DIURNAL TIME-ACTIVITY BUDGETS OF NESTING LEAST TERNS AND BLACK SKIMMERS

Melissa L. Leslie

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Approved by

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Chair

Accepted by

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Dean, Graduate School

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ABSTRACT

Time-activity budgets for Least Terns and Black Skimmers were determined for the 2004 and 2005 nesting seasons. These species had significantly different time-activity budgets. Least Terns spent more time engaged in incubation activities (72.89%), followed by brooding (9.53%), preening (6.65%), and standing (3.95%). Aggression, courtship, courtship feeding, flying, nest building, nest relief, sitting, tucking, and walking or running collectively accounted for 6.98% of their budget. Black Skimmers spent the majority of their time standing (28.86%) and incubating (28.70%), followed by brooding (15.73%), tucking (9.45%), sitting (5.98%), preening (4.99%), and walking or running (3.12%). Aggression, courtship, flying, nest building, and nest relief together totaled only 3.16% of their budget. Black Skimmer time-activity budgets also differed by sex; however, both sexes spent nearly identical amounts of time incubating, walking or running, and in aggressive acts. Both sexes spent 49% of the time with their mates. Week of the nesting season, time of day, air temperature, cloud cover, and wind speed significantly influenced Least Tern and Black Skimmer behavior. Air temperature was correlated with week of the nesting season. Least Terns displayed a pronounced sexual division of labor; females primarily were involved in incubation and brooding while males provisioned their mates and chicks. Black Skimmers did not display a sexual division of labor; both males and females shared incubation duties and provisioned their chicks.

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INTRODUCTION

Least Terns (*Sterna antillarum*) and Black Skimmers (*Rynchops niger*) are colonial ground nesting larids that frequently nest in mixed groups (Burger and Gochfeld 1990, Thompson *et al*. 1997). In North Carolina, Least Terns and Black Skimmers usually arrive at their breeding grounds in late April or early May. Both species tend to nest on sand or shell with little or no vegetation (Mallach and Leburg 1999, Schweitzer and Leslie 1999) and often use the same breeding sites year after year, although colony size, spacing patterns, and mating status may influence their nesting location (Burger 1988). Their favored nesting grounds are in considerable competition with human interests (Thompson *et al.* 1997).

Black Skimmers and Least Terns are monogamous and share parental duties, including incubation, brooding, nest defense, and feeding, although the extent to which each sex participates is arguable. About 90% of bird species are monogamous, with both parents investing in the care of eggs and chicks (Lack 1968). For monogamous species, biparental care is often necessary to successfully rear young (Emlen and Oring 1977). However, parental investment of the partners may differ due to differential rates of reproductive success. For example, females show slightly greater parental investment than males in most monogamous birds, probably due to the greater initial investment females provide by producing costly eggs (Trivers 1972). Recently, it has been argued that in some monogamous seabirds males may possibly invest as much as, if not more than, females throughout the breeding season. Examples of substantial male parental investment have been found in Common Terns (*Sterna hirundo*), where males perform extensive courtship and chick feeding (Wiggins and Morris 1986), and in Black Skimmers and Wandering Albatrosses (*Diomedea exulans*), where males have been found to incubate significantly more than females (Burger 1981b, Croxall and Ricketts 1983).

Black Skimmers exhibit sexual size dimorphism, with males being about ¼ larger than females (Erwin 1977), whereas Least Terns are not dimorphic. Darwin (1874) first proposed that sexual dimorphism occurs through sexual selection or ecological causation. According to sexual selection theory, selection favoring different body sizes in the two sexes occurs when it affects reproductive success. For instance, large males may have evolved due to male-male combat in order to achieve increased mating success. In contrast, ecological causation theory states that sexual differences in body size or morphology evolved to adapt the sexes to different ecological niches. Although sexual selection is the more recognized theory, Shine (1989) argues that both processes may work simultaneously on the same taxon to produce sexual dimorphism. Parental roles may be influenced by sexual dimorphism because size differences may better equip one sex for certain duties (Quinn 1990). Hence, pairs that allocate duties in this matter should raise more young and maximize their lifetime reproductive success.

Survival and reproductive rates are influenced by the amount of time and energy an animal devotes to different activities. Therefore, for a species in a given environment, there exists an optimal time and energy budget (Orians 1961, Verner 1965). How a species organizes its time can be determined by a time-activity budget, which is compiled by recording the time spent in various activities. Time-activity budgets have been collected on various shorebird species such as Kelp Gulls (*Larus dominicanus*) (Maxson and Bernstein 1984), American Avocets (*Recurvirostra Americana*) (Gibson 1978), and Black Oystercatchers (*Haematopus bachmani*) (Purdy and Miller 1988). Focal-Animal Sampling refers to a sampling method in which all occurrences of specified actions of one individual are recorded during a predetermined sample period (Altmann 1974). Data can then be used to construct a time-activity budget, which allows quantitative estimates of time and energy expenditures to be made of the animal under observation.

Previous behavioral studies on Least Terns have focused on breeding biology and reproductive behavior (Massey 1974, Wolk 1974), while those on Black Skimmers have focused on breeding ecology and behavior (Erwin 1977), sexual differences in parental activities (Burger 1981b, Quinn 1990), rates of aggression (Burger 1981a), and foraging efficiency and daily energy budgets (Blake 1985). Here, I investigated the diurnal behavior of nesting Least Terns and Black Skimmers to determine if reproductive behavior in these species varies over the course of the nesting season. In addition, I tested the hypothesis that weather patterns (air temperature, cloud cover, and wind speed) and time of day influence Least Tern and Black Skimmer behavior during the nesting season. Finally, I determined if male and female Black Skimmers or Least Terns and Black Skimmers have different time-activity budgets during the nesting season.

METHODS

Study Area

This study was conducted at the north end of Shell Island (34°14’N, 77°46’W), a part of Wrightsville Beach, North Carolina. This newly formed portion of the barrier island was created after the relocation of Mason Inlet in 2002 and has become important nesting habitat for Least Terns, Black Skimmers, Common Terns, American Oystercatchers (*Haematopus palliatus*), Wilson’s Plovers (*Charadrius wilsonia*), and Willets (*Catoptrophorus semipalmatus*). As a condition of the inlet relocation permit, New Hanover County had to provide a bird monitoring plan and a strategy to protect the nesting area for the life of the permit (30 years). Therefore, Shell Island is roped off and closed to beachgoers during the months of April through August, and monitored by the National Audubon Society and its volunteers. Growing numbers of birds have been nesting on the island each year since completion of the project. In 2004 and 2005, there were 369 and 614 Least Tern nests and 64 and 143 Black Skimmer nests, respectively. Vegetation on the island is meager, and consists mainly of sea rocket (C*akile harperi*), sea oats (*Uniola paniculata*), evening primrose (*Oenothera humifusa*), and saltmeadow cordgrass (*Spartina patens*).

Research Design

Least Terns were observed 7 May through 25 May 2004 and 3 May through 8 June 2005. Black Skimmers were observed 26 May through 14 July 2004 and 6 June through 14 July 2005. Three-hour observation intervals were performed three days a week from a portable fabric blind that was moved into the colony each day. Time intervals consisted of morning (0600-0900), afternoon (1100-1400), and evening (1600-1900) periods, when 20 randomly selected birds were videotaped, each for three minutes, within each three-hour time interval. Video recording aids in the critical analysis of behavior since observations of behavioral sequences may be viewed repeatedly, which greatly increases observer confidence and improves data reliability (Price and Stokes 1975). A random numbers table was used to select birds by counting in from either the far left or the far right of the colony. When each three-minute observation period was completed, the selection process was repeated from the opposite side of the colony. Subjects that left the viewing area before the observation period had ended were not analyzed. Videotapes were then reviewed and behavior was categorized to the nearest second. Since male and female Black Skimmers are sexually dimorphic, the sexes were distinguished visually in the field and from the videotape. Additionally, the number of incubation bouts (e.g. an incubating bird got up from the nest, engaged in other behavior, and came back to the nest to resume incubating during the observation period was counted as two incubation bouts) and whether or not skimmers were present with their mates was recorded for each three-minute observation period.

Least Tern and Black Skimmer behavior was classified into 14 categories. Stand: standing on one or both legs, eyes open or closed. Tuck: tucking their bill into the scapular feathers while standing. Sit: sitting, eyes open or closed. Fly: normal flapping flight or gliding. Walk and run: walking and running about the colony. Preen: actively manipulating feathers with bill, scratching, and stretching. Aggression: aggressive actions toward conspecifics or toward other species. Courtship: displays leading to copulations, attempted copulations, and successful copulations. Nest building: all behavior associated with nest-site selection and nest building. Courtship feeding: mate returned to the incubating partner with gifts of food. Incubation: sitting on or shading the nest when at least one egg was present. Nest relief: returning mate elicited departure of incubating partner. Brooding: all behavior associated with care of chicks. Other: any behavior observed that does not fit into one of the above categories. There were no records of this behavior for Least Terns and only 20 seconds for Black Skimmers, so this category was not included in the analyses for either species.

Three environmental characters (air temperature, cloud cover, and wind speed) were recorded at the middle of each observation period. Temperature categories were divided into cool (<23°C), moderate (23-28°C), and warm (>28°C). Cloud cover was based upon the amount of sky covered by opaque clouds, resulting in the categories of fair (<2/8), partly cloudy (2/8-5/8), cloudy (>5/8), and conditions of fog. Foggy conditions were not analyzed further since they only occurred once during Least Tern observations and once during Black Skimmer observations. Wind speed was categorized as light (<6.5 km/h), moderate (6.5-14.5 km/h), and strong (>14.5 km/h).

Analyses

Data were compiled and analyzed using SAS (version nine). The 2004 and 2005 data were combined for analysis. Contingency tables were generated to determine the percentage of time Least Terns and Black Skimmers spent in each behavior and the frequency with which each behavior was recorded. Chi-square was used to test the null hypotheses that the time-activity budgets of male and female Black Skimmers did not differ and the time-activity budgets of Least Terns and Black Skimmers did not differ. Simultaneous 95% confidence intervals were then calculated to detect significant differences between distinct behavior categories (non-overlapping intervals indicate significance at the 0.05 level). Chi-square was used to test the null hypothesis that week of the nesting season did not influence Least Tern or Black Skimmer behavior. Pearson correlation coefficients were generated to explore whether temperature, cloud cover, or wind speed were associated with time of season. Chi-square was also used to test the null hypotheses that time of day, temperature, cloud cover, and wind speed did not influence Least Tern or Black Skimmer nesting behavior. Again, simultaneous 95% confidence intervals were used to identify significant differences between categories. Null hypotheses were rejected when $P < 0.05$.

RESULTS

Environmental Data

Air temperature was significantly correlated with week of the nesting season ($r = 0.89$, $P < 0.001$; Fig. 1). However, cloud cover ($r = 0.26$, n.s.) and wind speed ($r = -0.32$, n.s.) were not correlated with week of the nesting season.

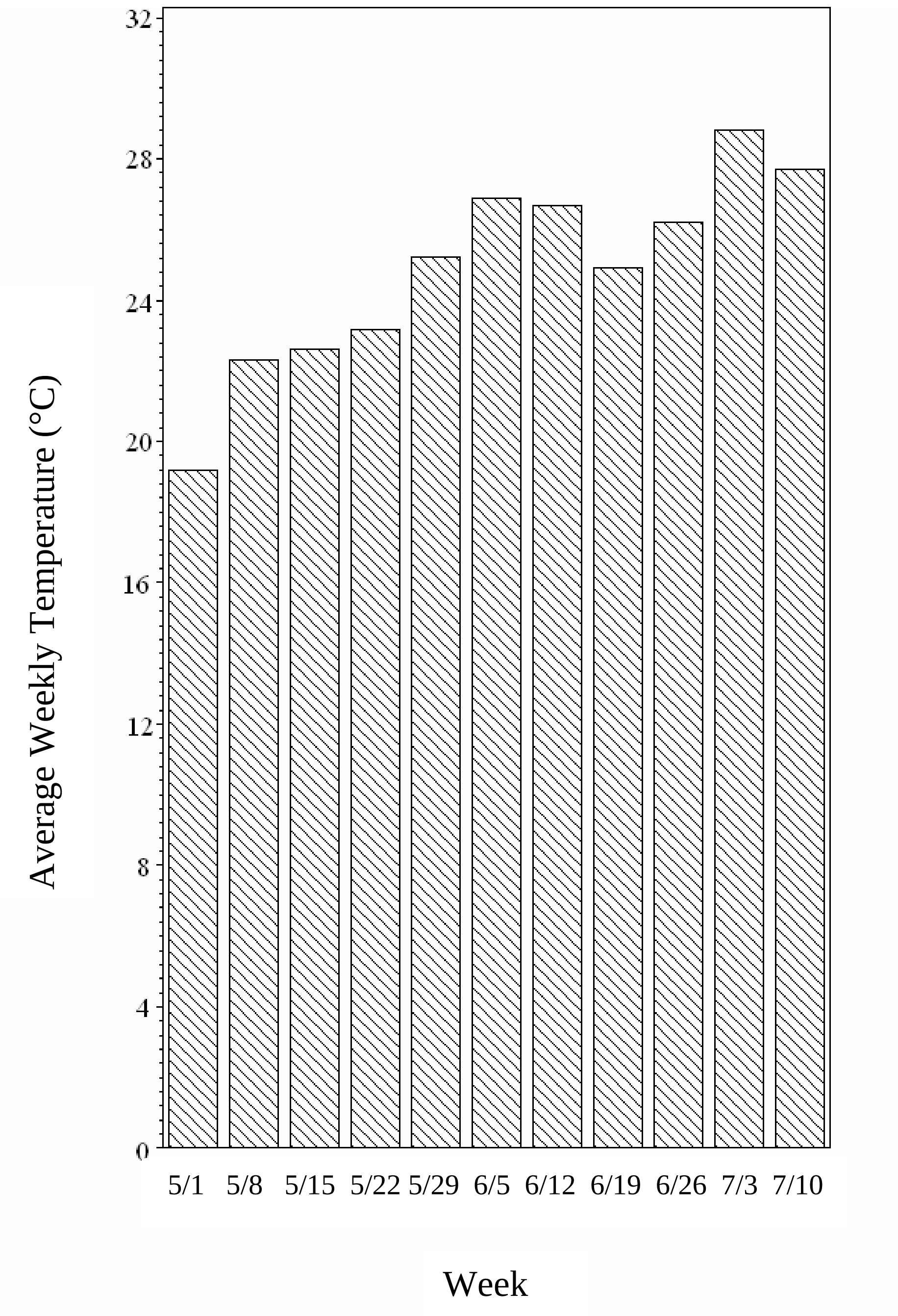

Figure 1. Average weekly temperatures at Wrightsville Beach, North Carolina, during the 2004 and 2005 nesting seasons (weeks aligned to the 2005 calendar year).

Least Tern Time-Activity Budget

A total of 469 Least Tern time-activity budget observations were taken over the 2004 and 2005 nesting seasons (Table 1). Incubation activities dominated the entire nesting budget while brooding, preening, and standing were the next three most common activities. The other nine behavioral categories collectively amounted to 6.98% of their nesting budget. Of the 357 Least Terns observed incubating, 330 performed one incubation bout, 26 performed two incubation bouts, and only one bird performed three bouts, resulting in a mean of 1.08.

Given that nine of the behavior categories accounted for less than 7% of the Least Tern nesting budget, only incubation, brooding, preening, and standing were analyzed with respect to time of day, temperature, cloud cover, and wind speed (Table 2). Least Tern behavior varied significantly with time of day (χ^2_{24} = 3,290.27, $P < 0.0001$). The most pronounced time of day effects were in brooding behavior, which decreased as the day progressed, and standing behavior, which increased. Least Tern behavior varied significantly according to temperature (χ^2_{24} = 4,267.31, $P < 0.0001$). During warm weather, incubation behavior decreased whereas preening increased. Least Terns spent significantly different amounts of time in various behaviors under different cloud cover conditions (χ^2_{36} = 4,281.42, $P < 0.0001$). Incubation behavior was observed the most under fair conditions, whereas the least amount of brooding was observed under fair conditions. Finally, Least Tern behavior varied significantly with wind speed (χ^2_{24} = 5,298.22, $P < 0.0001$). The majority of preening behavior was observed in light winds whereas most brooding behavior was observed in strong winds.

Least Tern behavior was significantly influenced by time of season (χ^2_{55} = 20,292.48, $P < 0.0001$). Figure 2 illustrates the average amount of time Least Terns spent incubating, brooding, preening, and standing over six weeks of the 2004 and 2005 nesting seasons. Incubation

Table 1. Least Tern time-activity budget at Wrightsville Beach, North Carolina, during the 2004 and 2005 nesting seasons (N = 469 three-minute observation periods).

Behavior	Time (seconds)	% of Time
Incubate	61530	72.89
Brood	8049	9.53
Preen	5615	6.65
Stand	3338	3.95
Fly	2389	2.83
Nest Build	945	1.12
Sit	827	0.98
Walk or Run	743	0.88
Courtship	558	0.66
Tuck	216	0.26
Aggression	108	0.13
Courtship Feed	61	0.07
Nest Relief	41	0.05
Total	84420	100

Table 2. Percent (simultaneous 95% confidence intervals) of time spent incubating, brooding, preening, and standing by Least Terns at Wrightsville Beach, North Carolina, during the 2004 and 2005 nesting seasons (N = 469 three-minute observation periods). Time Blocks: M = morning, A = afternoon, E = evening; Temperature: C = cool, M = moderate, W = warm; Cloud Cover: F = fair, PC = partly cloudy, C = cloudy; Wind Speed: L = light, M = moderate, S = strong.

Behavior	Time Block	%	Interval	Temp	%	Interval	Cloud Cover	%	Interval	Wind Speed	%	Interval
Incubate	M	73.20	(72.50-73.90)	C	78.10	(77.60-78.70)	F	76.90	(76.30-77.60)	L	64.50	(63.20-65.70)
	A	75.50	(74.80-76.20)	M	72.00	(71.40-72.70)	PC	70.50	(69.70-71.30)	M	76.80	(76.20-77.40)
	E	73.10	(72.30-73.90)	W	49.50	(47.20-51.90)	C	70.80	(69.80-71.80)	S	71.40	(70.60-72.10)
Brood	M	11.10	(10.60-11.60)	C	7.72	(7.34-8.10)	F	6.38	(6.00-6.76)	L	9.87	(9.06-10.70)
	A	10.60	(10.10-11.10)	M	12.10	(11.60-12.50)	PC	12.00	(11.40-12.50)	M	7.70	(7.32-8.08)
	E	7.92	(7.43-8.41)	W	12.00	(10.40-13.50)	C	14.80	(14.00-15.60)	S	14.50	(13.90-15.10)
Preen	M	5.97	(5.56-6.37)	C	5.63	(5.30-5.96)	F	6.92	(6.53-7.31)	L	17.20	(16.20-18.20)
	A	7.32	(6.90-7.75)	M	5.31	(4.99-5.63)	PC	6.79	(6.37-7.21)	M	3.06	(2.82-3.31)
	E	4.99	(4.60-5.38)	W	21.20	(19.30-23.10)	C	4.87	(4.39-5.34)	S	6.95	(6.52-7.38)
Stand	M	1.59	(1.38-1.81)	C	2.66	(2.43-2.88)	F	3.83	(3.53-4.12)	L	2.66	(2.22-3.09)
	A	3.67	(3.37-3.98)	M	4.44	(4.15-4.74)	PC	3.94	(3.62-4.27)	M	5.14	(4.83-5.46)
	E	6.22	(5.78-6.65)	W	8.07	(6.80-9.35)	C	3.01	(2.64-3.39)	S	2.62	(2.35-2.89)

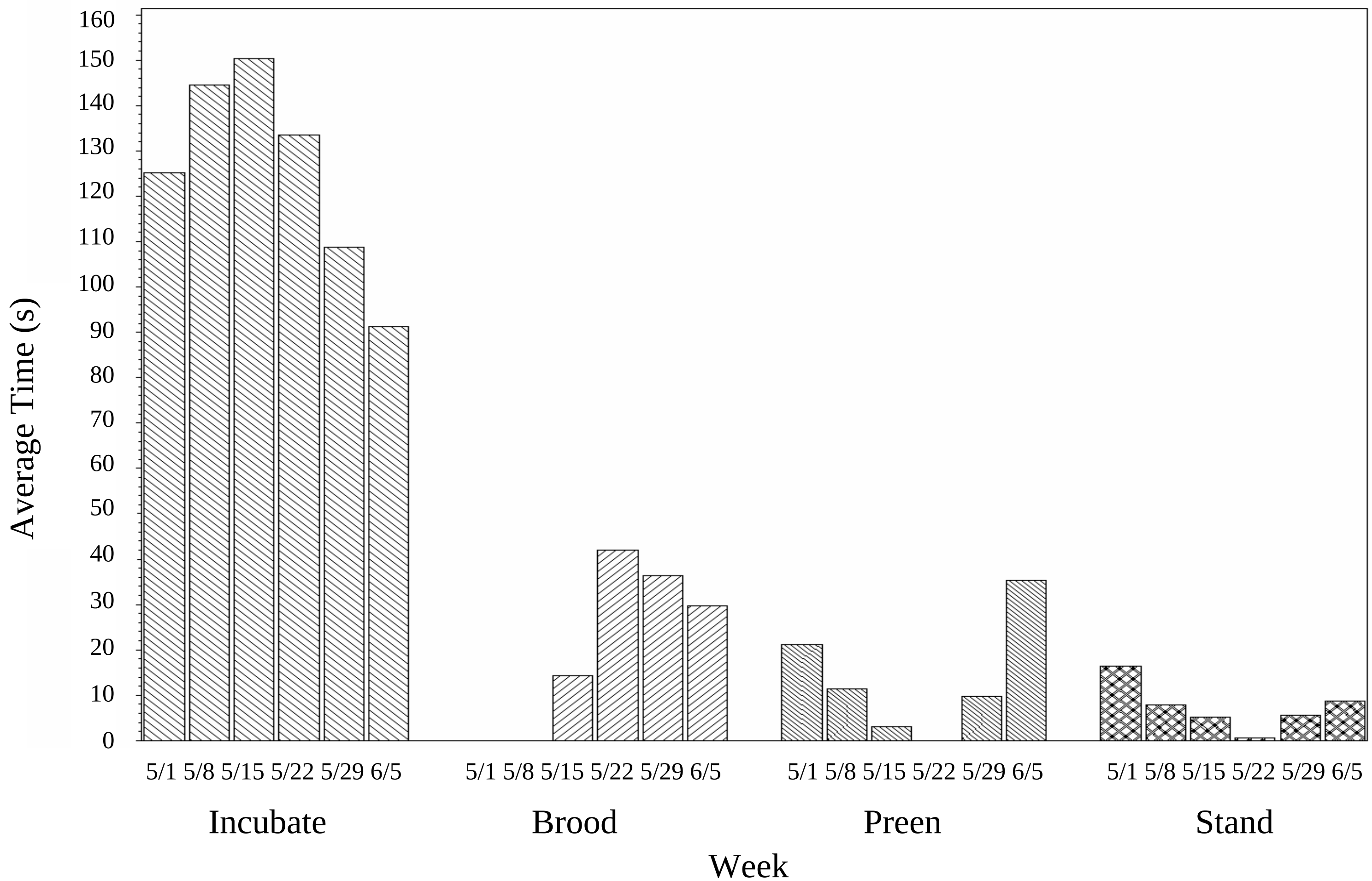

Figure 2. Average amount of time in seconds that Least Terns spent incubating, brooding, preening, and standing at Wrightsville Beach, North Carolina, over six weeks of the 2004 and 2005 nesting seasons (weeks aligned to the 2005 calendar year).

behavior peaked in the third week just as brooding behavior observations began. The majority of preening and standing behavior was observed in the first and last weeks of the nesting season, with little to none in the middle of the nesting season.

Black Skimmer Time-Activity Budget

A total of 786 Black Skimmer time-activity budget observations was taken over both nesting seasons (Table 3). Black Skimmers spent most of their time standing and incubating. The next highest categories were brooding, tucking, sitting, preening, and walking or running. Five other behavior categories together totaled only 3.16% of their entire nesting budget; courtship feeding was not observed. Of the 242 birds observed incubating, 236 performed one incubation bout, five birds performed two bouts, and only one bird performed three incubation bouts, for a mean of 1.03 for both sexes combined.

A total of 398 male and 385 female Black Skimmers were observed over the 2004 and 2005 nesting seasons. Three birds could not be accurately sexed and therefore were not included in the intersexual comparisons. The overall time-activity budgets of male and female Black Skimmers were significantly different ($\chi^2_{11} = 646.02$, $P < 0.0001$). Both sexes spent nearly identical amounts of time incubating, walking or running, and in aggressive acts; however, males spent significantly more time standing, sitting, preening, nest building, and engaging in nest relief, whereas females spent significantly more time brooding, tucking, flying, and in courtship activities (Table 4). The mean number of incubation bouts was 1.03 for each sex. Females were observed with their mate 45.66% of the time compared to 52.25% for males ($\chi^2_1 = 1.52$, n.s.). The overall percentage of time Black Skimmers were seen with their mates was 49.00%.

The chief categories of incubation, standing, brooding, tucking, sitting, preening, and walking or running were analyzed against time of day, air temperature, cloud cover, and wind

Table 3. Black Skimmer time-activity budget at Wrightsville Beach, North Carolina, during the 2004 and 2005 nesting seasons (N = 786 three-minute observation periods).

Behavior	Time (seconds)	% of Time
Stand	40827	28.86
Incubate	40599	28.70
Brood	22257	15.73
Tuck	13361	9.45
Sit	8466	5.98
Preen	7057	4.99
Walk or Run	4411	3.12
Fly	2023	1.43
Courtship	1283	0.91
Nest Build	700	0.49
Nest Relief	344	0.24
Aggression	132	0.09
Courtship Feed	0	0.00
Total	141460	99.99

Table 4. Percent (simultaneous 95% confidence intervals) of time spent in behaviors by male and female Black Skimmers at Wrightsville Beach, North Carolina, during the 2004 and 2005 nesting seasons (N = 398 males, N = 385 females).

	Males		Females	
Behavior	Percent	Interval	Percent	Interval
Stand	30.00	(29.60-30.50)	27.90	(27.40-28.30)
Incubate	29.00	(28.50-29.50)	28.30	(27.90-28.80)
Brood	14.80	(14.40-15.10)	16.90	(16.50-17.30)
Tuck	8.15	(7.86-8.43)	10.30	(10.00-10.70)
Sit	6.34	(6.08-6.60)	5.66	(5.42-5.91)
Preen	5.49	(5.25-5.73)	4.51	(4.29-4.73)
Walk or Run	3.26	(3.07-3.45)	2.99	(2.81-3.18)
Fly	1.30	(1.18-1.42)	1.57	(1.44-1.70)
Courtship	0.66	(0.58-0.75)	1.17	(1.05-1.28)
Nest Build	0.63	(0.54-0.71)	0.36	(0.30-0.43)
Nest Relief	0.30	(0.25-0.36)	0.18	(0.14-0.23)
Aggression	0.07	(0.04-0.10)	0.12	(0.08-0.16)

speed. Significant interactions were found between sex and the above categories, hence separate confidence intervals were generated for males and females. Males and females spent significantly different amounts of time in behaviors during the morning, afternoon, and evening time blocks (χ^2_{22} = 2,390.57, P < 0.0001; Table 5). The majority of male brooding behavior was seen in the morning, the majority of standing and incubating were seen in the afternoon, and the majority of preening was seen in the evening. Female brooding behavior was most often observed in the morning, incubating was most often seen in the afternoon, and standing and preening were most often seen in the evening. Males were observed sitting significantly more in the evening than were females. Tucking behavior was scarcely observed in the afternoon for either sex.

Male and female Black Skimmer behavior varied significantly during cool, moderate, and warm temperatures (χ^2_{22} = 1,198.01, P < 0.0001; Table 6). The majority of male standing, tucking, and walking or running behavior was observed during cool temperatures, the majority of preening behavior during moderate temperatures, and the majority of incubating during warm temperatures. Male brooding behavior was not observed in cool temperatures. The majority of female tucking, preening, and walking or running was observed during cool temperatures, whereas the majority of incubating, brooding, and standing was observed during warm temperatures. Females were much more likely to be seen incubating in cool weather than were males.

Male and female Black Skimmer behavior varied significantly under different cloud cover conditions (χ^2_{22} = 1,770.22, P < 0.0001; Table 7). The majority of male standing behavior versus the least amount of sitting was observed under fair conditions. The majority of male incubating and preening behavior was seen under partly cloudy skies. Male brooding behavior

Table 5. Percent (simultaneous 95% confidence intervals) of time spent in behaviors by male and female Black Skimmers during morning (0600-0900), afternoon (1100-1400), and evening (1600-1900) time blocks at Wrightsville Beach, North Carolina, during the 2004 and 2005 nesting seasons (N = 398 male, N = 385 female three-minute observation periods).

		Males		Females	
Behavior	Time	Percent	Interval	Percent	Interval
Stand	Morning	27.70	(26.90-28.60)	27.10	(20.80-22.50)
	Afternoon	34.10	(33.30-35.00)	27.70	(26.90-28.50)
	Evening	27.90	(27.10-28.70)	31.60	(30.70-32.40)
Incubate	Morning	20.70	(19.90-21.50)	20.20	(19.40-21.00)
	Afternoon	37.60	(36.70-38.50)	38.40	(37.50-39.20)
	Evening	28.30	(27.50-29.10)	26.00	(25.20-26.80)
Brood	Morning	22.90	(22.10-23.70)	23.30	(22.50-24.10)
	Afternoon	12.10	(11.50-12.70)	17.30	(16.70-18.00)
	Evening	11.20	(10.60-11.70)	12.20	(11.60-12.80)
Tuck	Morning	10.40	(9.86-11.00)	16.20	(15.50-16.90)
	Afternoon	3.30	(2.97-3.62)	1.04	(0.86-1.22)
	Evening	9.57	(9.04-10.10)	14.80	(14.20-15.50)
Sit	Morning	4.87	(4.46-5.28)	5.85	(5.38-6.32)
	Afternoon	4.67	(4.29-5.05)	7.36	(6.90-7.83)
	Evening	9.53	(9.01-10.10)	3.49	(3.15-3.83)
Preen	Morning	6.42	(5.95-6.88)	3.93	(3.54-4.31)
	Afternoon	1.75	(1.51-1.98)	3.31	(2.99-3.64)
	Evening	8.59	(8.08-9.09)	6.42	(5.97-6.87)
Walk or Run	Morning	3.70	(3.34-4.06)	4.08	(3.68-4.47)
	Afternoon	3.21	(2.90-3.53)	2.34	(2.07-2.61)
	Evening	2.70	(2.41-2.99)	2.73	(2.43-3.03)

Table 6. Percent (simultaneous 95% confidence intervals) of time spent in behaviors by male and female Black Skimmers during cool (<23°C), moderate (23-28°C), and warm (>28°C) temperatures at Wrightsville Beach, North Carolina, during the 2004 and 2005 nesting seasons (N = 398 male, N = 385 female three-minute observation periods).

		Males		Females	
Behavior	Temperature	Percent	Interval	Percent	Interval
Stand	Cool	38.00	(36.10-40.00)	25.40	(23.80-27.10)
	Moderate	27.00	(26.40-27.70)	27.30	(26.70-28.00)
	Warm	33.20	(32.40-34.10)	29.10	(28.30-29.90)
Incubate	Cool	14.30	(12.90-15.70)	30.60	(28.80-32.30)
	Moderate	29.20	(28.60-29.80)	25.80	(25.10-26.40)
	Warm	31.60	(30.80-32.40)	31.50	(30.70-32.30)
Brood	Cool	0.00		6.67	(5.71-7.62)
	Moderate	16.20	(15.70-16.70)	16.80	(16.30-17.40)
	Warm	15.40	(14.80-16.00)	19.00	(18.30-19.70)
Tuck	Cool	26.60	(24.90-28.40)	16.10	(14.70-17.50)
	Moderate	8.03	(7.65-8.40)	13.50	(13.00-14.00)
	Warm	4.70	(4.33-5.07)	4.85	(4.48-5.22)
Sit	Cool	7.28	(6.25-8.31)	6.94	(5.97-7.92)
	Moderate	7.07	(6.71-7.42)	4.40	(4.10-4.70)
	Warm	4.99	(4.61-5.37)	7.15	(6.71-7.60)
Preen	Cool	4.86	(4.01-5.71)	7.06	(6.08-8.03)
	Moderate	6.82	(6.47-7.17)	5.18	(4.86-5.51)
	Warm	3.49	(3.17-3.81)	3.06	(2.77-3.36)
Walk or Run	Cool	5.44	(4.54-6.33)	4.50	(3.71-5.29)
	Moderate	2.99	(2.76-3.23)	3.26	(3.00-3.52)
	Warm	3.26	(2.95-3.57)	2.32	(2.07-2.58)

Table 7. Percent (simultaneous 95% confidence intervals) of time spent in behaviors by male and female Black Skimmers during fair (<2/8), partly cloudy (2/8-5/8), and cloudy (>5/8) conditions at Wrightsville Beach, North Carolina, during the 2004 and 2005 nesting seasons (N = 398 male, N = 385 female three-minute observation periods).

		Males		Females	
Behavior	Cloud Cover	Percent	Interval	Percent	Interval
Stand	Fair	33.50	(32.60-34.30)	27.30	(26.50-28.20)
	Partly Cloudy	26.60	(25.80-27.50)	29.70	(28.90-30.60)
	Cloudy	29.90	(29.20-30.70)	26.70	(25.90-27.50)
Incubate	Fair	26.30	(25.50-27.10)	23.10	(22.30-23.90)
	Partly Cloudy	32.50	(31.60-33.40)	31.90	(31.00-32.70)
	Cloudy	28.40	(27.70-29.20)	30.00	(29.20-30.80)
Brood	Fair	15.00	(14.30-15.70)	25.60	(24.80-26.50)
	Partly Cloudy	15.50	(14.80-16.20)	13.50	(12.90-14.20)
	Cloudy	13.90	(13.40-14.50)	11.80	(11.30-12.40)
Tuck	Fair	10.60	(10.00-11.20)	8.12	(7.60-8.63)
	Partly Cloudy	4.41	(4.02-4.79)	8.73	(8.20-9.27)
	Cloudy	9.15	(8.65-9.64)	13.80	(13.20-14.40)
Sit	Fair	3.66	(3.31-4.01)	4.05	(3.68-4.42)
	Partly Cloudy	8.22	(7.70-8.74)	7.56	(7.06-8.06)
	Cloudy	7.03	(6.60-7.47)	5.43	(5.03-5.84)
Preen	Fair	4.83	(4.43-5.23)	5.38	(4.96-5.80)
	Partly Cloudy	7.12	(6.63-7.60)	3.91	(3.54-4.28)
	Cloudy	4.71	(4.35-5.08)	4.25	(3.89-4.61)
Walk or Run	Fair	3.09	(2.77-3.42)	2.68	(2.38-2.99)
	Partly Cloudy	3.05	(2.72-3.37)	2.43	(2.14-2.72)
	Cloudy	3.57	(3.26-3.89)	3.78	(3.44-4.12)

was not associated with cloud cover whereas females were seen brooding their chicks significantly more under fair conditions. The majority of female incubation behavior, standing, and sitting was observed under partly cloudy skies. Females were much more likely to be seen tucking under cloudy conditions compared to fair conditions for males. Walking or running behavior in males or females was not influenced by cloud cover.

Male and female Black Skimmer behavior varied significantly under differing wind speeds (χ^2_{22} = 1,072.97, P < 0.0001; Table 8). Male brooding behavior and walking or running were observed more in light winds whereas standing, incubating, and tucking were observed less in light winds. Males were more likely to be seen preening or brooding their chicks in light winds than were females. Female sitting and walking or running behavior were observed more in light winds, standing and preening behavior were seen significantly more in moderate winds, and incubating and brooding were seen significantly more in strong winds. Female tucking behavior was not associated with wind speed.

Black Skimmer male (χ^2_{77} = 25,236.39, P < 0.0001) and female (χ^2_{77} = 23,628.17, P < 0.0001) behavior varied significantly by week. Weekly changes in the average amount of time males and females spent in various activities over eight weeks of the 2004 and 2005 nesting seasons are shown in Figure 3 and Figure 4, respectively. Male incubation behavior was most abundant in weeks two through six and decreased as brooding behavior increased. A similar trend was seen in the incubating and brooding behavior of females. Incubation peaked at week four for females, which was followed by the initiation of brooding behavior in week five. Male Black Skimmers were observed sitting significantly more in the first week than were females. Tucking behavior of males and females also differed, in that males were observed tucking the

Table 8. Percent (simultaneous 95% confidence intervals) of time spent in behaviors by male and female Black Skimmers in light (<6.5 km/h), moderate (6.5-14.5 km/h), and strong (>14.5 km/h) wind at Wrightsville Beach, North Carolina, during the 2004 and 2005 nesting seasons (N = 398 male, N = 385 female three-minute observation periods).

		Males		Females	
Behavior	Wind Speed	Percent	Interval	Percent	Interval
Stand	Light	15.60	(14.10-17.10)	24.80	(23.10-26.60)
	Moderate	30.30	(29.60-30.90)	30.40	(29.80-31.10)
	Strong	32.50	(31.70-33.30)	25.50	(24.70-26.20)
Incubate	Light	24.00	(22.20-25.80)	21.90	(20.20-23.60)
	Moderate	29.90	(29.20-30.50)	28.40	(27.70-29.00)
	Strong	28.30	(27.50-29.10)	30.70	(29.90-31.50)
Brood	Light	33.10	(31.10-35.10)	15.20	(13.70-16.60)
	Moderate	11.70	(11.20-12.10)	13.00	(12.50-13.40)
	Strong	15.30	(14.70-15.90)	19.80	(19.10-20.50)
Tuck	Light	5.76	(4.78-6.73)	9.46	(8.26-10.70)
	Moderate	9.07	(8.66-9.48)	10.30	(9.84-10.70)
	Strong	7.86	(7.39-8.32)	11.20	(10.60-11.70)
Sit	Light	7.18	(6.10-8.26)	8.54	(7.39-9.69)
	Moderate	6.17	(5.83-6.51)	5.91	(5.56-6.25)
	Strong	6.98	(6.53-7.42)	5.11	(4.73-5.50)
Preen	Light	6.93	(5.87-8.00)	2.89	(2.20-3.58)
	Moderate	6.50	(6.15-6.85)	6.06	(5.71-6.40)
	Strong	4.11	(3.77-4.46)	2.74	(2.45-3.02)
Walk or Run	Light	5.24	(4.31-6.18)	6.78	(5.75-7.82)
	Moderate	3.29	(3.04-3.54)	2.98	(2.73-3.23)
	Strong	2.95	(2.65-3.24)	2.44	(2.18-2.71)

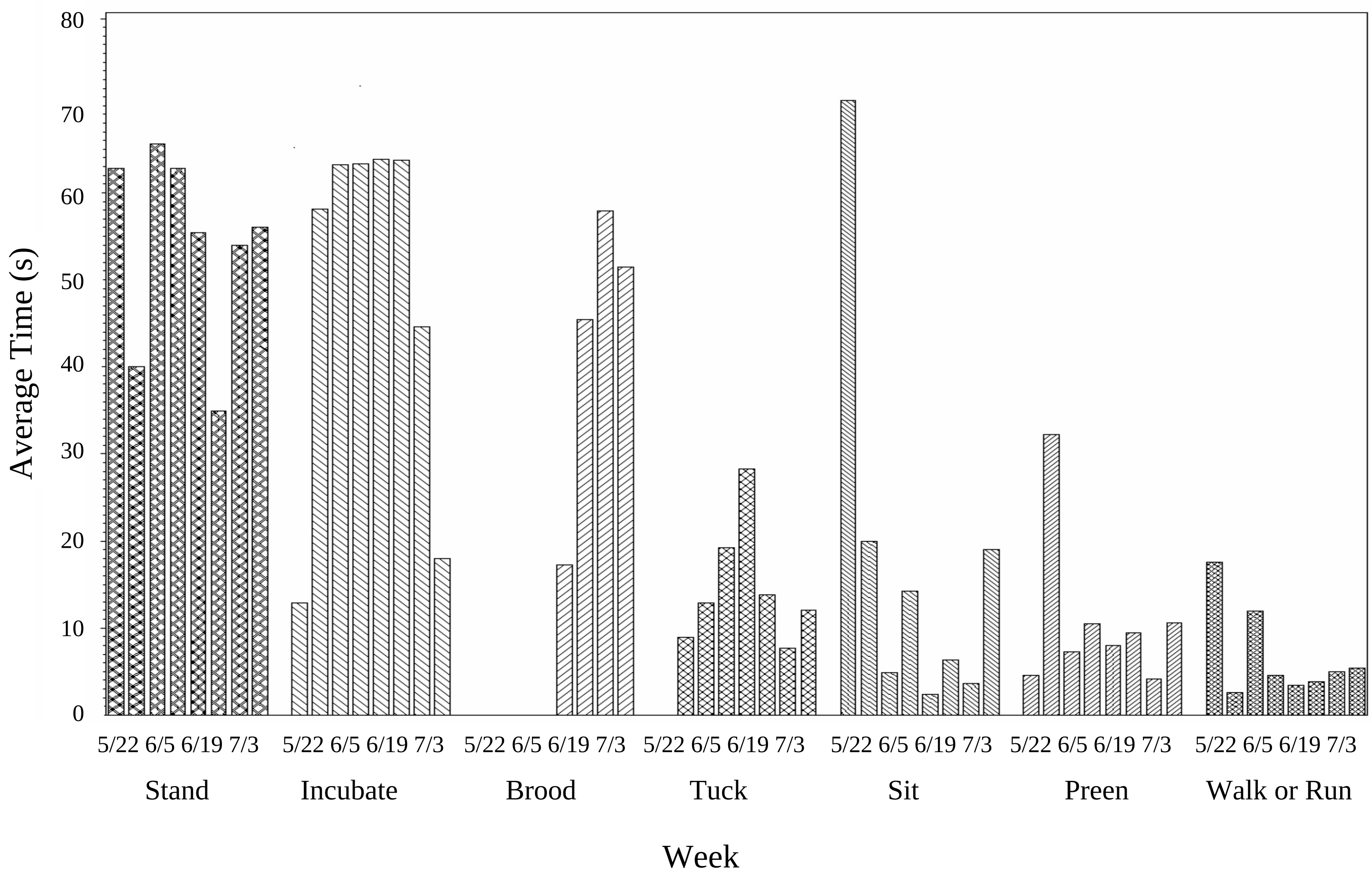

Figure 3. Average amount of time in seconds that male Black Skimmers spent standing, incubating, brooding, tucking, sitting, preening, and walking or running at Wrightsville Beach, North Carolina, over eight weeks of the 2004 and 2005 nesting seasons (weeks aligned to the 2005 calendar year).

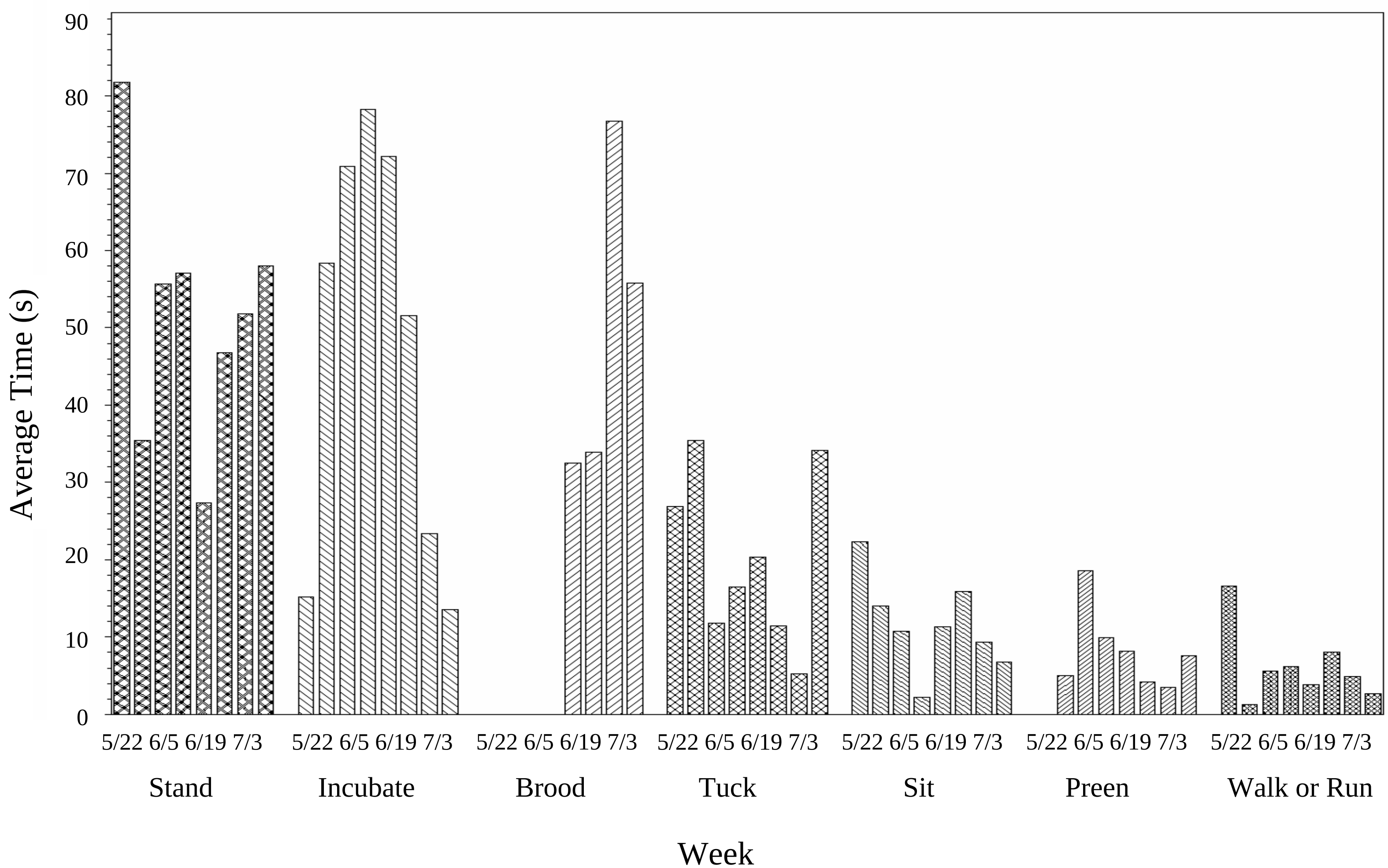

Figure 4. Average amount of time in seconds that female Black Skimmers spent standing, incubating, brooding, tucking, sitting, preening, and walking or running at Wrightsville Beach, North Carolina over eight weeks of the 2004 and 2005 nesting seasons (weeks aligned to the 2005 calendar year).

most in the middle of the season whereas females were observed tucking the most early and late in the season.

Least Tern Versus Black Skimmer Time-Activity Budgets

Least Terns and Black Skimmers had significantly different time-activity budgets during the nesting seasons (χ^2_{12} = 54,264.13, P < 0.0001; Table 9). Significant differences also were found between the time-activity budgets of Least Terns and female Black Skimmers (χ^2_{11} = 43,374.77, P < 0.0001) and male Black Skimmers (χ^2_{11} = 42,932.99, P < 0.0001; data not shown). Least Terns spent significantly more time than Black Skimmers incubating, preening, flying, and nest building. Black Skimmers spent significantly more time than Least Terns brooding, standing, tucking, sitting, walking or running, courting, and engaging in nest relief. There was no significant difference in the amount of time spent in aggressive acts by either species. Furthermore, Least Terns displayed courtship feeding 13 times, whereas it was not observed at all in Black Skimmers. Another behavioral difference was found in nest relief, where Black Skimmers were observed relieving their mates at the nest 41 times, compared to only five times with Least Terns.

DISCUSSION

The amount of time allocated to various behaviors by Least Terns and Black Skimmers changed over the course of their respective nesting seasons. In both species, incubation peaked in the middle of each season, followed by brooding, with the majority of other behaviors performed at the beginning and end of their nesting activities. Compared to Black Skimmers, Least Terns were more synchronized in their nesting activities and their peak nesting occurred two to three weeks earlier.

Table 9. Percent (simultaneous 95% confidence intervals) of time spent in behaviors by Least Terns and Black Skimmers at Wrightsville Beach, North Carolina, during the 2004 and 2005 nesting seasons (N = 469 Least Terns, N = 786 Black Skimmer three-minute observation periods).

	Least Terns		Black Skimmers	
Behavior	Percent	Interval	Percent	Interval
Incubate	72.90	(72.50-73.40)	28.70	(28.40-29.0)
Brood	9.54	(9.26-9.83)	15.70	(15.50-16.00)
Preen	6.66	(6.42-6.90)	4.99	(4.83-5.15)
Stand	3.96	(3.77-4.15)	28.90	(28.50-29.20)
Tuck	0.26	(0.21-0.30)	9.45	(9.23-9.66)
Sit	0.98	(0.89-1.08)	5.98	(5.81-6.16)
Walk or Run	0.88	(0.79-0.97)	3.12	(2.99-3.25)
Fly	2.83	(2.67-2.99)	1.43	(1.34-1.52)
Courtship	0.66	(0.58-0.74)	0.91	(0.84-0.98)
Nest Build	1.12	(1.02-1.22)	0.49	(0.44-0.55)
Nest Relief	0.05	(0.03-0.07)	0.24	(0.21-0.28)
Aggression	0.13	(0.09-0.16)	0.09	(0.07-0.12)

Despite these generalities, nesting Least Terns and Black Skimmers had different time-activity budgets. For example, Least Terns spent more time incubating and involved in courtship feeding than did Black Skimmers. Compared to Least Terns, Black Skimmers spent more time standing and sitting with their mates and engaging in nest relief. Also, Least Terns were rarely observed with their mates whereas nearly half of all Black Skimmer observations consisted of birds with their mates.

Both male and female Black Skimmers engaged in all parental duties, sharing incubation equally in the Mason Inlet colony. However, males incubated significantly more than did females at a colony in New Jersey (Burger 1981b). This difference may indicate yearly or geographic variability between sexes, or it may be a result of different sampling methods. By video recording all observations I was able to view behavioral sequences repeatedly, allowing identification of specific behaviors, such as the brief courtship feeding bouts of Least Terns, which might have been overlooked by an observer who was looking at a watch or field notebook rather than the focal bird. In this case, it is doubtful that the difference in Black Skimmer incubation is the result of sampling methodology, so perhaps incubation responsibilities vary across time or space.

Male Black Skimmers engaged in nest relief more often than did females, and due to their larger body size males were more successful than females at forcing their partners off the nest in order to assume incubation duties (Burger 1981b). However, not all Black Skimmer behaviors differed between the sexes. For example, Black Skimmers of both sexes were often observed standing next to their incubating mate, hence the high overall percentage of standing behavior. Courtship feeding was not observed, which suggests that birds forage independently of their mate. Black Skimmers frequently forage at night (Erwin 1977), which allows them more time to be present at the colony during the day to help with nest protection and engage in nest relief. Overall, nesting male and female Black Skimmers exhibited high levels of parental investment.

It was not possible to determine the sex of individual Least Terns in this study, but birds were rarely present with their mates at their nesting sites except during courtship, nest building activities, courtship feeding bouts, nest relief, and occasionally during brooding. In studies where the sex of individual Least Terns was known, females spent significantly more time on their nests than did males and males fed females at the nest (Davis 1974, Massey 1974, Keane 1987). Thus, females probably performed most of the incubation duties in the Mason Inlet colony, while males foraged and performed courtship feeding of the females. Moreover, nest relief was observed only five times over two nesting seasons, providing further evidence that the sexes do not share incubation duties equally. Energetic costs associated with incubation are low compared to those associated with other stages of the breeding cycle (Walsberg 1983). Therefore, in terms of parental investment, male Least Terns behave like male Common Terns (Wiggins and Morris 1986) in that males of both species contribute equal, if not more, reproductive effort by allocating considerable energy to foraging and feeding the female while she incubates the eggs.

Since Least Terns and Black Skimmers are monogamous and both sexes invest either directly or indirectly in the care of eggs and chicks, it is not clear why sexual size dimorphism evolved in one species and not the other. Again, sexual selection theory predicts that with increasing competition for mates, the relative size of the more competitive sex should increase. Furthermore, if differences in body size better equip one sex for certain duties, a greater division of labor would be expected in dimorphic species. In this study, the monomorphic species (Least Tern) exhibited a greater division of labor than the dimorphic species (Black Skimmer). This result may be explained by the aerial agility hypothesis, which states that type of courtship display moderates differences in body size between the sexes (Jehl and Murray 1986). For instance, monogamous male shorebirds that perform acrobatic aerial displays in courtship and aggression show reversed or a lack of sexual size dimorphism (Jehl and Murray 1986, Sandercock 2001).

Least Tern courtship includes a fish flight display, where a male is pursued by one to four other terns, and is followed by an aerial glide and a ground phase as the male approaches the female (Wolk 1974, Thompson *et al*. 1997). Smaller body size increases male agility and conveys important information to the female concerning his provisioning abilities. Least Terns are plunge divers, hence their foraging is based on visual cues and therefore limited to daylight hours. Smaller body size leads to increased foraging efficiency while decreasing competition for food with other tern species. Least Terns also exhibit aerial displays in aggression and antipredator behavior. They use intimidation responses and mobbing behavior in response to threats. When eggs and chicks are vulnerable to predation, adults dive and attack intruding predators (Burger 1989). Thus, smaller body size improves flight agility in courtship, foraging, and aggression, which possibly explains the lack of dimorphism in Least Terns.

The aerial agility hypothesis does not apply to Black Skimmers. Black Skimmer courtship lacks an elaborate aerial display and is characterized by a male simply presenting a fish or the gift of a leaf or a twig for the female to hold during copulation (Gochfeld and Burger 1994). Furthermore, Black Skimmers are surface skimmers so their foraging strategy is tactile and less active than Least Terns. Hence, a larger body size in males would not be as much of a detriment as it would for Least Terns. In addition, Black Skimmers do not usually exhibit extensive mobbing behavior and are more likely to use ground attacks and distraction displays when threatened (Gochfeld and Burger 1994). Black Skimmers may gain protection by nesting near birds such as terns that provide early warning of intruders and utilize intense mobbing behavior (Gochfeld and Burger 1994, Pius and Leberg 1998).

Since Black Skimmers do not have an elaborate aerial courtship ritual or foraging strategy, and do not exhibit mobbing behavior to the same extent as do Least Terns, male body size may have increased through sexual selection via competition for females. Females may assess male health and viability on the basis of body size. Males of large body size contribute to territory and nest protection and have also been shown to bring back larger fish to chicks (Quinn 1990). Therefore, sexual dimorphism in Black Skimmers may be merely a product of sexual selection.

Although time of day, temperature, cloud cover, and wind speed influenced Least Tern and Black Skimmer behavior during the nesting season, most of these effects were not particularly critical to the overall results of the study. For example, since Least Terns nest before Black Skimmers, Least Tern incubation behavior was associated with cooler ambient temperatures early in the nesting season, while Black Skimmer incubation behavior was associated with warmer ambient temperatures later in the nesting season. Also, as might be predicted, preening behavior was most often observed during light than strong winds in both species.

In future studies, Least Terns would need to be sexed and marked with colored dye to provide additional support for the division of labor observed in this study. Also, nocturnal time-activity budget studies of nesting Least Terns and Black Skimmers would be necessary to investigate whether their unequal and equal division of labor, respectively, exists through all hours of the day.

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