Ecology of Audubon's Shearwaters (Puffinus lherminieri) at San Salvador, Bahamas

Neville Anthony Trimm Jr.

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Ecology of Audubon's Shearwaters (*Puffinus lherminieri*) at San Salvador, Bahamas

by

Neville Anthony Trimm, Jr.

A Thesis submitted in partial satisfaction of the requirements for the degree of Master of Science in Biology

June 2001
Each person whose signature appears below certifies that this thesis, in their opinion, is adequate in scope and quality, as a thesis for the degree of Master of Science.

William Hayes, Associate Professor of Biology

Ronald Carter, Professor of Biology

David Cowles, Associate Professor of Biology
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ABSTRACT OF THE THESIS

Ecology of Audubon's Shearwaters (*Puffinus lherminieri*) at San Salvador, Bahamas

by

Neville Anthony Trimm, Jr.

Master of Science, Graduate Program in Biology
Loma Linda University, June 2001
Dr. William Hayes, Chairperson

The Audubon's Shearwater (*Puffinus lherminieri*), nearly pantropical in distribution, remains a poorly studied species. The subspecies *P. l. lherminieri* is endemic to the West Indies region. An estimated 5,000 pairs inhabit the Caribbean, but there has been a substantial decline with many colonies becoming extirpated. It is thought that as many as 3,000 pairs (60% of the West Indian population) nest in the Bahamas. In May and June of 2000, I collected data on shearwater demographics, colony site selection, burrow microhabitat, chick behavior and the effect of moonlight on the onset of calling of the Audubon's Shearwaters nesting on the satellite cays of San Salvador Island, Bahamas. The population of nesting shearwaters on the cays was estimated at 107 pairs. The size of the rock over a shearwater burrow and the percent of rock within a one-meter radius of the burrow entrance were two factors that distinguished between the burrow microhabitats of the different cays. The size of the colonies on individual cays was proportional to the availability of rocky habitat. Chick behavior varied significantly with time of day and age. Adults returned from offshore foraging areas to feed their young on 70% of the nights. Measures of chick activity were greater at
night than by day and increased during the three weeks of the study. The amount of ambient light on any given night did not significantly affect the time shearwaters arrived at the colony (i.e., started calling). The detailed behavior of chick feeding bouts was described, and data on morphometrics are also reported. The information gathered in this study is integral to understanding the biology of the Audubon’s Shearwater and aiding in the development of an effective conservation plan.
INTRODUCTION

Shearwaters belong to the avian order Procellariiformes, which includes "gull-like" pelagic birds that have external nostrils within tubes on the top or sides of the upper mandible. Their nostrils are associated with specialized salt-excreting glands that enable them to maintain an appropriate internal salt concentration. Procellariiforms are represented by about 93 species (Harrison, 1985) comprised of four families: albatrosses (Diomedeidae); petrels, fulmars, prions and shearwaters (Procellariidae); storm-petrels (Oceanitidae; formerly Hydrobatidae); and diving-petrels (Pelecanoididae).

The Audubon’s Shearwater (Puffinus lherminieri) is the most abundant nesting procellariiform in the West Indies (W.I.) region (Lee, unpublished manuscript). Despite its nearly pantropical distribution, this species has been the subject of few comprehensive studies. The breeding cycle (Snow, 1965; Harris, 1969), nesting success (Snow, 1965), survivorship (Harris, 1969), and food as a limiting factor in breeding (Harris, 1969) have been examined for the subspecies in the Galapagos Islands (P. l. subalaris) of the eastern Pacific. Distribution, abundance, nesting habitat characteristics and breeding biology have been described for the subspecies (P. l. bailloni) nesting on Reunion Island in the Indian Ocean (Bretagnolle et al. 2000). The few publications concerning the Caribbean subspecies (P. l. lherminieri) are comprised largely of distributional, abundance and breeding records based on anecdotal observations (Smyth, 1937; Wetmore, 1959; Lawrence, 1889; Collins, 1969; Lee and Clark, 1994).

Other shearwater species have been studied more extensively, and these can serve as reservoirs from which to draw ideas for study of Audubon’s Shearwaters.
Reproductive tactics (e.g., extra-pair fertilization, inbreeding, patterns of activity, burrow attendance, mate fidelity) have been studied in the Cory's (Thibault, 1994; Rabouam et al., 1998; Granadeiro et al., 1998), Wedge-tailed (Dyer and Hill, 1992) and Short-tailed (Austin et al., 1993) shearwaters. Demography and habitat use have been studied in the Wedge-tailed Shearwater (Ogden, 1994; Hill et al., 1996). Feeding and foraging strategies have been documented for the Cory’s (Granadeiro et al., 1998b; Hamer and Hill, 1993) and Little (Hamer, 1994) shearwaters.

Description

The Audubon’s Shearwater (Figure 1) is a small (length 30 cm; wingspan 67.5 cm) "gull-like" bird which has dark brown (appearing black) upperparts and white underparts, with brownish sides of breast and brownish undertail-coverts. Other aspects of coloration include a brown tail, black bill, brown iris and legs/feet that are flesh colored with the outer sides blackish (Harrison, 1985). The Audubon’s Shearwater could be mistaken for the Little Shearwater [Puffinus (assimilis) boydi] of the north-eastern Atlantic, based on plumage color; however, the ranges of the two do not overlap, and the Little Shearwater is slightly smaller (length 25 - 30 cm; wingspan 57.5 - 66.3 cm).

Taxonomy

The taxonomy of the Audubon’s Shearwater is not fully agreed upon. Nine or ten subspecies are listed according to Harrison (1985). Recent systematics suggests twelve
Figure 1. An adult Audubon’s Shearwater (*Puffinus lherminieri lherminieri*). Photographed by William K. Hayes.
subspecies (Warham, 1990; Sibley and Monrow, 1990; Mougin et al., 1992 all in Bretagnolle et al., 2000). Some authors have placed the Little Shearwater (P. assimilis) with this species (Mayr and Cottrell, 1979; see also Bretagnolle et al., 2000). According to Bretagnolle et al. (2000), as many as 40 taxa have been described for the iherminieri-assimilis complex. Behavioral and ecological differences, possibly at the species level, exist between the Galapagos and Atlantic subspecies, including the time of day that nests are attended (Lee, unpublished manuscript). The Galapagos race, for example, is diurnal at their breeding colonies (Harris, 1969) whereas the Atlantic race is nocturnal.

Natural History

Audubon’s Shearwaters spend most of their time out on the open seas. In the Caribbean populations, the birds fly to land at dusk where breeding activities occur during the dark hours. The peak activity period is from about 9:00-11:00 pm (D. Lee and W. Mackin, pers. comm.). At dawn the birds return to the open seas. During the daylight hours, the birds can be found at sea as solitary individuals or in small foraging flocks, often over Sargassum, feeding on fish and other inhabitants of the algal mats (Murphy, 1936). Non-feeding birds form extensive rafting aggregations on the ocean surface (Murphy, 1936). Except for a few anecdotal observations made in the Galapagos by Harris (1969), our knowledge of its feeding habits is limited. Examination of the stomach contents of 119 Audubon’s Shearwaters collected from the Gulf Stream off of North Carolina revealed that the species feeds largely on small fish and squid (Lee, unpublished manuscript).
Reproductive Phenology

Although studies have been conducted on other shearwater species, the reproductive phenology of the Audubon’s Shearwater is less understood. Audubon’s Shearwaters have formed breeding colonies on many islands in the W.I. The available information implies that breeding is initiated earlier in the more southern parts of the W.I. (Lee, unpublished manuscript). Whereas egg-laying begins in January or February in other Caribbean regions (Murphy, 1936), it probably does not begin until March in the Bahamas (Lee and Clark, 1994). In the Bahamas, the birds breed annually, possibly an adaptation to the high occurrence of hurricanes (Lee, 1996). No particular factor has been identified that synchronizes the onset of intracolonial breeding in this subspecies; however, in *P. l. sublaris* of the Galapagos, intracolonial breeding synchronization has been attributed to populous aerial displays (Snow, 1965).

In the Bahamas, courtship and prospecting for burrows begin in late November (Lee, unpublished manuscript). Egg-laying commences in early March and continues through late May (Lee and Clark, 1994). Both sexes have been reported to take turns incubating the single-egg clutch, with incubation bouts lasting up to 8-10 days (Palmer, 1962). Lee and Clark (1994) suspect that the mean incubation period is similar to that of the 48.5 days reported by Harris (1969) for the Galapagos subspecies and 51 days for the Bermuda population (Wingate, in Palmer, 1962). The mean fledging period in the Galapagos Islands is 75 days, with a range of 62-100 days (Harris, 1969). Chicks could be present in the Bahamas from late April thru late July or early August (Lee, unpublished manuscript).
Colony Site Selection

The "ideal free distribution" model of habitat selection proposes that, in situations of multiple habitat patches of varying quality, animals will settle where they will do best, assuming that they are free from interference by aggressive rivals (Alcock, 1998). The organisms take into account the presence of other individuals. When a prime habitat becomes saturated with settlers, new-comers may settle for a habitat of lower quality, but with fewer occupants and less competition. In contrast, the "despotic" model of habitat selection is one of aggression and territorial defense. The first arrival at a prime habitat site will set up a territory. New-comers, instead of settling for a habitat with less competition, will challenge the resident for the prime habitat (Krebs and Davies, 1993). Thus, both habitat structure and the presence of competitors can influence the choice of where an individual, or colony of birds, will settle.

Because the Audubon’s Shearwater is a species of special concern in the W. I., due to dwindling population size (Lee, 2000), the critical factors that dictate where a colony, or individual, will breed need to be better understood. Like many species that nest colonially, shearwaters often utilize only a portion of the available habitat for nesting. In the Exuma Islands of the Bahamas, Lee and Clark (1994) found that Audubon’s Shearwaters nested on some but not all of the numerous cays. On Reunion Island in the Indian Ocean, Bretagnolle et al. (2000) found that Audubon’s Shearwaters formed discrete colonies in multiple locations. All such colonies were found on cliffs below 1400 m elevation. Most colonies were at intermediate elevations (400-900 m) and most nests were at the base of cliffs (< 100 height). Cliffs covered by trees more than 10
m high were not colonized, whereas cliffs lacking vegetation were strongly preferred. The majority of colonies were along the southern part of the island and well inland from the coast. In the Bahamas, Audubon’s Shearwaters prefer to nest in rocky habitats but they are not restricted to cliffs (Lee and Clark, 1994; Mackin, pers. comm.).

The presence of predators or competitors may also influence colony site selection. Feral populations of Black Rats (*Rattus rattus*), for example, are widespread in the Bahamas (Lee and Clark, 1994). Rats are well-documented predators on nesting seabirds and often can wipe out entire colonies (Campbell, 1991; McChesney and Tersby, 1998). Other burrow-nesting seabirds may compete for nest sites with Audubon’s Shearwaters, including White-tailed Tropicbirds (*Phaethon lepturus*) and Bridled Terns (*Sterna anaethetus*).

Because nesting colonies are difficult to detect except by being present on an island at nighttime—a labor-intensive survey method—additional colonies would be more readily located with an improved understanding of the habitat features that make cays suitable for nesting.

Nest Microhabitat

Within a colony, one would expect microhabitat features to be critical in nest site selection. In the Bahamas, Audubon’s Shearwaters usually form nests in burrows, in recesses or holes in cliffs, under boulders (Snow, 1965), or simply in depressions where dry detritus has accumulated in the rocks (Lee and Clark, 1994). Mackin and Lee (pers. comm.) observed that nesting shearwaters on Long Cay of the Exumas preferred areas
that were sparsely covered with vegetation. Nests were most dense (1 nest/28 m²) on the eastern (seaward) side of the island and were few or absent from the dense thicket of short palms, gnarled buttonwood trees, and various shrubs on the western side of the island. Snow (1965) reported that most Audubon’s Shearwaters on South Plaza Island, Galapagos, nested in holes, recesses, or short tunnels in the broken lava cliff-face, from a few feet above the high tide line to the cliff tops (ca. 20 m). Some nests were among boulders at the foot of the cliffs, and a few more were found in holes a few feet back from the cliff-tops. Hill et al. (1996) conducted a study of the Wedge-tailed Shearwater (P. pacificus) on Heron Island, Australia. They classified habitat types on the entire island, measured burrow densities in the various habitats and then related burrow density to habitat type. Shearwaters in the undisturbed area had the highest breeding success, while those in the area disturbed by human presence had the lowest. In addition, those in the forested area had a higher breeding success than those in the area fringing the forest.

Chick Activity

Though little is known about chick activity in general, one would expect chicks to become more active as they become adults. For example, a study comparing the time budgets of Arctic Tern (Sterna paradisaea) and Common Tern (Sterna hirundo) chicks (Klaassen et al., 1994) showed that chicks of both species spent most (87%) of their time in quiescent activities (sitting quietly or being brooded). Parental brooding decreased but chick locomotion and preening increased with maturation in both species. These changes covaried with increasing mass but were statistically independent of age.
Audubon’s Shearwater chicks in the Bahamas appear to be quiet in their burrows when parents are absent from the nest (Mackin and Lee, pers. comm.). One might expect that the chicks spend most of their time sleeping or resting during the day to conserve energy and avoid detection by predators. Feeding is presumably limited to the hours of darkness when the adults return to the colony. However, the proportion of time spent active (e.g., preening, feeding) or inactive (sleeping or resting) should vary with time of day and age of the chick. For birds and other vertebrates, time devoted to sleep decreases during the course of ontogeny (Amlaner and Ball, 1983).

Effect of Ambient Light

Ambient levels of moonlight have variable effects on seabirds. Many species have improved foraging success on nights of greater moonlight, including gulls (McNeil and Rompre, 1995) and albatrosses (Klaer and Polacheck, 1998). The effect of moonlight on foraging success influences nest attendance and the feeding of young. Keitt (1998) found that nest attendance by Black-vented Shearwaters (Puffinus opisthomelas) was significantly reduced on nights of high ambient light. The percentage of burrows entered per night was lower on or near the full moon (10-30% for all burrows, 40% for active burrows) compared to other nights (80 - 100%). For Audubon’s Shearwaters on Reunion Island, Bretagnolle et al. (2000) found that both calling rate and duration of vocal activity into the night were reduced when the moon was visible. They also found that peak vocal activity was significantly decreased with increasing lunar phase when the moon was visible. In contrast to these studies, Day and Cooper (1995) concluded that the
effect of the moon on the movement rates of Dark-rumped Petrels (*Petrodroma phaeopygia*) and Newell’s Shearwaters (*Puffinus (auricularis) newelli*) on the island of Kauai, Hawaii, appeared to be small. In the Cory’s Shearwater (*Calonectris diomedea*), Granadeiro *et al.* (1998) concluded that no effect of moonlight on activity, hour of arrival at the colony or time spent inside the burrows in breeding birds was detected. The nocturnality of certain procellariiforms and alcids at their breeding sites may serve to avoid diurnal predators (Cody, 1973; Harris, S.W., 1974).

Objectives

The purpose of my thesis research was to study various aspects of the reproductive biology of Audubon’s Shearwaters nesting on the offshore cays of San Salvador Island, Bahamas. Specifically, I evaluated: 1) population size and distribution of nesting colonies; 2) the factors that influence colony site selection; 3) the microhabitat factors that influence nest site selection; 4) how the time budget of chicks varies with time of day and age; 5) the effects of ambient light on the onset of nightly vocalizations by the adults; and 6) the detailed behavior of chick feeding bouts.
MATERIALS AND METHODS

Study Site

San Salvador (Figure 2) is a relatively small island (156 km²) found on the eastern edge of the Bahamas (Figure 3). It is composed of limestone with many caves, sinkholes and fissures. The greatest elevation on the main island is 43 m (Smith, 1993). An extensive system of hypersaline lakes comprises most of the surface area of the island. Temperatures average 31 °C during summer and 17 °C during the coolest month, December (Smith, 1993). Annual precipitation ranges from 100-180 cm. There is a definite rainy (hurricane) season from August to September, and a lesser rainy season in May and June (Smith, 1993). There are 11 satellite cays just offshore from the main island (Figure 2), which range in size from 1 ha (Nancy Cay) to 15 ha (High Cay). These cays are the fragments of ancient, lithified Eolian sand dunes that formerly supported a dense forest, as is evident from the fossil flora (Hayes, pers. comm.). The plant diversity of these cays is highly variable, ranging from a mere 10 species on Green Cay to more than 40 species on Low and High Cays (Moyroud and Ehrig, 1994). The current vegetation of the offshore cays is similar in varying degrees to the coastal rock, the sand strand and sea oat, and the coastal coppice plant communities described for the main island (Smith, 1993). Although vegetation of the main island was heavily disturbed by cultivation in the nineteenth century (Olson et al., 1990), the impact of man on the satellite cays is unknown, except that regionally introduced moths (Cactoblastis cactorum) have decimated the Prickly-pear Cacti (Opuntia stricta) and Black Rats have been documented on Low Cay and High Cay (Hayes et al., 1995; Hayes, pers. comm.).
Figure 2. San Salvador Island and its satellite cays.
Figure 3. San Salvador's position in relation to Florida, the rest of the Bahamas and the Caribbean.
Capture, Processing and Marking

The capture and banding of shearwaters took place on three cays during the first week of the study (7-12 May, 2000). Captures were accomplished by searching for birds at night. The birds were usually detected audibly. Once located, they were captured by simply walking up to them and grabbing them. Some birds were found sitting on rocks in the open; however, most of them were found in crevices, under matted vegetation, or among and under rocks after they were heard calling. Once in hand, a coded band was placed on one of its legs and the following measurements were recorded: bill width (mm) at the culmen, bill length (mm), tarsus length (mm), tail length (mm) and flattened wing cord length (cm). Finally, the bird was placed in a cloth bag and weighed (g) on a Pesola spring scale. Immediately following this procedure, all birds were released at the site of capture. Headlamps were used to work at night. Nineteen adults were captured and banded.

Surveys of Breeding Colonies and Nest Microhabitats

I conducted surveys of nine off-shore cays during the first week of the study (6-14 May) with the help of two assistants. Up to three cays were surveyed on a given night (a minimum of one hour per cay depending on size) and each cay was sampled for only one night. The man-hours for surveys ranged from 3.0 (Catto, Middle Cays) to 10 (Green, Man Head Cays), and were restricted to the period of 2000-0200 hrs. Arriving at the cay was usually a late afternoon event. After setting up camp, we focused on placement of rodent traps (Sherman aluminum folding live capture traps, 25.4 cm length), before dusk,
in an effort to verify the presence or absence of feral rats on the cays. The live rodent traps were baited with peanuts and set out by dusk in a dispersed manner so as to cover representative areas of the island.

During the hours of darkness, we located shearwater burrows (by the calling of adult shearwaters) and marked them for microhabitat evaluation the following morning. In some cases, the precise burrow location could not be determined. All adults captured were marked and processed as described previously.

The next day we checked the traps for rats and recorded microhabitat variables for the shearwater nests. All rats found were euthanized by drowning (within trap) and then discarded in the sea. The following microhabitat features of each burrow were recorded: 1) height of the tallest vegetation (cm) within a 1 m radius of the burrow entrance; 2) percent vegetation cover directly above the burrow entrance (determined by densiometer placed at the base of the burrow entrance); 3) the estimated proportion of rock, sand, and vegetation substrate within a 1 m radius of the burrow entrance (the three measures summed to 1.0); 4) number of crevices within a 1 m radius of the burrow entrance; 5) relative size of rock over the burrow (based on area: small = <1 m²; medium = 1-3 m²; large = >3 m²); 6) the nearest distance (m) from each burrow to the bluff (or high tide line) as measured with a laser rangefinder (Intel Optics Laser 70); 7) relative nest density (distance in m from each burrow to its nearest neighboring burrow); and 8) altitude and GPS coordinates (with use of a Garmin GPS 12; GPS coordinates were within 5 m accuracy but altitude data were deemed unreliable).
Rocky habitats on the main island were surveyed at Dump Reef (2.6 man-hours, 28 May), where a colony of White-tailed Tropicbirds nests in the cliffs, and at North Point adjacent to Cut Cay (4 man-hours, 2 June). Both of these sites are on the north shore of San Salvador. Other rocky habitats on the mainland were not surveyed.

Nesting Biology: Chick Activity, Adult Arrival Times, and Feeding Behavior

Data concerning nesting biology were collected on Man Head Cay after the surveys of offshore cays were completed. From 14 May through 6 June, I camped on Man Head Cay, returning to the main island Friday nights through Sunday mornings. Initially, I conducted a survey that determined the presence or absence of eggs and chicks in burrows that had been marked the previous week during the surveys conducted by Hayes and myself. The burrows were examined by means of a custom-built, 12-V burrowscope with a miniaturized black/white CCD camera [the two models used were ProVideo CVC-120R (0.5 lux, 3.6 mm wide angle lens, 7/8" dia X 1-9/16) and ProVideo CVC-130R (0.1 lux; 3.6 mm wide angle lens; 1" dia. X 2-1/4")], five infrared-emitting LED’s affixed to the outside of the camera, and a 3-m cable. The unit was powered by a 7 amp-hour hip-pack battery and the signal was fed to a black-and-white monitor for viewing. The burrowscope was carefully introduced into each burrow entrance and maneuvered around the burrow until I determined whether the burrow was occupied by an adult (or pair), a chick or an egg. When applicable, comments on the nature of the interior of the burrow were recorded (i.e., a description of scat, egg shells, or other debris that might be noteworthy). Regularly throughout the duration of the study, the island was
"scouted" to ascertain its general population of Audubon's Shearwaters and to locate concentrations of nesting birds.

Burrowscopes were also used to evaluate circadian and ontogenetic variation in chick activity. After finding a burrow that housed a chick, a burrowscope was carefully introduced into the burrow and concealed as much as possible. Three chicks were monitored during the course of the study (chick 1: 5/17/00 - 6/6/00; chick 2: 5/15/00 - 6/6/00; chick 3: 5/16/00 - 6/6/00). Chick activity was monitored by time-sampling (10 minute periods of continuous observation) during six periods of the day (at 0400, 0800, 1200, 1600, 2000 and 2400 hrs.). During each observation period the following data were recorded for each burrow: 1) the presence of birds or eggs, and 2) chick activity. At times, detailed descriptions of feeding bouts were obtained. Chick activity was classified as follows: sleeping (motionless with eyes closed and head tucked), resting (awake but motionless with head raised and eyes usually opened), preening, feeding (receiving regurgitate from an adult), or active (eyes open, head raised, but not engaged in one of the aforementioned activities). These activities were deemed mutually exclusive (i.e., a chick could be classified within only one category at any given time). As the chick was viewed on the monitor, a stopwatch was used to record the start and stop times of its activities as classified above.

As sunset approached, a keen lookout was kept for the first sign of adult activity (usually detected audibly). Because adults were rarely found in burrows during daylight (N = 2), I assumed that the presence of adults was indicative of first arrivals from the sea. General notes were taken concerning this observation (time, general direction, over land
or at sea, sex if discernable). Scouting usually occurred until about midnight or 0100
during which careful attention was paid to making scheduled time-sampling observations.

A general description of the weather (cloud cover) was regularly noted. Data on
sunrise, sunset, moonrise, moonset, and moon phases were obtained from a weather
source on the internet (www.sunrisesunset.com) for Nassau. I was unable to make
corrections specific to San Salvador. The percent of lunar surface illuminated nightly was
obtained from another internet source
(http://aa.usno.navy.mil/data/docs/RS_OneYear.html) and was used to evaluate the effect
of ambient light on arrival times of adults at the breeding site.

Analyses

The data were evaluated initially to see if they met the assumptions of parametric
tests (i.e., normality, homoscedasticity, absence of outliers). Because much of the data
failed to conform to parametric assumptions, I relied largely on nonparametric tests
(Kruskal-Wallis ANOVAs and Spearman’s correlation coefficients). Questions that
required regression and discriminant function analyses were conducted as such because
these tests are largely robust against parametric violations. However, several variables
were rank-transformed prior to analysis to improve normality. All statistical analyses
were conducted with SPSS 8.0, and are discussed in detail in the results section.
RESULTS

Population Surveys: Density and Colony Site Selection

During the first week of the study (7-12 May), each of the cays was surveyed at night for nesting Audubon’s Shearwaters. Moonlight (percentage of lunar disk illuminated) during this period increased from 17% (7 May) to 70% (12 May). The number of burrows (nesting pairs) located on each cay and select geographical and biological attributes of each cay are summarized in Table 1. Middle Cay was the only cay on which no shearwaters were detected. Man Head Cay had the largest population, with 22 pairs detected. Even though some burrows contained a single bird, I assumed that each active burrow represented a breeding pair.

The ensuing weeks (14 May - 6 June) spent on Man Head Cay allowed for a more accurate estimation of colony size. By the time the study ended, a total of 31 burrows were detected on Man Head Cay, leading to the conclusion that there was a detection rate of 71% on Man Head during the single-night survey of the first week. Using this detection rate for all cays, the number of burrows detected during the first single-night survey on each cay was divided by 0.71 to yield the estimated population sizes reported in Table 1. Thus, the estimated total population of adult breeding shearwaters on the nine satellite cays surveyed was 107 pairs. The relative spatial distribution of the burrows on the various cays can be seen in Figure 4. The majority of nests, for which offspring were determined, contained chicks (81.3% of 16 nests; Table 1).

Stepwise linear regression analysis was used to evaluate the factors that influence colony size. The dependent variable (DV) was the estimated number of shearwater pairs
Table 1. Topographical, habitat and sampling data for single-night surveys of Audubon's Shearwaters on offshore cays.

| Cay       | Available habitat \(^a\) (%) | Light \(^b\) (%) | Area \(^d\) (ha) | Max elev \(^e\) (m) | Distance to main island \(^f\) (m) | Chicks found | Eggs found | Pairs found | Estimated pairs | Estimated density (pairs/ha) | Relative seabird density \(^d\) | Trap nights \(^e\) | Rats \(^f\) | Iguana density \(^f\) (N/ha) |
|-----------|-------------------------------|------------------|------------------|---------------------|-------------------------------|------------|-----------|------------|----------------|-----------------------------|----------------------|----------|----------------------|
| Man Head  | 60-80                         | 17               | 3.3              | 6+                  | 275                           | 6          | 1         | 22         | 31              | 9.4                         | 1                    | 66       | 0                     | 22              |
| Catto     | 0-20                          | 26               | 1.9              | 12+                 | 2050                          | 0          | 0         | 1          | 1               | 0.5                         | 3                    | 16       | 0                     | 0               |
| Gaulin    | 20-40                         | 26               | 1.6              | 3+                  | 2000                          | 0          | 0         | 17         | 24              | 15.0                        | 3                    | 6+5      | 0                     | 6               |
| Low       | 0-20                          | 37               | 10.8             | 6                   | 1013                          | 0          | 0         | 3          | 4               | 0.4                         | 1                    | 5+9      | 1+1                  | 7               |
| Middle    | 20-40                         | 37               | 2.7              | 6+                  | 963                           | 0          | 0         | 0          | 0               | 0.0                         | 1                    | 10+5     | 0                     | 0               |
| High      | 0-20                          | 37               | 13.4             | 18+                 | 575                           | 3          | 0         | 11         | 15              | 1.1                         | 1                    | 7+5      | 0                     | 0               |
| Green     | 60-80                         | 50               | 5.1              | 8                   | 1950                          | 3          | 1         | 18         | 25              | 4.9                         | 2                    | 0+11     | --                   | 49              |
| Cut       | 0-20                          | 70               | 3                | 16                  | 15                            | 1          | 0         | 1          | 1               | 0.3                         | 1                    | 1+0      | --                   | 0               |
| Goulding  | 40-60                         | 59               | 2.9              | 9+                  | 588                           | 0          | 1         | 4          | 6               | 2.1                         | 1                    | 15       | 0                     | 31              |
| Totals    | --                            | --               | 44.7             | --                  | --                            | 13         | 3         | 77         | 107             | --                          | --                   | 125+35   | 1+1                  | --              |

\(^a\) Proportion of cay consisting of rock crevice habitat, as visually estimated.

\(^b\) Available moonlight (percent of lunar disk illuminated) during the single night of survey during the period 7-12 May, 2000.

\(^c\) From maps published by the Lands and Surveys Department, Bahamas; area was measured by weighing paper cutouts; benchmark elevations are provided for some cays, but other elevations (indicated by +) are based on elevation contours (3 m intervals) and may be up to 2 m greater than indicated.

\(^d\) Relative density of other nesting seabird species: 1 = low; 2 = medium; 3 = high (Hayes, unpubl. data).

\(^e\) Trap nights from this study + additional trap nights from 1999 (Hayes, unpubl. data). Although rats have not been trapped on High Cay, their presence is apparent from a carcass found there in November 1995 (Hayes, pers. comm.); thus, rats are present on both High Cay and Low Cay, from North Point on the main island, 3 additional rats were captured in 22 trap nights during May 2000.

\(^f\) From Hayes et al., 1995
Figure 4. The distribution of Audubon’s Shearwater burrows on eight of San Salvador’s satellite cays.
(for each cay), which was rank-transformed to normalize the data. The following
geophysical and biological factors were treated as independent variables (IV’s): 1) cay
size (rank-transformed from hectares); 2) maximum elevation of cay (m); 3) distance
from the main island (rank-transformed from meters); 4) the north-south orientation of
each cay (1 = northern cays, 2 = Goulding Cay, 3 = High, Low and Middle Cays); 5)
habitat availability (as defined below); 6) relative density of other nesting seabirds [up to
5 species of terns, two species of boobies and Magnificent Frigatebirds (*Fregata
magnificens*): 1 = <5 pairs/ha, 2 = 10-40 pairs/ha, 3 = >100 pairs/ha; Hayes, unpublished
data]; 7) presence vs. absence of rats; and 8) the density (N/ha) of San Salvador Rock
Iguanas ([*Cyclura rileyi rileyi*]; ranked transformed from data Hayes *et al*., 1995).
Because nests were found only in rocky areas, nest habitat availability was measured as
the proportion of the cay that was covered by rocky areas, as estimated visually in 20%
increments (0-20%, 20-40%, 40-60%, 60-80% and 80-100%). However, several IV’s had
to be removed from the regression equation because of multicolinearity. These included
distance of cay to the main island (which covaried with density of other seabirds),
presence vs. absence of rats (which covaried with size of cay), and iguana density (which
covaried with habitat availability). The results indicated that habitat availability was the
only variable that explained the number of shearwater pairs ($F_{1,7} = 6.23$, $P = 0.041$). The
coefficient of determination (adjusted $r^2$) indicated that 39.5% of the variance in
shearwater numbers was explained by this variable.
The status of shearwaters on the main island of San Salvador is uncertain. At least two individuals were detected at North Point (adjacent to Cut Cay), but nest burrows were not located. Neither shearwaters nor nests were found at Dump Reef cliffs.

Of the variables that were omitted from the regression, only iguana density was significantly correlated (Spearman’s rho = 0.682; P = 0.043; N = 9 cays) with the estimated shearwater population of the individual cays. Both distance of the cay from the main island (Spearman’s rho = -0.050; P = 0.898; N = 9 cays) and rats (Spearman’s rho = -0.126; P = 0.766; N = 9 cays) were negatively, but not significantly, correlated with the DV. A Mann-Whitney U test revealed no difference in numbers of shearwaters on cays with rats present (N = 2) versus rats absent (N = 6; U = 5.0, P = 0.739). Both cays on which rats are present (High and Low Cays) supported small numbers of shearwaters (Table 1). Although no rats were trapped on High Cay (12 trap-nights total), a carcass was found there in November 1995 (Hayes, unpubl. data). Rats were more readily trapped on Low Cay (2 of 14 trap-nights; 14.3%) and on North Point on the main island (3 of 22 trap-nights; 13.6%), where rat populations seem to be more dense.

Nest Site Selection

Microhabitat features of burrows on the various cays are compared in Table 2. These data were subjected to discriminant function analysis. The intent here was to determine whether or not the microhabitat features of a burrow can be used to determine which cay the burrow was most likely to be found on. Such an analysis can be helpful to understand which factors are most shared among colonies and, therefore, may be most
Table 2. Summary of microhabitat data (mean ± s.e.) collected for the burrows on the satellite cays.

<table>
<thead>
<tr>
<th>Cay</th>
<th>Vegetation height (cm)</th>
<th>Vegetation cover (%)</th>
<th>Substrate cover (%)</th>
<th>Distance to bluff (m)</th>
<th>Distance to nearest neighbor (m)</th>
<th>Crevices (N)</th>
<th>Rock size (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gaulin</td>
<td>46 ± 10 n = 17</td>
<td>53 ± 11 n = 17</td>
<td>41 ± 10 n = 17</td>
<td>1 ± 0 n = 17</td>
<td>58 ± 10 n = 17</td>
<td>12 ± 1 n = 17</td>
<td>11 ± 3 n = 17</td>
</tr>
<tr>
<td>Goulding</td>
<td>0 n = 3 100 ± 0 n = 3</td>
<td>0 n = 3</td>
<td>0 n = 3</td>
<td>0 n = 3</td>
<td>18 ± 3 n = 4</td>
<td>4 ± 0 n = 4</td>
<td>--</td>
</tr>
<tr>
<td>Green</td>
<td>91 ± 9 n = 6</td>
<td>86 ± 13 n = 6</td>
<td>4 ± 3 n = 6</td>
<td>1 ± 1 n = 6</td>
<td>80 ± 14 n = 6</td>
<td>20 ± 5 n = 6</td>
<td>19 ± 8 n = 7</td>
</tr>
<tr>
<td>High</td>
<td>56 ± 15 n = 5</td>
<td>40 ± 20 n = 5</td>
<td>42 ± 15 n = 6</td>
<td>5 ± 3 n = 6</td>
<td>53 ± 16 n = 6</td>
<td>7 ± 2 n = 7</td>
<td>12 ± 6 n = 6</td>
</tr>
<tr>
<td>Low</td>
<td>49 ± 49 n = 2</td>
<td>0 n = 2</td>
<td>98 ± 3 n = 2</td>
<td>3 ± 3 n = 2</td>
<td>0 n = 2</td>
<td>9 ± 4 n = 2</td>
<td>460 ± 0 n = 2</td>
</tr>
<tr>
<td>Man Head</td>
<td>64 ± 12 n = 24</td>
<td>37 ± 9 n = 25</td>
<td>52 ± 8 n = 24</td>
<td>7 ± 4 n = 24</td>
<td>41 ± 9 n = 24</td>
<td>9 ± 3 n = 25</td>
<td>10 ± 1 n = 26</td>
</tr>
</tbody>
</table>
critical. Accordingly, the cays were used as the DV and the following microhabitat features were used as the IV's: 1) height of the tallest vegetation within a 1 m radius of the burrow, 2) percent vegetation cover directly above the burrow entrance, 3) relative proportion of substrate cover occupied by rock, sand, and/or vegetation within a 1 m radius of the burrow entrance, 4) number of crevices within a 1 m radius of the burrow entrance, 5) relative size of rock over the burrow, 6) nearest distance from each burrow to the bluff, and 7) relative nesting density. Only four of the nine cays (i.e., Man Head, Gaulin, High and Green) surveyed were used in the analysis. I omitted Low Cay because of the low number of burrows found on this cay (N = 2). Goulding Cay was left out because each of its burrows was missing data for at least one of the discriminating variables. Data were not collected from the remaining cays. Because of time constraints, microhabitat measures were not taken from all burrows located. Of the 77 burrows detected, data for 62% (N = 48) were entered in the analysis.

The results suggested that microhabitat features of the burrows were distinctive among the four cays (Wilks' $\lambda = 0.193; \chi^2 = 66.709; P < 0.05; N = 48$). The size of the rock over the burrow and the percent of ground covered by rock in a 1 m radius were the two variables with the most discriminating power. The number of crevices (i.e., potential nesting burrows) within a 1 m radius of the burrow entrance was the variable with the least predictive power. The variables used allowed for the discriminating function to correctly predict 68.6% of the cases. Gaulin Cay had the most correct predictions (13 cases; 76.5%) and was most likely to be mis-predicted (3 cases; 17.6%) as High Cay.
High Cay had the least percentage of correct predictions (2 cases; 40%) and was most likely to be mis-predicted (2 cases; 40%) as Man Head Cay.

Morphometrics

Measurements were taken of 19 adult shearwaters from three cays (i.e., Man Head, Green and Gaulin). The data are summarized in Table 3. The sample size was \( N = 19 \) for all variables except wing length (\( N = 18 \)). The birds could not be reliably sexed.

Chick Activity and Nest Attendance by Adults

The data on chick activity are summarized in Figures 5 and 6. Chicks devoted most of their time to sleeping (\( F = 7.769; P = 0.001; N = 146 \)) and the least amount of time to feeding. A discriminant function analysis was conducted to learn if there was a difference in the amount of time each chick spent in the various activities. Such an analysis could be useful to evaluate distinctive chick behavior related to general health or age. For this test, the five classifications of chick behavior (i.e., sleeping, feeding, resting, preening and active) were used as IV's and the DV was "chick" (i.e., chick 1, chick 2, and chick 3). The results indicated that there was a significant difference between chicks in the amount of time spent in the various activities (Wilks' \( \lambda = 0.750; \chi^2 = 40.584; P < 0.05; N = 146 \)). Time (s) spent resting (mean ± s.d.; chick 1: 199 ± 175; chick 2: 90 ± 162; chick 3: 278 ± 220) and time (s) spent sleeping (mean ± s.d.; chick 1: 162 ± 209; chick 2: 312 ± 262; chick 3: 152 ± 209) were the two variables with the most discriminating power. The inclusion of all five variables allowed for the discriminating
Table 3. Morphometric data (mean ± s.e.) for adult Audubon’s Shearwaters captured on three cays.

<table>
<thead>
<tr>
<th>Cay</th>
<th>Birds (N)</th>
<th>Mass (g)</th>
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<td>39 ± 2</td>
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</tr>
<tr>
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The change of chick activity over time was analyzed at two levels: circadian differences and weekly differences (age of chicks). Due to the nonparametric nature of the data, the Kruskal-Wallis test was used in these analyses with the assumption that all observations were independent within and between individual chicks. To analyze the circadian changes in chick activity, the day was divided into six four-hour periods (i.e., 0400, 0800, 1200, 1600, 2000 and 2400). All observations that occurred between 0400 and 0759 were classified in the 0400 category (N = 22); observations between 0800 and 1159 were put into the 0800 category (N = 29), and so on. The time categories were used as the IV (grouping variable) and the five behavioral categories were used as DV's (test variables). Chick 1 represented 38% (N = 56) of all data cases, chick 2 comprised 45% (N = 66) of the observations, and chick 3 accounted for 18% (N = 24) of the data set. The results indicated that the percent of time (s) spent feeding ($\chi^2 = 17.3; P = 0.004; N = 146$), sleeping ($\chi^2 = 32.1; P < 0.05; N = 146$) and active ($\chi^2 = 27.5; P < 0.05; N = 146$) varied significantly during the day. The percent of time (s) spent preening ($\chi^2 = 4.6; P = 0.464; N = 146$) and resting ($\chi^2 = 5.2; P = 0.387; N = 146$) did not differ significantly with time of day (Figure 5).
Figure 5. Graphs showing how the percent of time (s) spent by chicks feeding (top left), active (top right), resting (bottom left), sleeping (bottom right) and preening (center) varied with time of day. The bars represent means. The error bars show the 95% confidence interval of the mean. N = 146 observations.
Chick behavior also changed as they got older (Figure 6). In considering how the chicks' behavior changed as weeks progressed, the entire period of chick behavior observation (i.e., 16 days spanning May 15 - June 6, 2000) was divided into four weeks Sunday through Saturday. Week 1 contained 26% (N = 39) of all observations; 41% (N = 61) of the observations were conducted in week 2, 16% (N = 24) in week 3, and 15% (N = 22) came from week 4. A Kruskal-Wallis test using the weekly categories as the IV (grouping variable) and the percent of time (s) spent in each of the five behavioral categories as the DV’s (test variables) revealed that the percent of time (s) spent sleeping ($\chi^2 = 8.371; P = 0.039; N = 146$) and resting ($\chi^2 = 10.651; P = 0.014; N = 146$) changed significantly as the chicks got older. The percent of time (s) spent feeding ($\chi^2 = 4.400; P = 0.221; N = 146$), active ($\chi^2 = 1.405; P = 0.704; N = 146$) and preening ($\chi^2 = 7.149; P = 0.67; N = 146$) did not vary with chick age.

Nest attendance was evaluated as the percentage of nights adults were present at the nests of the three chicks studied (Table 4). Chicks 1 and 2 were attended on 73% of the nights and chick 3 was attended 64% of the nights. For all three chicks, mean nest attendance was 70%. Of the eleven nights on which data were collected, there was only one night (9%) on which none of the chicks were attended. Due to some difficulty in detection (the adults were sometimes heard but not seen; the camera was situated to view the chicks), these values are likely to be underestimates of actual nest attendance.
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Table 4. (A) Number of adults that attended chicks 1, 2 and 3 on 11 nights that nest attendance data were collected on Man Head Cay. (B) The proportion of nights (N = 11) chicks 1, 2 and 3 were attended by 0, 1 or 2 adults on Man Head Cay.

### A.

<table>
<thead>
<tr>
<th>Chick</th>
<th>5/15/00</th>
<th>5/17/00</th>
<th>5/18/00</th>
<th>5/21/00</th>
<th>5/23/00</th>
<th>5/24/00</th>
<th>5/25/00</th>
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</tbody>
</table>

### B.

<table>
<thead>
<tr>
<th>Chick</th>
<th>Adults present (%)</th>
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<th>Two</th>
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<tr>
<td>1</td>
<td></td>
<td>27.3</td>
<td>27.3</td>
<td>45.5</td>
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<tr>
<td>2</td>
<td></td>
<td>27.3</td>
<td>54.5</td>
<td>18.2</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>27.3</td>
<td>63.6</td>
<td>9.1</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>27.3</td>
<td>48.5</td>
<td>24.3</td>
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</table>
Effect of Ambient Light on Calling

To analyze the effect of ambient light on the onset of shearwater calling, data were collected for 13 evenings on Man Head Cay (5/1500 - 6/5/00). The onset of calling for each night, calculated as minutes after sunset, varied from 51 - 304. Sunset, moonset and moonrise times were obtained from the website www.sunsetsunrise.com. Percent of lunar surface illuminated (relative amount of ambient light available) was obtained from the U.S. navy website (www.aa.usno.navy.mil). When the moon was not present above the horizon during the first two hours of the night, the amount of ambient light available was effectively considered 0, despite its actual phase. A linear regression (Figure 7) of calling time on the percent of ambient light available indicated that there was no relationship between the onset of shearwater calling and amount of ambient light at the breeding colony (t = 1.904; P=0.083; beta=0.498; N=13). However, only three evenings had moonlight levels greater than 0.2.

Description of Feeding Bouts

Five complete and two incomplete feeding bouts were observed during the study period. Two of the feeding bouts were not part of the scheduled time-sampling observation periods. The mean duration of a feeding bout (i.e., from adult’s entrance into the burrow, to the ignoring of chick) was 336.4 seconds (range = 266 - 420; N = 5). In all cases the adult landed near the nest (usually within a meter or so) and “waddled” into the burrow. The chicks instantly became alert upon the adult’s landing. As the adult entered the burrow, the chick began to chirp vigorously. This chick calling was so soft that it
Figure 7. Regression depicting the relationship between the percent of moonlight available and the time of the onset of shearwater calling.
could only be heard within a few meters of the burrow. Older chicks (observations later in the study period) would violently peck at the adult's bill and head. This pecking appeared to be food solicitation and possibly stimulated regurgitation by the adult as the adult usually commenced regurgitation at a heightened state of chick pecking/begging. Regurgitation would begin with a suite of simultaneous behaviors. With bill wide open, the adult would engage in a vigorous forward/backward head bobbing motion accompanied by rapid gular fluttering. This regurgitation behavior was further accompanied by raising of the rump and lowering of the adult's head. In smaller burrows, elevation of the rump was not as noticeable as it was restricted by the height of the burrow. As the adult's bill opened wide the chick would stop pecking and place its opened bill inside the adult's bill. Regurgitation bouts would begin relatively slowly, increase in speed, then slow down again. As the motion slowed, the chick would remove its bill from the adult's throat and immediately commence pecking at the adult's head. The regurgitation process would be repeated, delivering multiple portions of food to the chick before the adult left. An average of 10.5 regurgitations (range = 7 - 16; N = 4) were completed during each feeding bout, and each regurgitation event lasted an average of 4.3 sec. (range = 3 - 6 ;N = 6). After the last regurgitation, the chick would persist in calling and pecking at the adult until the adult turned away from the chick and seemingly ignored it. This could serve as a cue to the chick that feeding had ended, as the chick stopped begging even though the adult was still present. Additional data (on frequency of feeding bouts and sex of feeding adult) were not obtained.
DISCUSSION

Population Size

Results of the population surveys suggest a breeding population of 107 pairs on nine of San Salvador’s cays. This estimate is seven times larger than that (15+ pairs) given by Lee and Clark (1994) for San Salvador Island. My estimate for San Salvador represents 2% of the estimated maximum of 5000 pairs nesting in the West Indies (Lee, 2000). West Indian colonies for which shearwater numbers are reported range from less than 10 individuals on a few cays in the British and U.S. Virgin Islands (Lee, 2000), to 3000 on Long Cay, Exumas, Bahamas (Mackin, pers. comm.).

Colony Site Selection

The amount of available habitat was the most important factor predicting the number of nesting shearwaters that occupied the various cays. Cays with a higher proportion of available habitat had higher numbers of nesting shearwaters. Other geophysical factors were unimportant for determining colony size, including size of cay, maximum elevation of cay, distance from the main island, and north-south orientation. Nevertheless, several cays appeared to have considerable habitat but supported only a handful of shearwater pairs (e.g., Goulding Cay) or none at all (Middle Cay). In spite of its small size, Gaulin Cay (1.6 ha) supported the most dense colony of shearwaters (15 pairs/ha).

I found no evidence that other vertebrate species exert an influence on location of colonies or on the numbers of nesting shearwaters within a colony. For example, some
cays harbor dense seabird colonies (Table 1), but their relative abundance was independent of shearwater abundance. However, there are two species that nest in rock crevices on San Salvador that might be expected to compete for nest sites with shearwaters. Bridled Terns nest in small numbers on most of the cays occupied by shearwaters (Hayes, unpublished data), and have been reported to occupy abandoned burrows of Audubon’s Shearwaters (Bonhote, 1903, in Haney et al., 1999). Unfortunately, my analyses did not allow me to evaluate whether nest site competition occurs between these two species. However, White-tailed Tropicbirds nest in the bluffs above Dump Reef, where the absence of shearwaters suggests that competitive exclusion is occurring. Despite what appears to be suitable habitat, tropicbirds do not nest on any of the offshore cays (Hayes, pers. comm.). Lee and Walsh-McGehee (1998) reported that in Bermuda the tropicbirds compete for nest sites with the smaller Bermuda Petrel (Pterodroma cahow)--a bird similar in size to Audubon’s Shearwater--and may kill the petrel’s chicks and take over the nest site when the adult petrels are feeding at sea. Tropicbirds nest at other localities on the main island of San Salvador, and more surveys are needed to determine whether shearwaters nest among them.

Another large vertebrate, the San Salvador Rock Iguana, also occurs on the cays and has been observed to retreat into the same rock crevice occupied by nesting shearwaters (Hayes, pers. comm.). However, my regression analyses showed that the abundance of both iguanas and shearwaters covaried with habitat availability. Although iguanas occasionally feed on small prey and carrion, they are largely vegetarian and have not been observed to prey on seabird chicks or eggs (Cyril, 2001; Hayes et al., 1995).
Bridled Terns are successful at chasing iguanas away from their nests (Hayes, pers. comm.), but no such interactions between shearwaters and iguanas have been observed. The fact that both shearwaters and iguanas coexist on the same cays and covary in abundance with habitat availability suggests that neither has a significant impact on the other species.

I was unable to detect predation on shearwaters in my study. Rats are well-documented predators on nesting seabirds and often can wipe out entire colonies (Campbell, 1991; Lee and Haney, 1996; McChesney and Tersby, 1998), but I found no statistical evidence that rats affect San Salvador's shearwater colonies. However, our samples for rat trapping are minimal and we do not know whether larger colonies might have existed on infested cays (High Cay, Low Cay) prior to rat invasions. Nevertheless, studies of other shearwater populations confirm their vulnerability to natural predators and invasive species. In the Galapagos, Audubon’s Shearwaters are preyed upon by the Galapagos Short-eared Owl (Asio flammeus galapagoensis). Snow (1965) reported that over the course of 15 months, the wings of more than 100 freshly killed shearwaters were found. He suggested that this heavy predation may partially explain the diurnal nature of the Galapagos subspecies. In addition to the owls, the Galapagos Hawk (Buteo galapagoensis) is an occasional diurnal predator of shearwaters (Harris, 1969). On San Salvador, Barn Owls (Tyto alba) are occasionally seen on several offshore cays (Hayes, pers. comm.) but none were seen during the time of my study. On Nativity Island, Mexico, Western Gulls (Larus occidentalis) were the most frequent predators on Black-vented Shearwaters, but Peregrine Falcons (Falco peregrinus) and Common Ravens
(Corvus corax) were occasional predators as well. Feral cats, however, inflicted the greatest levels of mortality (Keitt, 1998).

Other factors that may affect colony size were not considered in this study but may be important for explaining colony size. One such factor is proximity to the birds’ foraging grounds, as the birds may prefer to minimize travel distance. Unfortunately, I do not know where the birds forage at sea. If the majority of adults forage either to the north or to the south of San Salvador (no such data are available), there was no association between colony size and a north-south gradient. Further studies involving telemetry would be necessary to determine where at sea the birds forage. Another factor might be historical disturbance of the colonies by humans. Activities such as hunting and egging could influence present-day habitat use.

There are several reasons why the population estimates in this study are likely to be underestimates of the total population size on San Salvador. First, several cays (White Cay, Nancy Cay, and a few rocky outcrops off High and Middle Cays) were not sampled, and these may support small colonies. Second, several or more colonies may exist on the main island. No shearwaters were detected at the Dump Reef bluffs, and the single individual seen in flight from North Point may have been a resident of nearby Cut Cay. However, an abundance of suitable habitat exists on San Salvador’s eastern and southern shores, and these areas need to be surveyed. Finally, the single-night detectability estimate of 71% may be in error, though it corresponds well with the rate of nest-attendance by one or more adults (70%). However, because some cays were sampled during moderate levels of moonlight (Table 1), detectability (calling) rates might have
been reduced, as has been reported for Audubon’s Shearwaters in the Indian Ocean (Bretagnolle et al., 2000).

It would be helpful to identify key criteria by which Audubon’s Shearwater colonies could be more readily located. Apart from the need for isolation and the presence of rocky habitat with crevices, no further useful criteria were discerned from my analysis. My impression is that the available habitat does not limit shearwater numbers, but more detailed evaluation of the habitat on each cay is necessary to help understand why some cays support larger numbers of shearwaters than others.

Nest Site Selection

Nest microhabitats varied significantly among cays. The analysis of burrow microhabitats suggests that the size of the rock over the burrow and the percent of rock covering the ground around the burrow (1 m radius) were the two most important burrow microhabitat features in discriminating between which cay any given nest could be found. Thus, these two variables were the most distinctive among the cays and indicate their relative unimportance for nest site selection. The microhabitat feature that had the least discriminating power was the number of crevices--or potential nesting burrows--around the entrance of the active burrow. This feature was the most similar from cay to cay and suggests that the presence of one or more crevices is critical for selection of a nest site, regardless of the size of the rock or the substrate cover.

Apart from the need for rock crevices, many of the microhabitat features of nest burrows appeared to be associated with the unique habitat of each cay (Table 2).
Shearwaters nesting on Green Cay and Gaulin Cay, for example, utilized relatively small rocks, which were the only ones available. In contrast, those on Goulding Cay utilized subterranean passageways (cracks) in the exceptionally large cliffs even though smaller rocks were abundant. This might suggest a preference for cracks in large rocks compared to openings beneath small rocks when both habitats are available.

Vegetation differences were also apparent amongst the cays (Table 2). For example, the small rocks above the burrows on Green Cay were nestled amongst considerable vegetation. Mean vegetation height and cover were greatest on Green Cay. The nests in the cliffs of Goulding Cay, in contrast, lacked vegetation altogether. On Man Head Cay, the shearwaters were absent from the more densely vegetated western side of the island and nested within the vegetation only on the eastern and northern periphery. I suspect that the shearwaters avoid more densely vegetated areas. On Gaulin Cay, a substantial portion of the area where burrows were found was comprised of rocks covered by Sea Purslane (*Sesuvium portulacastrum*), which forms a dense “mat” of low-growing ground cover. The burrow entrances here were well hidden, which may help explain why Gaulin Cay supported such a dense population.

Many of the nests were situated at the periphery of the islands, as reflected in the relatively short distances to the bluffs or high tide line (Table 2 and Figure 4). On some cays, suitable habitat was present only on the periphery (e.g., Gaulin, Low and High Cays). Suitable habitat was present in the interior of other cays (e.g., Green Cay), where shearwaters were more likely to be nesting some distance from the periphery of the
island. Some clustering of nests is evident from Figure 4, which was also apparent in the small distances to nearest neighbor.

Unfortunately, my analyses cannot confirm how selective shearwaters are in their choice of nest sites other than their dependence on some kind of rock crevice that offers shelter. To demonstrate selectivity, it would be necessary to survey the abundance and distribution of crevices on each of the cays and show that the characteristics of nest sites were distinct from a random selection of available crevices. A more detailed study could eliminate some of the observer bias in my study. For example, a higher proportion of burrows were detected on Man Head compared to other cays because more time was spent there, allowing for a more thorough search of the vegetative habitats. On the other cays where less time was spent searching, the burrows in exposed habitat were perhaps more readily detected. A more thorough search of the vegetated habitats might have revealed more burrows present. In addition, searching efficiency and burrow detectability are influenced by the number of researchers looking for burrows.

Complex issues are involved in determining the theoretical habitat selection model (i.e., ideal free distribution or despotism) that determines where a breeding pair of Audubon’s Shearwaters would nest. One essential challenge is to define what the preferred habitat might be. This might best be elucidated using an inductive approach as I have attempted that considers factors at two levels: colony site selection and microhabitat selection. This would all be more meaningful if the differences in shearwater fitness between preferred and less optimal habitats can be shown. Other important considerations include the presence or absence of territoriality or a dominance hierarchy.

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among conspecifics, and the effects of interspecific competition for resources. A wealth of ecological and behavioral data need to be collected to determine the roles that the varying factors play in habitat selection. The present study does not thoroughly address these factors but represents a useful beginning. Given the tolerance on some cays for close neighbors (e.g., Goulding, Man Head; Table 2), the substantial amount of habitat that appears under-utilized, and the lack of evidence for interspecific competition for nest sites (with the possible exception of tropicbirds on the main island), I suspect that the shearwaters settle in accordance with the ideal free distribution.

Morphometrics

Bretagnolle et al. (2000) suggested that morphometric data might be useful in delineating taxonomic relationships. Lee (2000) noted variation in Audubon’s Shearwaters foraging offshore from Cape Hatteras, North Carolina (U.S.), and pointed out the need for more precise measurements from different parts of the range. The data presented here are useful primarily for future comparisons.

Chick Activity and Nest Attendance by Adults

Statistically distinguishable differences indicate that chick 2 spent significantly less time resting than the others while chick 3 spent more time resting. These behavioral differences could be attributable to differences in age, health or individual behavior. One would expect the amount of time spent in quiescence to decrease with age. However, the ages of the chicks are unknown. One plausible reason for the significantly greater amount
of time spent by chick 3 in quiescence is its lower nest attendance rate by its parents.

Chicks 1 and 2 were attended 74% of the nights while chick 3 was attended 64% of the
nights. Assuming that this lower attendance rate is indicative of a lower feeding rate, it
could be concluded that chick 3 spent more time in quiescence because it was fed less and
was conserving its lower energy resources.

The percent of time chicks devoted to each of the five behavioral categories varied
significantly with time of day (Figure 5). Feeding was only observed between 1600 and
0400 hours, and was observed most frequently from 2000 to 2400 hrs. This is most likely
a result of the tendency of adults to feed chicks about the time they arrived at the colony.
The percent of time chicks spent sleeping tended to increase during the day and decrease
during the dark hours. Considering the nocturnal nature of the species, it is expected that
the chicks be awake at night, especially when the adults arrive. Chicks, then, would need
the day to sleep. Sleeping during the day would also serve an adaptive advantage as it
would reduce detection by predators and conserve energy. The percent of time spent
active was exactly opposite to what was observed for sleeping. Time spent active
decreased during the daylight hours. The percent of time spent preening and resting did
not vary significantly with time of day; however, the data indicate that these proportions
were lower during the day (e.g., 1200 hrs.) when the chicks devoted a significant amount
of time to sleep.

The change in chick behavior as they got older is portrayed in Figure 6. Time
spent preening was greatest in the final week of the study, after the down was being
replaced with feathers. Resting was highest in the third week, and is probably correlated
with the percent of time spent sleeping, which was lowest in the same week. The percent
of time spent active was lowest in the first week, as can be expected for young nestlings.
Feeding decreased as the chicks got older. This was an unexpected finding as it would
seem intuitive that chicks need more food as they get older. However, other factors that
affect the rate of feeding were not analyzed here, such as food availability and foraging
success of the adults.

Effect of Ambient Light

The scientific literature has indicated that differing amounts of ambient light
affect animals’ behavior. The results of the regression analysis conducted in this study on
the effect of ambient light on shearwater calling did not indicate a significant relationship.
However, most of the calling occurred on nights when there was less moonlight available,
and on these nights the calling generally started earlier. The issue of shearwater detection
rate as it relates to the effect of ambient light on calling is further complicated when one
considers that the prevailing weather affects the relative ambient light availability. Is
calling affected by cloud cover (i.e., clouds block the moon causing a darker night), or a
lunar eclipse? Another concern when considering the effect of ambient light on
shearwater activity at the breeding colony is the effect of ambient light on foraging
efficiency. If the birds spend more time at the foraging grounds on brightly lit nights (due
to increased foraging efficiency), then their arrival at the colony site would be delayed on
those days, resulting in the observed relationship between ambient light and time of
arrival at the colony site. In order to get a better understanding of shearwaters’ whereabouts on dark versus bright nights radio, or satellite, telemetry studies are needed.

Feeding Bouts

The scientific literature on shearwater chick feeding is relatively limited. Hamer (1994), in a study conducted on Selvagem Grande, reported on the feeding of Little Shearwater chicks. Individual meals fed to chicks averaged 23.2 g (s.d. ± 4.7). Over a period of 18 nights, he estimated that the mean interval between feedings was 1.05 nights (range = 0 - 3). Chicks required an average of 16 g of food per day to maintain constant mass. Details of that nature were not evaluated in the present study; however, detailed notes were taken on the description of feeding bouts. I was unable to find comparably detailed notes on feeding bouts in the literature. Although I was unable to confirm whether multiple feeding sessions occur throughout the night, I was able to document that a single session of food transfer is relatively brief, lasting up to 7 min. The information presented here should not be taken as final, considering the small number of observations on which it is based.
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