DAILY ACTIVITY PATTERNS OF SOUTH POLAR AND BROWN SKUAS NEAR PALMER STATION, ANTARCTICA

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ABSTRACT.—I conducted a behavioral study of sympatrically nesting South Polar (*Catharacta maccormicki*) and Brown skuas (*C. lonnbergi*) near Palmer Station, Antarctica. A total of 4,058 bird-hours of observations was made on eight South Polar, three Brown, and one mixed-species pair during the 1979–1980 and 1980–1981 austral summers. I used subsets of these data to analyze various aspects of skua activity patterns.

South Polar Skuas exhibited maximum resting and minimum foraging activity during the twilight period around 2400. Brown Skuas appeared to rest and forage more randomly. Members of the mixed pair exhibited patterns similar to those of their respective species. Several hypotheses are suggested to account for species differences in activity patterns; most of these relate dietary differences and differential foraging abilities at low light levels.

In both species, agonistic and preening activities occurred at all hours. South Polar Skuas, however, were most often observed bathing in early afternoon and preening in afternoon and twilight. Pairing activity showed no discernible relationship with time.

Foraging bouts averaged 13 min for Brown Skuas with feeding territories and about 1 h for those without. South Polar Skuas averaged feeding trips of 2–3 h when the sea was open and over 7 h during heavy ice cover.

The timing of an individual's activity was correlated negatively with that of its mate during incubation, brooding, and postbrooding. A nonbreeding pair and breeders that had suffered nest failure showed more positive correlations. Thus, individual activity patterns were shaped by reproductive priorities as well as by feeding ecology and light levels. *Received 13 March 1985, accepted 18 March 1986.*

AN extensive literature exists on the relationship between daily activity patterns of birds and various light regimes (see reviews by Aschoff 1967, Daan and Aschoff 1975, Gwinner 1975, Rusak 1981). Nevertheless, little research has been done on activity patterns of birds under natural conditions of continuous light, as occurs in polar regions in summer. Three decades ago, Armstrong (1954) noted that such information from arctic regions was meagre, while that from the Antarctic was too scarce to warrant discussion. Since then, antarctic researchers have examined activity patterns of Adélie Penguins (*Pygoscelis adeliae*; Muller-Schwarze 1968), Blue-eyed Shags (*Phalacrocorax atriceps*; Bernstein and Maxson 1984), and Southern Black-backed Gulls (*Larus dominicanus*; Maxson and Bernstein 1984, Fraser pers. comm.). Literature on skuas in Antarctica contains only an incidental comment on timing of activity (Spellerberg 1969).

At Palmer Station (64°46′S, 64°03′W) on Anvers Island, Antarctica, I had an opportunity to observe South Polar (*Catharacta maccormicki*) and

Brown skuas (*C. lonnbergi*)[1] where they nest sympatrically and occasionally form mixed pairs. Investigations of allopatric populations suggest that the activity patterns of these species are very different. Spellerberg (1969) noted that South Polar Skuas on Ross Island (77°33′S, 166°09′E), the southern extreme of their breeding range, showed a 24-h cycle of activity even during continuous daylight: "Between 01:00 and 05:00 ... all breeding pairs are roosting, incubating, or brooding and little or no foraging takes place." On the other hand, Young (1978) documented Brown Skuas feeding regularly during hours of darkness on the Chatham Islands, New Zealand (44°22′S, 176°11′W).

STUDY AREA AND METHODS

This study was conducted during the 1979–1980 and 1980–1981 austral summers on several small is-

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[1] Pending resolution of their taxonomic status, I refer to these as separate species. For discussions of skua systematics and nomenclature, see Pietz (1984, 1985).

lands and peninsulas within 5 km of Palmer Station, Antarctica. The ice-free areas provided nesting sites for nearly a dozen bird species (Parmelee et al. 1977), including South Polar Skuas (approx. 250 pairs) and Brown Skuas (up to 12 pairs). From late November to late January there is enough light at Palmer to conduct fieldwork 24 hours a day, despite the fact that the sun dips below the horizon for a short period around 2400.

Skuas were color-banded to allow recognition of individuals at a distance. Most of these birds had been banded in previous years and thus had documented breeding histories. Sexes of birds were determined by copulatory position and courtship feeding.

Skua feeding habits also had been documented at Palmer in previous years (Parmelee et al. 1978, Neilson 1983). Brown Skuas here, as in many other areas (e.g. Stonehouse 1956, Moors 1980, Sinclair 1980, Trivelpiece et al. 1980), concentrated on penguin eggs and chicks and sometimes defended penguin colonies near their nests as feeding territories. Some South Polar Skuas feed on penguins in areas where Brown Skuas are few (Parmelee pers. comm.) or absent (e.g. Eklund 1961, Le Morvan et al. 1967, Trillmich 1978). At Palmer, however, most South Polars fed at sea on fish and krill, a common habit in much of their range (Eklund 1961, Young 1963, Trivelpiece and Volkman 1982).

Between 8 December 1979 and 22 January 1980, we documented the behavior of 4 South Polar Skua pairs, 2 Brown Skua pairs, and 1 mixed-species pair. A total of 50 bird-days of observations was obtained for South Polar Skuas, 14 for Brown Skuas, and 8 for the mixed pair. All were observed for 24-h periods.

Between 27 January and 9 March 1980, when increasing darkness prevented 24-h observations, we watched each of the 7 pairs for 6 dawn-to-dusk periods. From 7 January to 6 March 1981, I made additional observations using sample periods of 3–14 h. Eight South Polar Skua pairs, 2 Brown Skua pairs, and 1 mixed pair constituted the sample in the second season. The mixed pair, 1 of the Brown, and 4 of the South Polar pairs were observed in both years.

During all observation periods, the behavior of each bird was noted every 30 s using a metronome (Wiens et al. 1970). From these observations hourly and daily time budgets were constructed for each individual.

Only data collected during 24-h observation periods of the 1979–1980 season (1,691 bird-hours) were used for assessing relationships between activities and time of day. For resting and foraging behaviors, the mean and standard error were calculated by hour for each individual and for each pair. Weighted hourly means were determined for both species using pair data, and for each sex of both species using individual data. Mean hourly standard error estimates were weighted across individual or pair standard errors

that had been pooled over the 24 h. Finally, weighted hourly means were used to calculate angular-linear correlations (Johnson and Wehrly 1977), in a test for 24-h patterns related to either sine or cosine functions.

Agonistic, preening, bathing, and pairing behaviors occurred too rarely to examine variation among individuals or pairs. For each of the first three of these behavioral groups, data on all individuals from all observation days were combined by hour within species. For pairing behaviors, only data for the male of each pair were combined.

Dawn-to-dusk observations from 1980 (1,406 bird-hours) and the shorter observation periods of 1981 (805 bird-hours) were included only in calculating lengths of foraging trips (or time away from the nest territory) and in evaluating correlations of activity between pair members.

Activity correlations between pair members were assessed for 3,860 bird-hours of observations on 8 South Polar, 3 Brown, and 1 mixed skua pairs over two seasons. Behavioral data were sampled from the time budgets once every 30 min, at the end of each 30-min interval. For each pair at each stage of the breeding cycle, I constructed a 2 × 2 contingency table and tabulated presence or absence of a specified behavior by the male and the female. Product moment correlation coefficients and their standard errors were calculated for each table (Bishop et al. 1975); the weighted means of these coefficients, with their associated error terms, were calculated across pairs for each species.

For the purposes of these analyses, the breeding season was divided into (1) pre-egg-laying, (2) incubation (from the time the first egg was laid), (3) brooding (from the hatching of the first chick until it was no longer regularly brooded), (4) postbrooding (until the time the first chick flew well enough to avoid capture), and (5) fledging. A sixth category (failed-nest) contained observations on pairs following loss of eggs or chicks.

Of the 4 South Polar Skua pairs observed in 1979–1980, 1 courted and defended a territory but failed to produce eggs. For purposes of comparison with the three breeding pairs, this pair's season was divided into sections reflecting the average timing of incubation and brooding observed in the breeders.

In several cases, related behaviors were combined before analysis. Grouped behaviors included resting (i.e. sitting, incubating, brooding), foraging (i.e. procuring, transporting and eating prey, activity out of view off the nest territory), pairing (i.e. courtship and courtship feeding, copulation, attempted copulation), agonistic displays (i.e. long call, alarm call, bent neck, wing raising), and agonistic encounters (i.e. running or flying displacement, swooping, aerial chasing, fighting).

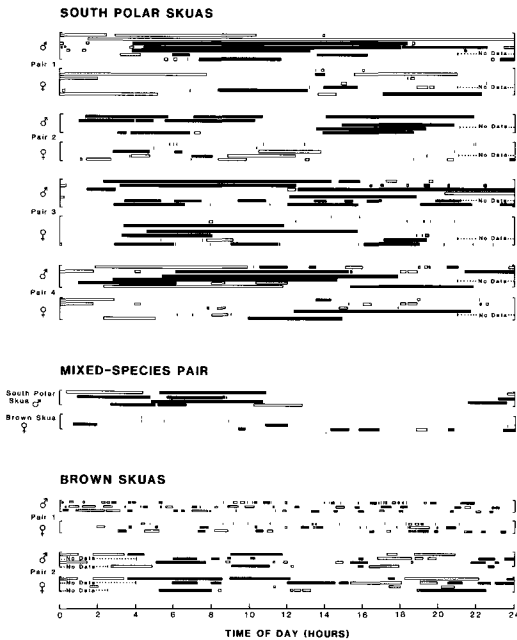Assessment of foraging behavior presented special

Fig. 1. Daily foraging activity of skua pairs. Each row represents one individual during one 24-h observation period. Horizontal bars denote time spent away from the nest area; solid bars indicate evidence of foraging (see Methods) and open bars indicate unknown location off territory.

Fig. 2. Daily patterns of resting and foraging. Band width indicates ±1 SE of hourly means weighted across pairs. The 24-h pattern is repeated to facilitate imaging.

problems. Direct observations could be made in the vicinity of each pair's territory, but foraging at sea or at penguin colonies on other islands could only be inferred from flight direction or regurgitation of food when the bird returned. Periods when the birds were off their territories and out of view were divided into those for which there was evidence of foraging (from flight direction or food regurgitation) and those for which there was not. While both types of absences were included in total foraging time, they were distinguished in the representation of daily foraging activity (Fig. 1). In calculating lengths of foraging bouts, absences of the latter type were excluded. Courtship feedings were included in Fig. 1 because, for much of the early season, this constituted the females' primary means of food intake. These feedings were not included in measures of foraging bouts.

RESULTS

Resting and foraging behaviors comprised the two largest components of skua time budgets. The timing of these behaviors varied greatly from day to day for each individual (Fig. 1).
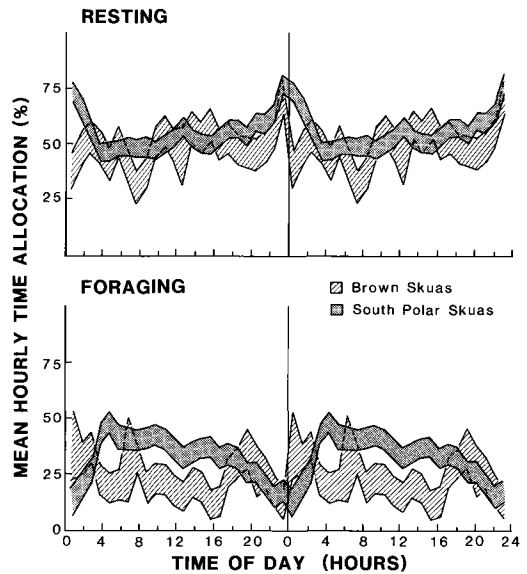
There was no hour in which all birds were always foraging or always at rest.

Despite this variation, the activity of South Polar Skuas exhibited a significant correlation with time of day (Table 1). On average, both breeding and nonbreeding pairs showed a short peak in resting behaviors around 2400 (Fig. 2); foraging activity moved from lowest to highest levels between 0000 and 0500, then gradually declined toward midnight.

Resting and foraging of Brown Skuas was not correlated with time of day (Table 1). An abrupt peak in resting levels at 2300–2400 (Fig. 2) appeared as an outlier in relation to the other 23 h. Although activity seemed to fluctuate more sharply than for South Polar Skuas, this probably was due to the smaller Brown Skua sample size.

Male and female South Polar Skuas both showed the tendencies described for the species as a whole, but the pattern was much stronger in males (Fig. 3A, Table 1). The lack of a significant correlation between resting and time of day in females reflected their propensity to stay on the territory during pre-egg-laying and early incubation, while males procured food at sea for both of them. Because most of the 24-h

TABLE 1. Angular-linear correlations (Johnson and Wehrly 1977) between activity and time of day for South Polar and Brown skuas near Palmer Station, Antarctica.[a]

	Resting	Foraging	Preening	Bathing	Agonistic	Pairing
South Polar Skua pairs	0.67**	0.83**	0.57*	0.62*	0.34	0.19
Males	0.71**	0.77**	—[b]	—	—	—
Females	0.46	0.67**	—	—	—	—
Brown Skua pairs	0.35	0.39	0.42	0.13	0.46	—
Males	0.36	0.43	—	—	—	—
Females	0.07	0.12	—	—	—	—
Mixed-species pair						
South Polar Skua male	0.83**	0.95**	—	—	—	—
Brown Skua female	0.41	0.30	—	—	—	—

[a] * = $P < 0.05$ for F with 2 and 21 df; ** = $P < 0.005$, for F with 2 and 21 df.
[b] Not calculated.

observations of South Polars occurred early in the breeding season, patterns of this period dominated the data set. Nevertheless, females showed an abrupt resting peak at 2300–2400, like that described for Brown Skuas.

In Brown Skuas, activity of both sexes showed the main features noted for the species (Fig. 3B), but a sex-related difference in pattern strength was not apparent. Although some Brown Skua females may fit the South Polar trend, the evidence was inconclusive because relatively few observations were made early in the Brown Skua breeding cycle. In an early-season study on nearby King George Island (62°10′S, 58°30′W), however, Brown Skua females spent more time at the nest site and less time foraging than males (Trivelpiece et al. 1980).

Members of the mixed pair showed tendencies of their respective species and sexes (Fig. 3C, Table 1). The South Polar Skua male exhibited strong time-related patterns, with foraging highs and resting lows in midmorning. Activity of the Brown Skua female was not correlated with time, and her levels of foraging were generally lower than those of her mate.

Foraging bouts, or trips away from the nest territory, were typically shorter for Brown than for South Polar skuas (Table 2, Fig. 1) ($t = -7.83$, df = 6, one-tailed $P < 0.00025$). This difference also was observed in earlier seasons. In 1977–1978 Neilson (1983) recorded Brown Skua foraging bouts that averaged less than 20 min, and in 1976–1977 South Polar bouts that averaged 1–2 h.

Further distinctions occurred within species. During most of the season, Brown Skuas with feeding territories adjacent to their nests foraged for less than 13 min per bout, while birds without adjacent feeding territories averaged over 60 min ($t = -4.58$, df = 2, one-tailed $P < 0.025$). In Fig. 1 these two conditions are illustrated by Brown Skua pairs 1 and 2, respectively. Similarly, Neilson (1983) documented average bout lengths of 8–13 min for a pair with an adjacent feeding territory and 16–21 min for a pair feeding about 1 km away.

After all the penguin fledglings had departed (late February), differences in the length of foraging bouts between Brown and South Polar skuas decreased substantially. Brown Skuas that had maintained feeding territories still made short scavenging trips to the deserted penguin colonies (weighted $\bar{x} = 16.2$ min, SE = 2.05, $n = 3$ pairs; 21 bouts). In addition, like the other skua groups, they now made trips away from their territories that averaged over 3 h (weighted $\bar{x} = 180.3$ min, SE = 28.42, $n = 3$ pairs; 13 bouts). Some observations suggested that these birds searched for penguins on more distant islands. In addition, seaward flight direction and subsequent regurgitation of fish to chicks indicated some foraging at sea. The average duration of these longer trips was an underestimate because of the inclusion of several trips that started before or ended after the observation period. Nevertheless, the long trips significantly increased average bout length in this period (on log-transformed data, paired $t = -8.89$, df = 3, one-tailed $P < 0.0025$). The Brown Skua pair without a feeding territory also showed an increase in bout length ($t = -2.64$, approx. df = 6, one-tailed $P < 0.025$).

For South Polar Skuas, foraging-trip length

RESTING   FORAGING

A. SOUTH POLAR SKUAS

B. BROWN SKUAS

C. MIXED-SPECIES PAIR
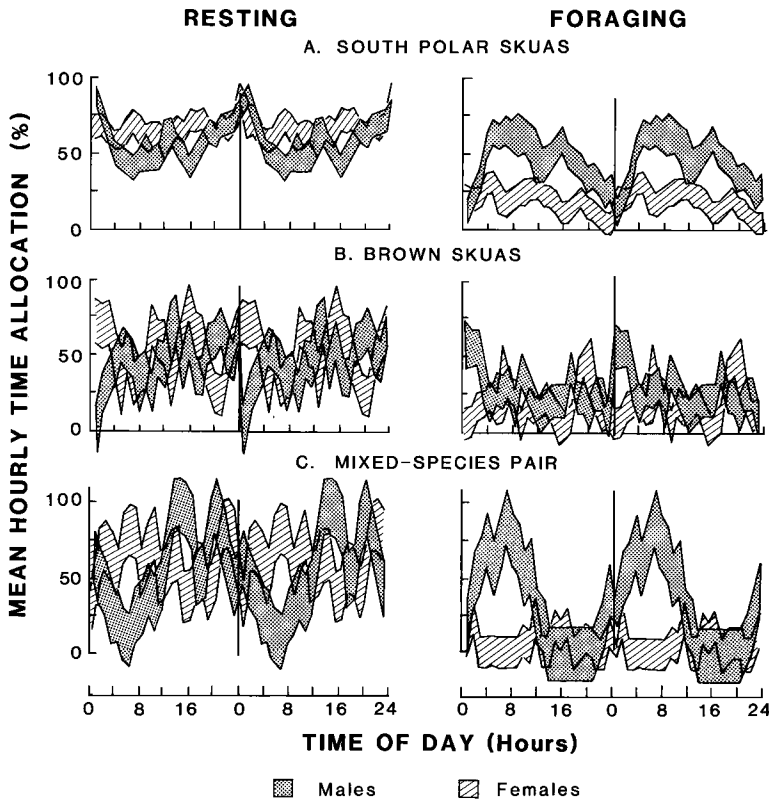
TIME OF DAY (Hours)

▦ Males   ▨ Females

Fig. 3.   Daily patterns of resting and foraging for males and females. Band width indicates ±1 SE of hourly means weighted across individuals. The 24-h pattern is repeated to facilitate imaging.

reflected the variable availability of their food resources. Early in the 1979–1980 season, foraging at sea was extremely difficult due to extensive pack-ice cover (Pietz 1984), and trips away from the nest area averaged 7.6 h. Later, when local waters were relatively clear of ice, foraging trips averaged 2.4 h (paired t = 3.57, df = 3, one-tailed P < 0.025).

Early in the 1980–1981 season, when nest initiation dates, nest densities, and clutch sizes indicated that food was more plentiful (Pietz 1984), average trip lengths were shorter than in the previous year. Because of short observation periods in the second year, accurate estimates of mean trip length could not be calculated; however, 25% of the trips were under 1 h during 1980–1981, compared with 12% in 1979–1980.

Previous investigators noted the impact of ice and storms on the foraging efficiency of South Polar Skuas. In 1976–1977 foraging bouts of three South Polar pairs averaged 58 min in

a period of calm weather and 112 min in a period of late-season storms (Neilson 1983). The impact of extensive ice cover was most dramatic in 1977–1978, when birds were sometimes absent from their territories for days, resulting in a total reproductive failure (Parmelee et al. 1978).

Members of the mixed-species pair showed bout lengths and diets characteristic of their respective species. The Brown Skua female, foraging primarily on penguins at neighboring islands, averaged trips of less than 1 h from mid-December to late February, and over 3 h afterwards (t = −3.57, approx. df = 4, one-tailed P < 0.025). The South Polar Skua male, foraging at sea, averaged trips of about 4 h during the period of extensive ice cover and 2.8 h during periods of open water (t = 2.4, df = 23, one-tailed P < 0.025).

Finally, female Brown Skuas averaged longer foraging trips than males (on log-transformed data, paired t = 4.33, df = 3, two-tailed

TABLE 2. Average duration of foraging bouts for South Polar and Brown skuas near Palmer Station, Antarctica.

	$\bar{x}^a$ (min)	SE (min)	No. of pairs	No. of bouts[b]
Brown Skuas				
Overall	32.3	11.52	4[c]	355
Pairs with feeding territories				
Penguins nesting	12.7	0.74	3[d]	277
Penguins gone	76.7	17.71	3[d]	34
Pair without feeding territory				
Penguins nesting	61.0	10.52	1	38
Penguins gone	239.1	66.73	1	6
South Polar Skuas				
Overall	198.0	17.43	4	123
Heavy ice cover	453.2	77.04	4	24
Ice out	145.1	12.72	4	99
Mixed-species pair				
Brown Skua female				
Penguins nesting	52.8	7.48	1	21
Penguins gone	216.8	45.28	1	4
South Polar Skua male				
Overall	185.0	15.11	1	25
Heavy ice cover	244.1	36.12	1	6
Ice out	166.4	14.33	1	19

[a] Weighted means given where sample includes more than one pair.
[b] Summed for all individuals in sample.
[c] Two pairs for 1 yr and one pair for 2 yr.
[d] One pair for 2 yr and one pair for 1 yr.

$P < 0.05$), but male and female South Polar Skuas showed no consistent differences in length of foraging trips (on log-transformed data, paired $t = -1.32$, df $= 3$, two-tailed $P > 0.20$). This difference may hinge on the sexual size dimorphism that was clearly visible in Brown Skuas (females are larger) but difficult to detect in South Polar Skuas.

Agonistic displays and encounters occurred during nearly all hours (Figs. 4A and 5A). No significant correlations were found between levels of agonistic activity and time of day (Table 1). There was some indication of a lull in agonistic activities during twilight, probably because the fewest potential intruders were active then (Fig. 2).

Episodes of preening activity occurred at all hours in both species, with no decline near 2400 (Figs. 4B and 5B). Some lulls in preening activity coincided with peaks in foraging, suggesting that time spent off territory occasionally
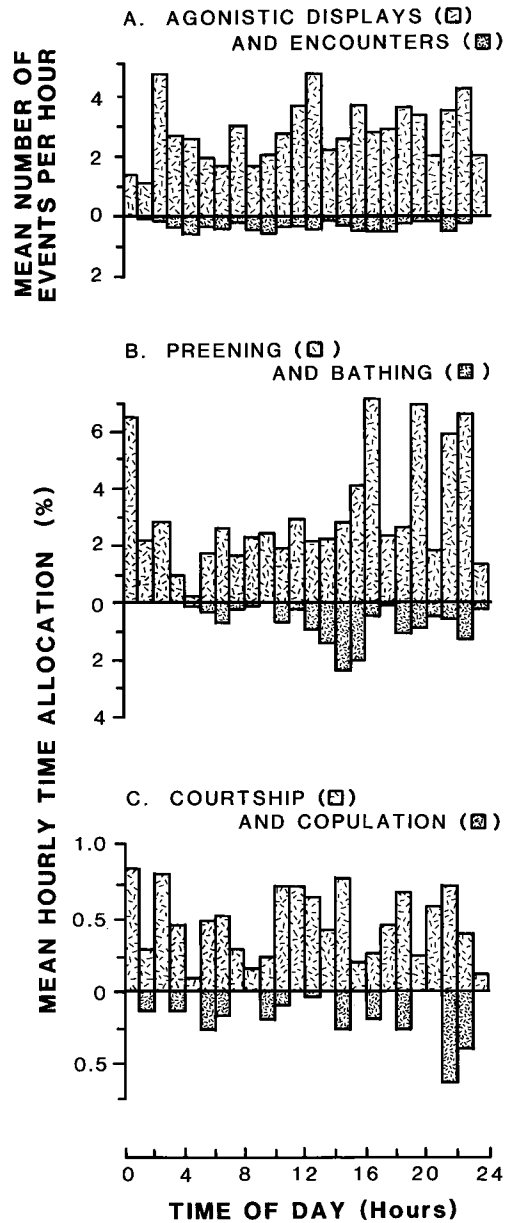

Fig. 4. Timing of agonistic (A), preening and bathing (B), and pairing (C) activities of 8 South Polar Skuas. In A, bar height represents hourly counts of agonistic behaviors, averaged across 50 bird-days of observations. In B and C, bar height represents the percentage of each hour allocated to an activity, averaged across 50 (B) or 25 (C) bird-days.

constrained the timing of preening as well as resting.

Among South Polar Skuas, bouts of bathing activity showed highest levels in midafternoon

A. AGONISTIC DISPLAYS (▣)
AND ENCOUNTERS (▣)

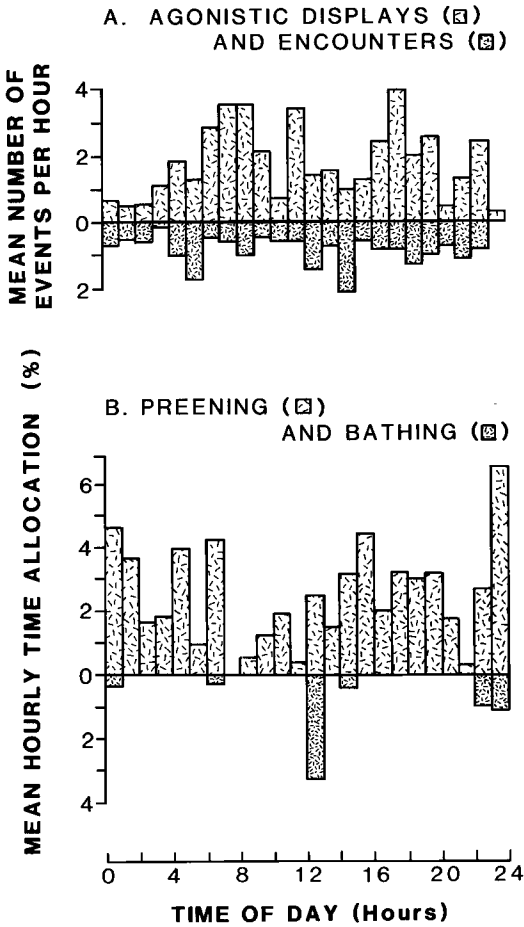## B. PREENING (▣)
AND BATHING (▣)

TIME OF DAY (Hours)

Fig. 5. Timing of agonistic (A) and preening and bathing (B) activities of 4 Brown Skuas. In A, bar height represents hourly counts of agonistic behaviors, averaged across 14 bird-days of observations. In B, bar height represents the percentage of each hour allocated to that activity, averaged across 14 bird-days.

and a sustained low in the early morning (Fig. 4B). Brown Skua bathing patterns could not be assessed because observed bathing was very rare as well as episodic. The six hours in which bathing activity appeared (Fig. 5B) represented only six episodes of bathing.

Pairing behaviors of South Polar Skuas, although among the rarest activities observed, occurred randomly (Fig. 4C, Table 1). Brown Skua pairing could not be evaluated because the pre-egg-laying period, when most courtship and mating occurred, was poorly represented in the sample.

In skuas, as in many seabirds, pair members share the tasks of incubation, brooding, and guarding of young. When one bird leaves, the other must remain until its mate returns or risk losing the eggs or chicks. The activity of male and female skuas appeared to be coordinated in this way. It was most striking in Brown Skuas (Fig. 3B), where a peak in the activity of one sex frequently concurred with lowered activity in the other, but was only weakly visible in South Polar Skuas (Fig. 3A). Presumably, with a larger sample of observation days and observed pairs, these compensatory patterns would average out and disappear. Then only the time-related patterns of each species and sex would be apparent.

Direct examination of activity within pairs showed that the nature and strength of within-pair correlations depended primarily on the stage of breeding (Fig. 6). Most sample correlations were weakly positive during pre-egg-laying and negative during incubation, brooding, and postbrooding. Pairs that lost eggs or chicks again showed more positive correlations.

For both species, the strongest negative correlations between activity and breeding stage occurred in resting behavior during incubation and brooding. This reflected the dominance of incubating and brooding in the time budgets of the skuas at these stages (recall that these two behaviors were part of the resting category in the analyses). Members of a nonbreeding South Polar pair generally showed weak positive correlations all season, further indicating the importance of reproduction to the timing of activity between mates.

The importance of nest attendance for breeding skuas was demonstrated by how seldom both pair members were off the nest territory. For South Polar pairs whose eggs or chicks survived, simultaneous absences occurred less than 0.02% of the observed time during incubation (284 h, 6 pairs), 0.07% during the brooding period (112 h, 5 pairs), and about 4% during postbrooding (182 h, 4 pairs). By contrast, simultaneous absences rose to 13% (92 h, 6 pairs) for pairs that suffered total nest failure, and averaged 14% (169 h) in the nonbreeding pair.

DISCUSSION

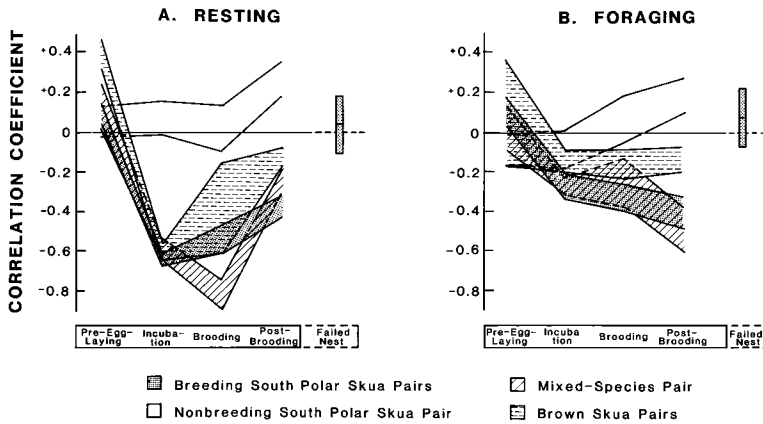During this study near Palmer Station, breeding South Polar Skuas did not show an

Fig. 6.   Correlations between pair members in resting (A) and foraging (B) skuas. Band width indicates ±1 SE of the means weighted across pairs within each group. The "failed nest" category, shown discontinuously from the rest of the breeding chronology, represents 6 pairs of South Polar Skuas.

activity lull from 0100 to 0500 as reported for birds at Cape Royds, Ross Island (Spellerberg 1969). Instead, averaged data for resting and foraging indicated a period of relative quiescence around 2400. In the absence of darkness, one might expect skuas to be equally active at all hours. Instead, South Polar Skuas at Palmer showed a strong relationship between foraging activity and time of day that Brown Skuas did not.

The differences in activity patterns between species most likely stem from differences in their feeding ecology. Searching for fish at sea presents problems for South Polar Skuas that Brown Skuas, feeding on land, do not face.

These problems may relate, directly or indirectly, to diel changes in light intensity. Even during continuous daylight, light intensities may shift markedly; at Ross Island, as much as 8-fold changes in irradiance were measured between 1200 and 2400 under various degrees of cloud cover (Steven Kottmeier pers. comm.). At Palmer, where some twilight occurs even in midsummer, the range of light intensities was greater. Gallardo and Piezzi (1973) recorded January light levels near Palmer (64°53′S, 62°53′W) ranging from 30,000–50,000 lux at noon to less than 1,000 lux at 2200 when twilight began.

At the lowest light levels there are several conceivable deterrents to fishing at sea. It is possible that (1) lower temperatures associated with lower light require birds to conserve heat;

(2) lower air temperatures freeze water on feathers after birds splash-dive for fish; (3) lower angles of incidence of light rays, which cause more reflection and less penetration of the water surface, make it more difficult for skuas to see prey; (4) prey show behavioral changes related to light (e.g. vertical movements) that make them less available to skuas at certain times of day; or (5) light cues trigger an intrinsic activity "clock" that may have evolved in response to some other, more strongly rhythmic environment.

The first hypothesis was suggested by the observation (Spellerberg 1969) that the lowest atmospheric temperatures at Cape Royds coincided with a 0100–0500 period of skua inactivity. Atmospheric temperatures from November to March ranged between −15°C and 5°C. At Palmer, however, summer temperatures rarely fell below −2°C, and at warmer times incubating skuas sometimes panted to dissipate excess body heat. The high frequency of early morning activity in individuals of both species (Fig. 1) makes it unlikely that heat conservation was a primary concern for Palmer skuas.

The second hypothesis also involves temperature as a deterrent to fishing. Young (1963) noted that

The plunge into the water immersing much of the head and lower part of the body accounts for the ice masses that encrusted the upper mandible and

forehead and the jugulum and breast feathers of many birds. This icing was most commonly observed during early and late summer when air temperatures were lower. Some birds had so much ice about the beak and forehead when they returned to the territory that vision was seriously impaired.

This suggests a reason for Cape Royds skuas to avoid fishing during the coldest hours of the day. At Palmer, where the lowest temperatures were often above freezing, I never saw birds with ice on their feathers. Nevertheless, the fact that records of bathing were rare between 2400 and 0400, and peaked from 1400 to 1600, suggests that skuas may have avoided getting wet during the early hours of the day.

The third hypothesis relates light intensity and sun position to the visibility of prey below the water surface. This may be more important at Palmer than Ross Island, because the height of the midsummer sun ranges much more widely at 65°S than at 78°S. As sun position moves toward the horizon, the proportion of light reflected from the water's surface increases and the proportion penetrating the water decreases. If the water surface is disturbed, reflection at low sun angles is even greater (Hutchinson 1957). Coupled with lower light intensities at this time of day, these effects may severely reduce skuas' ability to see underwater prey. The high proportion of cloudy days at Palmer [mean of about 22 cloudy and 8 partly cloudy days/month in December–January of 1979–1980 and 1980–1981 (Anon. 1980, 1981)] may reduce the importance of reflection off the water, but increase the importance of light intensity for seeing prey.

The feeding habits of South Polar and Brown skuas offer circumstantial support for this hypothesis. Penguin colonies provide a closer and more predictable food source than marine prey, allowing Brown Skuas to find their food with less searching and, probably, with less light.

The fourth hypothesis implicates diel changes in marine prey availability; prey are available to skuas only when they occur within 1 m of the water surface. The primary food source for South Polar Skuas at Palmer is the nototheniid fish *Pleuragramma antarcticum* (Neilson 1983, Pietz 1984). Its movements in response to light, food, and other environmental factors are not well known, but other notothenoid fishes migrate vertically to feed on krill (*Euphausia su-*

perba; Permitin 1970, Karl-Hermann Kock pers. comm.). Krill, a secondary food source of the skuas (Pietz 1984) and a major food of *Pleuragramma* (Dewitt and Hopkins 1977), migrate vertically (e.g. Witek et al. 1981). In most areas, krill aggregate in upper water layers at night and disperse to deeper water in the day.

Such movements would indicate that skuas at Palmer feed when krill are least available. The situation is probably more complicated, however. First, diel krill migrations may be much less important when there is continuous light. Witek et al. (1981) observed no distinct dependence of the vertical krill distribution on the intensity of daylight. In addition, Pavlov (1974) observed a second surface migration at noon, and Mauchline (1981) noted several studies that suggest krill move irregularly, perhaps reacting to varying concentrations of phytoplankton.

The fifth hypothesis relates light intensity to skua activity and implies that proximal causes now may be missing but that an internal clock still responds to changing light cues. Experimental evidence of circadian rhythms in skuas is lacking; however, 24-h rhythms in their physiology and behavior may reflect the influences of an internal clock. At Cape Royds, Spellerberg (1969) found that the core body temperature of an adult male skua peaked at 42.4°C at midday and fell to 41.0°C at 0200–0400, implying a daily cycle. On the other hand, Eklund (1942) measured body temperatures of two South Polar Skuas on the Antarctic Peninsula (68°11'S, 67°12'W) and recorded lows of 39.9°C in the hours just before midnight. Eklund mentioned that the South Polar Skuas observed during continual daylight were "more or less active for 24-hour periods, and ... could always be observed eating and fighting among themselves over seal-meat scraps near the husky sledge-dog kennels."

These findings, together with individual variability noted at Palmer, suggest that the activity patterns of South Polar Skuas are not controlled by one 24-h pattern. A light-synchronized internal clock may be involved in the timing of activity, but use of this clock may depend on local foraging conditions and opportunities. Brown Skuas display this opportunistic flexibility to extremes. Brown Skuas on the Chatham Islands, New Zealand, forage primarily during hours of darkness (Young 1978).

This allows them to prey on locally abundant, night-active petrels, which they catch on the ground near the petrels' burrows. Similarly, Brown Skuas on Gough Island in the South Atlantic (40°S, 10°W) feed primarily at night on Procellariiformes (Furness pers. comm.).

I believe that light levels ultimately influence the activity of South Polar Skuas, although the proximate mechanism may vary. The effect of light on air temperature may cause the activity lull at 0100–0500 on Ross Island (hypotheses 1 and 2), while the effect of light on prey visibility may produce the midnight low at Palmer (hypothesis 3). Alternatively, light may trigger an internal clock that produces both patterns. Diet is a proximate factor influencing South Polar and Brown skua activity patterns at a local level. For both species, the large variance in the timing of individuals' activities suggests a behavioral flexibility suited to an opportunistic life style.

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A **symposium on Birds of Evergreen Forest,** organized by the Southern African Ornithological Society, will be held **8-10 September 1987** at The Wilderness, Cape Province, South Africa. Papers and posters will be presented on the following topics: forest bird communities, biogeography of forest birds, population biology of forest birds, and conservation of forest avifaunas. Prospective participants should contact the **Symposium Organising Committee, E.C.W.B.S., P.O. Box 1305, Port Elizabeth 6000, South Africa.**

The **Third New England Regional Hawk Conference** will be held **4 April 1987** at the Holiday Inn, Holyoke, Massachusetts. Registration forms are available from **HAWKS, P.O. Box 212, Portland, Connecticut 06480.** There are special rates for lodging at the Conference center. Registration will be limited.

The **Third World Conference on Birds of Prey** will be held **22-27 March 1987** at Eilat, Israel. It will be organized by the World Working Group on Birds of Prey in conjunction with the Israel Raptor Information Center and the U.S. Hawk Mountain Sanctuary Association. The conference will consist of 7 paper sessions on conservation, migration, population biology, education, and legislation. For further information write to the Hon. Secretary of the World Working Group: **Mr. R. D. Chancellor, 15 Bolton Gardens, London SW5 0AL, U.K.**