability after the storm, may explain the low feeding rates of those brood-age categories in 1982.

In both species high levels of parental investment (Trivers 1972) were provided by both sexes. Difficulties with the definition and use of parental investment measures have been noted previously (Knapton 1984, Quinn and Sakaluk 1986). My results provide an example of another related dilemma. Parental investment is defined in terms of costs to the investing parent and benefits to the recipient offspring (Trivers 1972). As such, chick-feeding represents one component of parental investment. Chick-feeding by male Caspian Terns exceeded that by females, both in terms of apparent costs (numbers of items delivered) and benefits to the young (mass of prey delivered). Therefore, parental investment in chick-feeding by male Caspian Terns seems to exceed that by females. Chick-feeding by female Black Skimmers exceeded that by males, in terms of the number of items delivered (though some of the difference may be diminished by larger flight costs of males; Peters 1983). In contrast, chick-feeding by male skimmers provided more benefits

to the young because greater prey-mass was delivered by males. Parental investment in chick-feeding by female Black Skimmers probably exceeded that by males in terms of costs. This is the critical measure of parental investment (Trivers 1972), but it does not reflect benefits to the young.

Male Caspian Terns were more heavily involved in the energetically expensive tasks of feeding their chicks than their skimmer counterparts were. On the other hand, male Black Skimmers generally shared solo-brooding duties equally with their mates, whereas Caspian Tern males generally did less than their mates. These parental differences may relate to the dual skimmer advantages of predator protection by males and small-prey delivery to the young chicks by females. The skimmer pattern of parental care supported qualitatively the hypothesis tested. The Caspian Tern pattern of parental care was not predicted by the sexual specialization hypothesis, which suggests that other important factors influence parental care patterns.

Heavy male parental investment may be related to benefits of long-term pair-bond maintenance. Some Caspian Tern pairs are known to remain intact from season to season, although the separation rate can be quite high (Cuthbert 1985), perhaps when breeding sites are not stable. In this species, previous reproductive success did not correlate with the likelihood of remating (Cuthbert 1985). If parental care provided by one's mate is an important determinant of pair-bond maintenance, then only parents willing to invest equitably would garner the benefits of long-term pair bonding. Selection as a result of such benefits could favor increased male care to the extent that male parental investment matches that of females and asymmetries ultimately due to anisogamy have been overcome (Trivers 1972, Parker et al. 1972). Selection for equitability has also been suggested for Herring Gulls (Burger 1986), Western Gulls (*Larus occidentalis*; Pierotti 1981), and Great Black-backed Gulls (*Larus marinus*; Butler and Janes-Butler 1983).

Some interspecific differences in parental care patterns could stem from differential size-dependent costs of parental duties (Reynolds 1972, Andersson and Norberg 1981), or from differences in the probability of mixed paternity among broods of the two species (Quinn 1988). Elsewhere I summarized some indirect evidence that suggests a greater likelihood of mixed

paternity in Black Skimmer than Caspian Tern broods (Quinn 1988: appendix A).

Sexual dimorphism may better equip one sex for certain parental duties. Pairs that apportion duties in such a manner will tend to raise more young. However, if costs to future reproduction are greater on one sex, as a result of parental roles, selection on that sex should oppose such extravagant investments. The expected pattern is a compromise between the production of young of the year and parental survival, maximizing lifetime reproductive success (see Stearns 1976, Winkler 1987).

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 ERRATA

The AOU Check-list Committee acknowledges that it erred in the Thirty-seventh Supplement (*Auk* 106: 532-538) in assigning the English name MAS AFUERA PETREL to *Pterodroma e. externa* (p. 532). That form should continue to be known as JUAN FERNANDEZ PETREL. *Pterodroma defilippiana* (p. 537) should be called DEFILIPPE'S PETREL. More information will be in the Thirty-eighth Supplement in 1991.