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ROOSTING BY PELAGIC SEABIRDS: ENERGETIC, POPULATIONAL, AND SOCIAL CONSIDERATIONS[1]

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Abstract. Great Frigatebirds (*Fregata minor*) and Red-footed Boobies (*Sula sula*) roost in large numbers on the guy wires of the LORAN-C tower on Sand Island, Johnston Atoll, in the central Pacific Ocean. We quantified the diurnal pattern of movement to and from the atoll by the roosting, but nonnesting birds. The total number of birds using the atoll is difficult to determine but must be considered when making population estimates. By counting the roosting birds at 10 min after sunset a reliable estimate can be made of the maximum number of birds which will roost that evening. The number of roosting birds increases significantly when the trade winds decrease in velocity. Utilizing energy from winds and thermals is critical to these species for efficient flight, and energetic considerations may determine roosting patterns. Social interactions probably are secondary and result from the scarcity of suitable roost sites in the pelagic zone.

Key words: Red-footed Booby; Sula sula; *Great Frigatebird;* Fregata minor; *roosting; flight energetics; population dynamics; seabirds.*

INTRODUCTION

Seabirds are among the most aerial of all birds. Many spend virtually their entire lives at sea and return to land only to nest, and in some species, to roost. Accurate population estimates of seabirds are difficult to obtain (Croxall et al. 1984; Nettleship and Birkhead 1985), but are critical to studies of population dynamics and establishment of valid conservation policies. Censuses of roosting populations on central Pacific islands or other oceanic locales are rare. Our data have broad implications for obtaining and interpreting such population estimates. Further, the sociological implications of communal roosting by birds have received considerable attention (Morrison and Caccamise 1985, and references therein). Our data provide another hypothesis for why birds form communal roosts.

STUDY SITE AND METHODS

Johnston Atoll consists of a fringing reef with two small (less than 231 and 8 ha) natural, but highly modified islands, and two small entirely man-made islands (9.7 and 6.9 ha), all with low vertical profile (Amerson and Shelton 1976). The atoll lies at 16°45′N, 169°30′W. The nearest landfall is French Frigate Shoals in the Leeward Hawaiian chain, 450 nautical miles to the north northwest. Sand Island (ca. 8 ha) is the major seabird nesting area, and through the effort of the Smithsonian Institution's Pacific Ocean Biological Survey Program (POBSP), ranks among the best studied colonies in the world. Sand Island is dominated by a 196.6 m high LORAN-C transmitting tower with 24 external guy wires radiating from the top of the tower to bases in the lagoon forming a ca. 300 m diameter circle. To the northeast, southeast, and west a series of inner guy wires support the tower.

POBSP personnel made hourly counts of Great Frigatebirds (*Fregata minor*) and Red-footed Boobies (*Sula sula*) once a week from 0700 to 1900, from September 1964 through March 1965. We use those data to illustrate the diurnal cycle in the numbers of birds present.

The counts used to analyze evening arrivals were made by RWS from 3 to 29 January 1967, at 1200, and 60, 30, and 15 min before sunset, at sunset, 10 min after sunset, and at midnight.

The counts used to correlate the number of birds present at midnight, dusk (10 min after sunset), and noon were made by RWS from 22 December 1966 through 31 January 1967. The midnight data were collected only when sufficient moonlight was present to ensure accurate counts. As the birds were difficult to census in low light, and flushed readily when artificial light was directed on them, we estimate that figures presented for midnight for Red-footed Boobies are accurate to ±20%, and for Great Frigatebirds to ±10%. Data used for correlating the numbers of birds present and environmental parameters were taken by RWS from 22 December 1966 to 10 February 1967 at 10 min after sunset.

Daily mean wind speed, percent possible sunshine, sky cover from sunrise to sunset, mean temperature, and precipitation were obtained from the U.S. Department of Commerce Weather Bureau on Johnston Island, ca. 2 km from the LORAN tower. Rainfall of less than 0.25 mm was listed in the records as "trace"; we substituted the value of 0.01 mm

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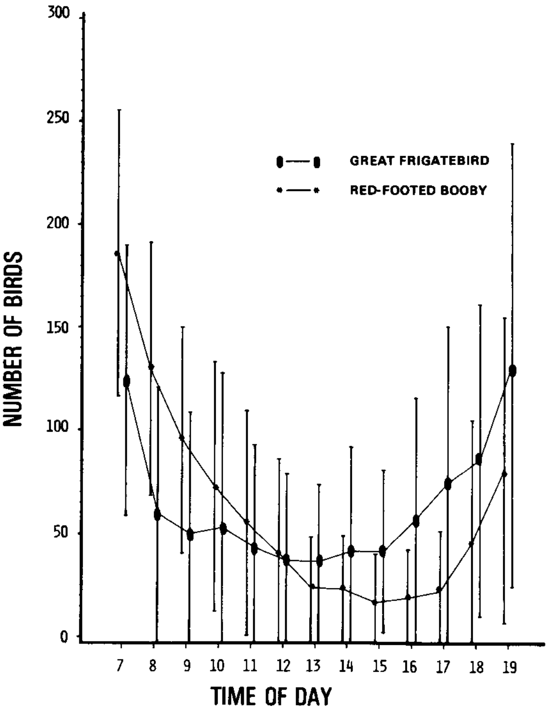

FIGURE 1. The number of Red-footed Boobies and Great Frigatebirds roosting on Sand Island, Johnston Atoll, central Pacific Ocean, in relation to time of day. The mean ±one SD is graphed.

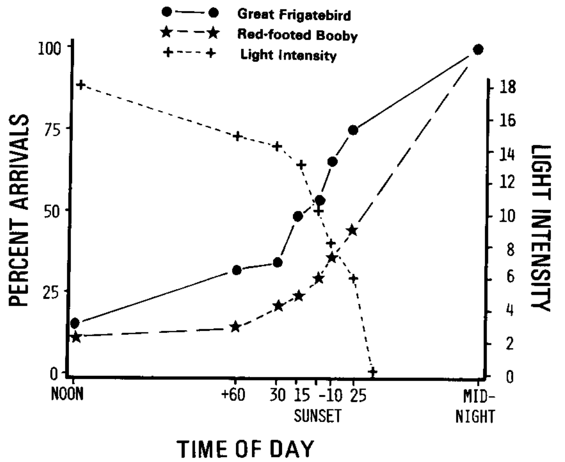

FIGURE 2. Time of arrival, based on a percent of the daily maximum population, in relation to time of day and light intensity (measured in LUX).

for trace, six times during each of two correlation analyses.

RESULTS

During this study, roughly a dozen pairs of Red-footed Boobies and fewer than 100 pairs of Great Frigatebirds nested on Sand Island. However, the roosting populations were considerably larger and were composed of individuals coming from outside the immediate atoll on a daily basis (Harrington 1977).

Verner (1965) found a diurnal movement pattern for boobies at Half Moon Cay, Belize. We also documented a predictable diurnal pattern of movement to and from a roost site by Great Frigatebirds and Red-footed Boobies (Fig. 1). The majority of both species of birds left the wires near dawn and returned after sunset, reaching maximum numbers after last light, based on counts at midnight (Figs. 2, 3). We found that the number of birds counted at 10 min after sunset was correlated to the maximum numbers counted at midnight ($r = 0.747$, $t = 2.75$, $P < 0.05$), and can be used to predict the maximum bird population for that evening. A significant negative correlation exists between the percent arrival of both species and light intensity (Fig. 2) (Great Frigatebirds: $r = -0.980$, $t = 11.02$, $P < 0.01$; Red-footed Booby: $r = -0.986$, $t = 13.18$, $P < 0.01$.)

The evening arrival time of maximum numbers of birds is significantly different between the two species: Great Frigatebirds return earlier than the Red-footed Boobies. This was quantified by ranking the percent of birds arriving for each time interval based on the total number that were present at midnight, and using the Wilcoxon's test for unpaired data, $P < 0.05$, for a one-tailed test (Fig. 2). For Great Frigatebirds, approximately half the daily arrivals occurred by sunset, 65% by 10 min after sunset, and 75% at last light (25 to 30 min past sunset). For Red-footed Boobies, only one quarter of the daily arrivals occurred by sunset, 30% by 10 min after sunset, and 45% by last light. Only 12 to 18% of the total roosting population of both species was present during mid-morning to early afternoon. Early morning departures occurred at such low light levels and so rapidly that estimates from counts taken at that time are unreliable.

Our data indicate that numbers of roosting boobies and frigates increase over several days when winds remain calm (i.e., Fig. 3: 25 to 31 December, 15 to 23 January), and the birds do not leave in the morning when winds are light. For both species, the numbers of birds and mean daily windspeeds are significantly negatively correlated (Figs. 4, 5) (Great Frigatebird: $n = 45$ days, $r = -0.799$, $P < 0.01$; Red-footed Booby: $n = 33$ days, $r = -0.8157$, and $t = 7.846$, $P < 0.01$).

Numbers of frigatebirds and percent possible sunshine, amount of sky cover and air temperature were not significantly correlated. Numbers of frigatebirds and precipitation levels were negatively correlated ($r = -0.345$, $t = 378$, $P < 0.05$). Numbers of boobies were not significantly correlated with temperature or amount of rainfall. Numbers of boobies and

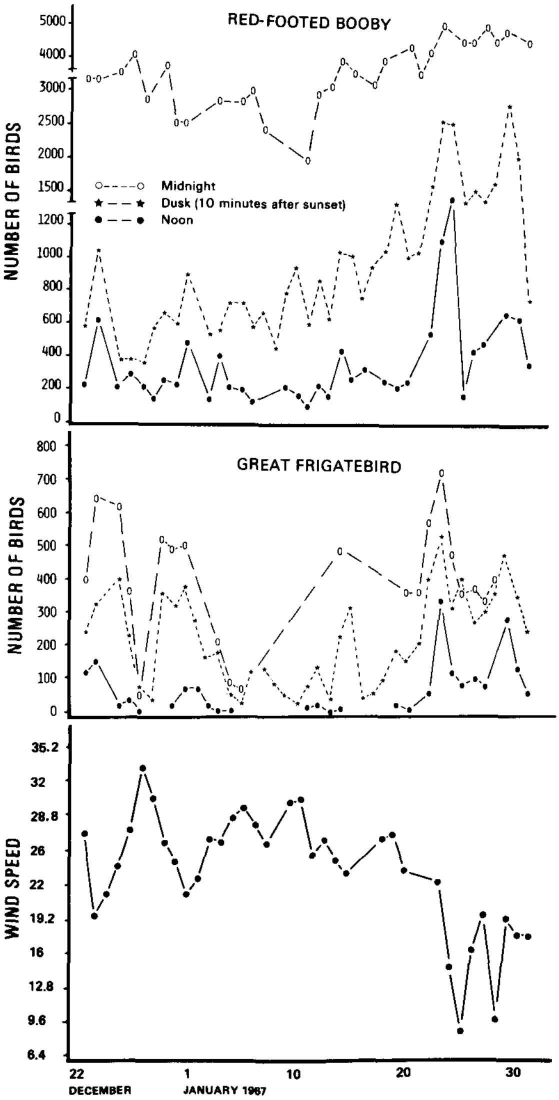

FIGURE 3. The numbers of Red-footed Boobies and Great Frigatebirds roosting at noon, dusk (10 min after sunset), and midnight from 22 December 1966 to 31 January 1967, in relation to wind speed (km/hr).

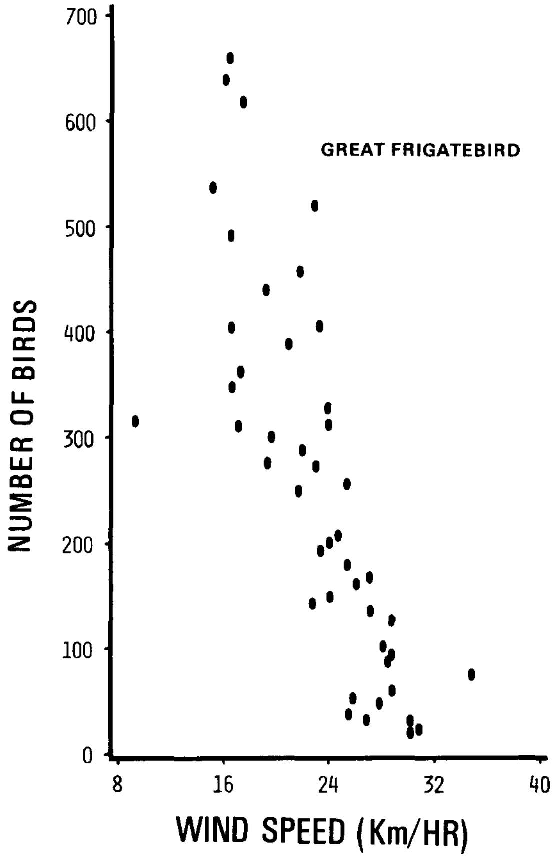

FIGURE 4. The relationship between wind speed and number of roosting Great Frigatebirds based on counts at 10 min after sunset.

percent possible sunshine (an index to cloud cover) are negatively correlated ($r = -0.429$, $P < 0.05$). We found no significant correlations between precipitation, cloud cover, and wind speed for boobies. Our counts do not indicate higher populations of either species present in relation to phases of the moon.

DISCUSSION

POPULATION ESTIMATES: IMPLICATIONS OF DIURNAL CHANGES

Amerson and Shelton (1976) quantified the Red-footed Booby and Great Frigatebird populations on Johnston Atoll, but pointed out the difficulties in accounting for birds arriving after dark. We found that counts made at 10 and 25 min after sunset do provide a good index to the numbers of birds roosting on a given night, at all seasons of the year.

Estimating the total population of boobies and frigatebirds using Johnston Atoll is probably impossible because of the movement of individual birds through the region (Harrington 1977). Data collected at sea in this region of the central Pacific indicate that within about 120 to 160 km of an atoll, distinct movements by Red-footed Boobies occur in the mornings away from land and in the evenings toward land. Inward movement continued to occur after dark. At greater distances such movements were not noted. Densities of birds are greatest near land and decrease with increasing distance from land (King 1970, Harrington 1977, R. Pitman, pers. comm.). Few at-sea data are available for this region but at the time of this study, in a region 200 km southwest of Johnston, densities of 0.0 to 1.04 boobies and 0.12 to 0.21 frigates per km^2 were obtained, with a distinct seasonal variation in density (Amerson and Shelton 1976). In an area approximately 1,300 km east of Johnston, King (1970) calculated boobies as four times more common than frigatebirds (0.90 vs. 0.25 birds per 1.6 linear km) and boobies were com-

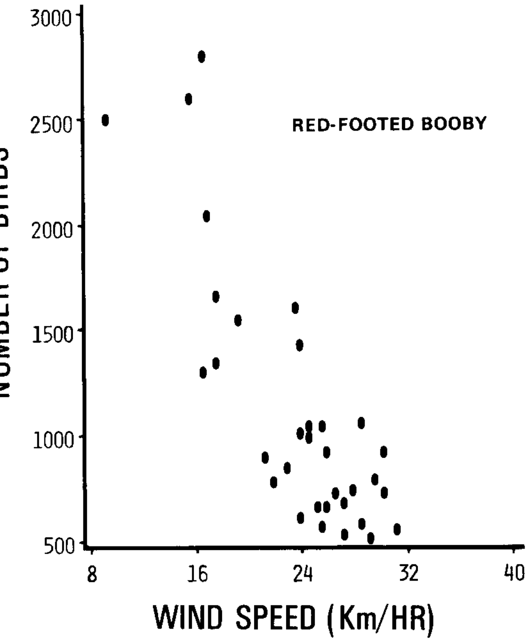

FIGURE 5. The relationship between wind speed and number of roosting Red-footed Boobies based on counts at 10 min after sunset.

puted at 6.57 birds per km². Those data, and the roost counts presented here, indicate that boobies are four to six times more abundant than frigatebirds in this region. Evidence indicates that the booby and frigate populations have increased on Johnston Atoll since the LORAN-C tower was erected (Amerson and Shelton 1976, Harrington 1977, Schreiber and Schreiber, unpubl. data). The height provided by the guy wires may assist in take-off since both species require an elevated perch to readily become airborne (Verner 1965, Pennycuick 1983, Schreiber, unpubl. data). Is it possible that the lack of vertical stratification on coral atolls is a limiting factor to populations of certain species of seabirds?

Numbers of seabirds can fluctuate widely under various synoptic weather factors (Schreiber and Schreiber 1984), and only long term studies can give reliable estimates of population trends. When presenting data on seabird populations, caution must be used to state precisely the method used to delineate the population size: nesting pairs in one season (for discussion of the problems of making even such estimates see Floyd and Swanson 1983); total population associated with nesting (adults, nestlings, juveniles, subadults); or total number of birds utilizing the island (Diamond 1975). Actual nest counts give a repeatable figure for the number of nesting seabird pairs in a given season but obviously a huge, more difficult to estimate, nonbreeding population also exists, at least on Johnston Atoll. The diurnal pattern of movement of this nonbreeding population must be taken into consideration when discussing population sizes and censusing seabirds (Croxall et al. 1985). Our methods control for the diurnal changes in numbers of roosting birds.

ENERGETIC CONSIDERATIONS

Pennycuick (1983) studied wing shapes and flight characteristics of the Magnificent Frigatebirds (*Fregata magnificens*) in Panama, and used data on distribution of Lesser Frigatebirds (*Fregata ariel*) (Sibley and Clapp 1967) to "imply that frigates must be able . . . to remain airborne continuously, day and night for extended periods." Pennycuick (1983, in litt.) further stressed the importance of trade wind zones with their resultant trade wind cumulus clouds and rising thermals over the sea as an important source of energy enabling frigates to remain in the air (see also Harrington et al. 1972). Frigates circle in these thermals and gain altitude. They glide off, losing height but gaining distance over the ground, and must find another thermal to rise upward again. When wind speeds increase, the thermals are broken up, rendering it difficult for frigates to take advantage of this type of flight, and they must rely on flapping, which is energetically more costly, to move from place to place. In light winds, thermals drift downwind of an island and birds upwind can move to land easily. However, those birds which are downwind or crosswind must resort to flap flying to reach the atoll. It would seem that nonnesting birds, with no incentive to return to the island, might find it easier to continue to soar through the night (Pennycuick, in litt.). That idea is not supported by our data.

Our data clearly show that roosting frigatebirds and Red-footed Boobies are more abundant on Johnston Atoll on calm nights. Furthermore, on calm days, when they seemingly would be able to take advantage of strong thermal development, they stay perched later in the morning (Schreiber, unpubl. data). If soaring flight is more efficient, why do frigates return to the roost, rather than soar on thermals through the night? It appears that frigates roost in highest numbers when daily minimum wind speeds fall below 15 to 18 km/hr, the time of greatest thermal development and stability.

Larger numbers of Red-footed Boobies also remain at the roost in calm periods. The wing shape, wing loading, and flight dynamics of boobies appear different from frigates. Boobies do not use thermals, but rather flap fly or slope soar along wave tops. With little or no wind, waves are not generated, and consequently boobies roost in large numbers. Thus, it is interesting that both Great Frigatebirds and Red-footed Boobies roost in larger numbers under the same weather conditions.

Our roosting data clearly indicate that both Red-footed Boobies and Great Frigatebirds in the central Pacific remain at sea when it is windy and roost in calm periods. We believe they find this pattern to be energetically efficient since they thus avoid having to flap fly in calm weather. Another possibility is that on calm days and nights these species, for some reason, cannot feed efficiently. We would find the same effect of more birds roosting, but the reason might not be related to flight so much, as to the lack of foraging efficiency (J. E. Heyning, pers. comm.).

Clearly, the relations between thermal development, wind velocity, bird use of thermals and wind, and bird flight energetics in the pelagic zone need further investigation. This better understanding of the activities of birds at sea is critical to our understanding of what we observe on islands.

SOCIAL CONSIDERATIONS

Communal roosting is a common phenomenon in birds that has received considerable attention in recent studies. It has become obvious that different species roost for various reasons and under various conditions. The result of this diversity has led to considerable discussion about the functional and adaptive significance of roosting (Evans 1983, Caccamise and Fischl 1985, Hockey 1985, Keister et al. 1985, Morrison and Caccamise 1985, and references therein) and the various theories to explain roosting are not mutually exclusive (Weatherhead 1983). Most of the data involve landbirds, especially passerines. We wish to discuss briefly several of these ideas as they relate to frigatebirds and boobies in the pelagic zone.

Predation. Communal roosting has been assumed to be a method of avoiding predation away from the roost, and most studies have primarily dealt with differential predation within the roost (Weatherhead 1983, reviewed in Møller 1985). Roosting on land may be a method of avoiding predation at sea since sharks eat birds sitting on the water (Mote Marine Laboratory, unpubl. data). If the birds remained in the air over the ocean at night, and were then forced into the water by a change in weather patterns (calm wind conditions), the chance of predation occurring away from the roost would be increased. We suspect this threat at sea is significant and thus gathering on land is a method to avoid predation. An individual's place within seabird roosts is unimportant as a predator avoidance mechanism and the size of the roost is not related to predation pressure since there are no terrestrial predators at the roost.

Dominance within the roost. Weatherhead's (1983) suggestion that superior foraging ability leads to dominance and thus access to central roosting positions does not seem applicable in our situation. It is logical to assume that frigates and boobies with "superior foraging ability" would spend less time in foraging and thus would return early to roost. However, at Johnston Atoll most movement to the roost occurs only over a relatively short period of time. Additionally, these early arrivals are usually displaced from their perch by the later arrivals and thus must move to a higher, more vertically inclined portion of the guy wires. This is especially true of the frigates, which arrive earlier than the boobies and first roost low on the wires in the most horizontal positions. After the boobies arrive and land in these lower sites, the displaced frigates move onto higher perches which are probably not as easy to grasp (Amerson and Shelton 1976). Thus, we see no advantage in arriving early. In fact, it would appear that arriving late may be advantageous since those arrivals are in a dominant position when landing.

Information centers. While our data do not actually test the information center hypothesis (Ward and Zahavi 1973), we cannot see how information exchange is important in this case (Bayer 1982). These species do feed on an ephemeral food source while in flocks (conditions that could lead to the usefulness of information exchange). However, exchange of information might *result* from roosting together but is not a *cause* for roosting communally. Exchange of information on feeding is difficult to document, but because of the nature of the roost situation it could be examined on Johnston Atoll.

CONCLUSIONS

Our observations indicate that the underlying reason for roosting in the Great Frigatebird and Red-footed Booby is flight energetics. Frigates are adapted to sustained soaring flight. Boobies are adapted to slope soaring along wave tops. If wind velocity is not favorable, it is energetically advantageous to roost. In these species, inhabiting the pelagic oceans, roost sites are definitely limited. Whatever sociological events that occur do so as a result of the birds roosting in close proximity at night. These interactions would appear to be the *consequence* of limited roost sites and the energetic need to perch at night, rather than a *cause* for their social communal gathering.

As biologists, rather than searching for the one explanation for evolutionary events, we should expect that multiple factors, including those based especially on energetic considerations, would explain the variability we observe in ecological systems. Our suggestion that conservation of energy is the major causal factor in frigate and booby roosting does not exclude any "social" hypotheses. Since islands are widely scattered in the central Pacific and roost site availability is limited, we believe that communal roosting may be a major factor in the evolution of seabird foraging distribution. Further, the relationship between limited roost sites and the adaptive significance of coloniality needs to be investigated (but see Wittenberger and Hunt 1985).

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