NIH grant HD 06552 to K. A. Sullivan, the American Philosophical Society, and the Frank M. Chapman Foundation.

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NAVIGATION TO NEST SITE IN THE SNOW PETREL (PAGODROMA NIVEA)^{1,2}

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Key words: Snow Petrel; Pagodroma nivea; olfactory navigation; visual navigation; breeding colony; Antarctica.

Procellariiform birds have a well-developed olfactory apparatus (Bang 1966, 1971), suggesting that olfaction is of vital importance to these birds. Experiments made at sea (Hutchison and Wenzel 1980, Hutchison et al. 1984, Jouventin and Robin 1984) and in captivity (Jouventin 1977) strongly support the view that procellariiforms use olfaction in locating food. Evidence also supports the view that an olfactory guidance system is utilized to locate nesting burrows at night in the Leach's Petrel, *Oceanodroma leucorhoa* (Grubb 1974). Birds of this species approached their island upwind at twilight or after dark, plummeted through the heavy wooded cover and landed a few meters downwind of their burrows, finally walking upwind the last short distance.

When the ratio of olfactory bulb diameter to the largest diameter of the cerebral hemisphere was measured, the Snow Petrel, *Pagodroma nivea*, ranked high-

est among the 151 species from 23 orders studied, even higher than the Brown Kiwi, *Apteryx australis* (rank 2), and the Turkey Vulture, *Cathartes aura* (rank 10), both of which have been shown to be capable of discriminating between relevant food odors (Stager 1964, Bang and Wenzel 1985, Houston 1986).

During the Norwegian Antarctic Research Expedition in January to February 1985 to the Mühlig-Hofmann Mountains, in Queen Maud Land on the Antarctic continent, we had the opportunity to study a population of Snow Petrels, roughly estimated as 500 pairs (Mehlum et al. 1985). The colony was situated at Svarthamaren (71°53'S, 5°10'E), where the Snow Petrels were nesting close to and partly within a huge colony of the Antarctic Petrel, *Thalassoica antarctica*. The distance to the open sea was about 200 km.

To test whether the Snow Petrels depend on olfaction for navigation to their hidden nests, we carried out a small-scale experiment. Because of the 24-hr continuous daylight during the breeding season (the sun being continually above the horizon from 15 November to 27 January), we hypothesized that the birds should be able to locate the nests by vision alone, using learned landmarks. The results of our experiments in fact support this view.

METHODS AND MATERIALS

The majority of the Snow Petrels were nesting under large boulders on the ice-free, north-exposed hillside

¹ Received 12 June 1987. Final acceptance 4 December 1987.

² Publication no. 90 of the Norwegian Antarctic Research Expeditions (1984–1985).

of Svarthamaren. Out of a total of 42 nests inspected during the period 16 to 18 January 1985, 34 each contained one egg, in three other nests the egg was at the point of hatching, and the remaining five nests contained small chicks. This finding is consistent with the statements of Brown (1966) and Sømme (1977) that hatching in the Snow Petrel occurs about mid-January.

Altogether 24 incubating birds were caught, between 10:00 and 15:00, on three different dates (17, 18, and 23 January) on nests containing eggs. The birds were ringed and color-marked by painting the head feathers. The nostrils of half of the birds (12) were blocked, following the method described by Grubb (1974). In short, we used plugs of modelling clay, which was inserted with a blunt probe and sealed with a layer of waterproof, nontoxic cement (Ceramco polycarboxylate cement). The respective numbers of birds caught on the above-mentioned dates were 10, 10, and 4, of which 5, 5, and 2, respectively, had their nostrils blocked. The birds were randomly assigned to treatment and control groups. They were all released 1 to 2 km away from the breeding colony at Svarthamaren, 90 min to 4 hr after capture.

The cyclones that reached the shelf edge further north only occasionally caused strong wind in the Svarthamaren area. However, strong katabatic winds from the Antarctic plateau to the south occurred almost every evening and night, and flowed down an icefall 2 km to the southeast of Svarthamaren. Here wind velocities normally reached 6 to 10 m sec⁻¹, but in the immediate area of the colony velocities were about 50% less (Mehlum et al., in press). At the time of day when the experimental birds were released the wind velocity was low.

RESULTS

Four of the 12 experimental birds successfully returned to their own nests, three within 5 hr after release, the fourth one 5 to 7 hr afterwards. Four of the 12 control birds also returned to their nests, the first two 5 to 7 hr after release, the third one 7 to 14 hr afterwards, and the last one 22 to 34 hr afterwards. Thus, exactly the same number (four) and proportion (one third) of birds from each group returned to their nests. All eight of these birds reappeared before any of their unbanded mates were observed back at the colony.

At 14 of the remaining 16 nests to which the captured birds did not return, new unmarked birds appeared and took over the experimentally interrupted incubation within 6 days after their presumed mates had been removed. The first of these unmarked birds settled on the nest about 6 hr after its presumed mate had been caught, the second one about 30 hr afterwards, while five other birds appeared after 2 to 3 days, three more after 4 to 5 days and four more after 5 to 6 days. None was observed to return to the final two nests. The returned experimental birds were all checked for bilateral retention of their nostril plugs.

DISCUSSION

After capture on the nest and release 1 to 2 km away from the breeding colony, the same proportion of the experimental and control birds, viz. one third of each group, returned successfully to their respective nests. All these eight birds returned within 7 hr of their removal, except for two of the control group birds, which arrived 7 to 14 and 22 to 34 hr afterwards. The result of the experiment thus indicates that the birds with blocked nostrils were not inferior to the control birds in relocating their nests. It therefore seems that the Snow Petrel is quite able, by visual navigation alone, to locate nests hidden under boulders, probably using characteristic markings in the surroundings. This finding accords with what would be expected in an environment with 24-hr continuous daylight during the breeding season.

Our experiment could be criticized for not including an additional experimental group of birds that were prevented physiologically from using their sense of smell. This could have been achieved by transecting the olfactory nerves, as was done by Grubb (1974). However, the results of his orientation experiments with the Leach's Petrel (Grubb 1974) lend little support to the argument that birds with blocked nares may still be able to discriminate between odors. None of Grubb's experimental birds returned to their burrows, whether or not their nares had been sealed or their olfactory nerves severed. Admittedly, three of the Leach's Petrels released with plugged nares did come back, but the plugs had evidently become dislodged before return.

One may speculate why only one third of our captured birds did finally return to their nests. One possible explanation could be that the birds which failed to return happened to be captured on the nest at a final stage of their current incubation session and consequently were only slightly motivated for an immediate resumption of incubation. A comparison of the body condition of the birds that returned and those that disappeared, as adjudged from the relationship of body weight to wing length, however, did not support this tentative explanation, as no significant difference was found between the two groups (two-tailed *t*-test, P > 0.40).

Another variable which indirectly might indicate whether a bird had been captured early or late in its current incubation spell, is the period of time which elapsed between capture of the bird on nest and the arrival of its presumed mate. For those eight birds (four experimental and four controls), which returned to their nests after release, this period lasted on average $3.4 \pm$ SD 0.9 days (range 2.5–4.5 days). For those 14 birds which disappeared altogether after release, the mean was 3.5 ± 1.7 days (range 0.3–5.5 days). In other words this variable, too, discloses no difference between the two groups (Mann-Whitney U-test, two-tailed, P >0.50).

Most likely, sensitivity to serious disturbances when at the nest (capture, handling) provide the explanation for the overall low rate of return, although this view is inconsistent with the experience of Cowan (1981), who captured and measured many Snow Petrels at Casey and found that they returned at once to their nests when released.

We thank two anonymous referees for valuable comments to the manuscript. Ph. Tallantire kindly improved the English.

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IMITATIONS OF WHITE-CROWNED SPARROW SONGS BY A SONG SPARROW

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Key words: Song Sparrows; allospecific song; Whitecrowned Sparrow; mimicry; song.

Although cardueline finches are known to incorporate vocalizations of many allospecific species into their advertising song (Knecht and Scheer 1968, Güttinger 1974, Remsen et al. 1982), records of emberizid finches imitating allospecific songs in the wild are rare (Baptista et al. 1981, Cooper and Murphy 1985).

The resistance to learning allospecific syllables appears to vary among species in the genus *Melospiza*. Naive Swamp Sparrows (*M. georgiana*) exposed to both taped conspecific song and song of the sympatric Song Sparrow (*M. melodia*) produced conspecific song as adults, rejecting allospecific song as learning stimuli (Marler and Peters 1977).

The song repertoire of an adult Song Sparrow consists of a number of themes. A theme is defined as "a particular set of notes always rendered in the same order and with set pitch relationships" (Nottebohm 1969:302).

Marler and Peters (1977, 1987) also exposed Song Sparrows to tapes of conspecific and alien Swamp Sparrow songs. As adults, the experimental subjects sang mostly themes containing Song Sparrow syllables, although a few themes included syllables typical of Swamp Sparrows. No themes contained exclusively allospecific syllables however, indicating that Song Sparrows possess a genetic predisposition to learn conspecific syllables.

On 11 April 1987, I tape-recorded a "mimetic" Song Sparrow on the campus of the State University of San Francisco, California, singing White-crowned Sparrow (Zonotrichia leucophrys) songs, Song Sparrow songs, and songs containing syllables borrowed from both species (Fig. 1). I describe herein the song repertoire

¹ Received 24 June 1987. Final acceptance 4 December 1987.