CENSUS OF WEDGE-TAILED SHEARWATERS *PUFFINUS PACIFICUS* AND AUDUBON'S SHEARWATERS *P. LHERMINERI* ON COUSIN ISLAND, SEYCHELLES USING CALL-PLAYBACK

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SUMMARY

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We counted shearwaters on Cousin Island, Seychelles, and tested the call-playback method for determining nest occupancy. Wedge-tailed Shearwaters *Puffinus pacificus* nest synchronously and were counted during early incubation in October 1999. Audubon's Shearwaters *P. lherminieri* nest year-round and were counted in February 2000. We made five refinements to the call-playback method that are applicable to other cavity-nesting seabirds. First, to minimise errors associated with the method, we applied call-playback only where cavity occupancy could not be determined by looking or feeling into the nest cavity (i.e., in 17% of Wedge-tailed Shearwater cavities, but 76% of the smaller Audubon's Shearwater cavities). Second, we combined daytime visits to the census plots, which facilitated location of cavities, reduced disturbance to birds and minimised damage to fragile burrows, with night visits to determine occupancy. Responses to call-playbacks were significantly higher at night than by day. Third, we timed the bird's responses to derive the optimal duration of a playback test (120 s in Wedge-tailed and 80 s in Audubon's Shearwaters). Fourth, we used the proportions responding at night for both occupied cavities (R_o) and cavities with unknown contents (R_u) to formulate a response coefficient (R_u/R_o) used to estimate occupancy in cavities with unknown contents. For Wedge-tailed, $R_o = 0.774$, $R_u = 0.170$ and $R_u/R_o = 0.220$, and for Audubon's, $R_o = 0.714$, $R_u = 0.164$ and $R_u/R_o = 0.229$ (i.e., 22.0% of Wedge-tailed and 22.9% of Audubon's Shearwater cavities with contents unknown were likely to be occupied). Fifth, we reported the density of several categories of nest cavity, including cavities occupied by birds, those with failed eggs or chicks, and empty potential cavities. This allows a wider range of monitoring options and comparisons with other studies. The total number of cavities occupied by Wedge-tailed and Audubon's Shearwaters on Cousin was 13 066 (95% confidence limits 9259–16 873) and 5100 (95% CL 3976–6625), respectively. We lack an accurate method to estimate the year-round breeding population of Audubon's Shearwater. The Wedge-tailed Shearwater population was similar to a 1996/97 estimate, but considerably less than the 1973/74 estimate of 30 000–35 000 pairs, which might have been an overestimate. There have been no previous estimates of the Audubon's Shearwater population on Cousin Island. Continued monitoring of the Cousin Island shearwaters is recommended.

Key words: Wedge-tailed Shearwater, *Puffinus pacificus,* Audubon's Shearwater, *Puffinus lherminieri,* Seychelles, call-playback, population census

INTRODUCTION

Call-playback is commonly used to count a variety of land-birds and has recently been applied to count procellariiform seabirds which nest in cavities (James & Robertson 1985, Warham 1996, Gibbons & Vaughan 1998, Ratcliffe *et al*. 1998, Vaughan & Gibbons 1998). We applied call-playback in counting Wedge-tailed Shearwaters *Puffinus pacificus* and Audubon's Shearwaters *P. lherminieri* breeding on Cousin Island, Seychelles. This island supports one of the highest densities of both species in the Indian Ocean. Our study thus provides essential baseline data for monitoring population changes in these species. We also confirmed that the call-playback method is applicable to these tropical shearwaters, and we provide refinements for the wider application of the method for these and other cavity-nesting seabirds.

Monitoring the populations of these two shearwaters, and developing reliable methods for doing so, is important for several reasons. They are among the most common seabirds in the western Indian Ocean, and can serve as valuable indicators of offshore ocean conditions. They forage over large tracts of ocean and often in feeding flocks associated with tuna and other large fish.

Changes to their food supply, either through changes in marine productivity or through declines in tuna stocks, are likely to affect shearwater populations although these effects might be obvious only after many years of monitoring. The effects of accidental by-catch in fisheries operations is not known for seabirds in Seychelles. The killing of shearwater chicks for human consumption, once common, is no longer legal in Seychelles, but poaching is likely to impact populations on some islands. Many present and past colonies are in a state of flux, due to changes in the habitat, as former coconut plantations revert to forest, or changes in predation rates, with eradication of introduced domestic cats *Felis catus* and rats *Rattus* sp. (Burger & Lawrence 2000).

Census methods for shearwaters generally involve counting burrows or other nest cavities within sample plots or transects, determining the proportion of cavities occupied by breeding birds, and then extrapolating these results to the area of the colony (Walsh *et al*. 1995, Warham 1996). For Wedge-tailed and Audubon's Shearwaters in Seychelles there are problems in determining both the density of nests and the proportion occupied. The bulk of the populations nest on the granitic central islands of Seychelles (Rocamora & Skerrett 2001). Here they use a wide variety of nest sites, including burrows dug into soil and cavities beneath or among rocks and tree roots. Counting nest sites is particularly difficult among the huge granite boulders, many metres in diameter, where five or ten pairs might nest beneath a single large boulder.

Determining occupancy is difficult because many nests of both species are not visible from the surface and are out of reach of even the longest arm. Cavities of Audubon's Shearwaters are often too narrow for manual checking. Large centipedes and, on some islands, scorpions within the cavities also deter manual checking of cavities. The call-playback method is ideal for estimating occupancy under these conditions. Briefly this involves playing taped calls of the species near the entrance of a possible nest cavity and recording whether or not a bird responds. Since not all birds respond, and in some species only males respond (James & Robertson 1985), the proportion of responses from nests known to be occupied has to be measured and applied to the responses recorded in census plots.

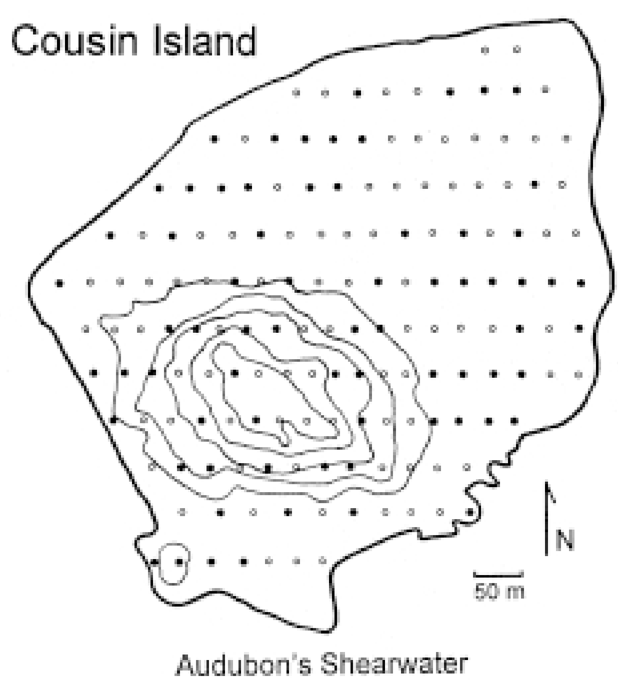
METHODS

Study area

Cousin Island (4°20'S, 55°40'E) is one of the smaller (27 ha) of the central granitic islands, but supports the second-highest number of breeding seabirds in Seychelles (Rocamora & Skerrett 2001). Nests of Audubon's Shearwaters are scattered across the entire island, on both the granite hillside and the flat coastal plateau, whereas those of Wedge-tailed Shearwaters are found only on 9.7 ha of hillside and associated granite outcrops (Fig. 1). The plateau is covered with dense forest, dominated by *Pisonia grandis* and other large trees, but the hillside is more sparsely vegetated with grass, ferns and woodland (Diamond 1975).

Timing of censuses

In Seychelles most of the Wedge-tailed Shearwaters breed synchronously, laying in September or October after several months spent courting and establishing nest sites (Wilson 1980, Rocamora 1997, pers. obs.). A few pairs lay out of sequence and newly laid eggs can be found from June to December. Our count of Wedge-tailed Shearwaters was done between 7–22 October 1999 when most pairs were in early incubation. Audubon's Shearwaters nest year-round in Seychelles, but the proportions active in any month are not known. Our count of this species was done between 6–22 February 2000.



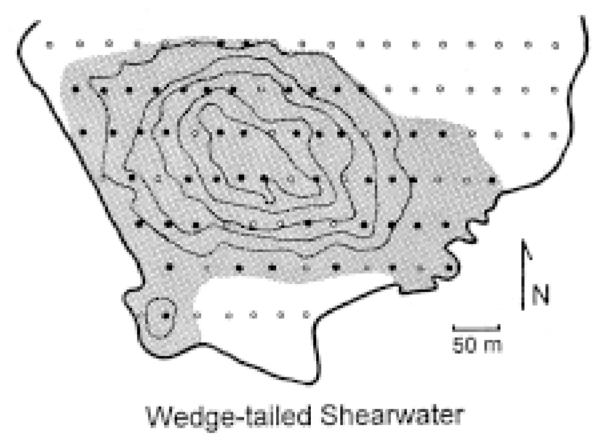


Fig. 1. *Cousin Island, Seychelles, showing the grid of 158 census points (small open circles), the 70 points randomly selected to count Audubon's Shearwaters (black-filled circles on left hand map), the 50 points for counting Wedge-tailed Shearwaters (black-filled circles on map above), and the area of the Wedge-tailed Shearwater colony (stippled area). Audubon's Shearwater nests were scattered throughout the island. The contour lines show 10-m elevation intervals.*

Census plots

A grid of 158 sample points was established in 1999 to count seabirds on Cousin (Burger & Lawrence 1999, 2000). These points were situated at 30-m intervals along east–west transect lines placed 50 m apart (Fig. 1). Preliminary testing on Cousin showed that White-tailed Tropicbirds *Phaethon lepturus* and White Terns *Gygis alba*, with densities and distributions similar to those of Audubon's Shearwaters, were most efficiently counted using 70 plots of 200 m^2 in order to optimise the mean and variance of density measures (Burger & Lawrence 1999, 2000). Consequently, to sample Audubon's Shearwaters we randomly selected 70 of the 158 points to locate 200-m^2 circular plots. At 17 plots with high densities of potential nest cavities and complex boulder topography, we reduced the plot size to 100 m^2 to facilitate sampling. Wedge-tailed Shearwaters, which nest at higher densities in a more restricted area, were sampled within 100-m^2 circular plots at 50 randomly selected grid points within the 9.7-ha hillside area where other studies (Diamond 1975, Rocamora 1997) and our preliminary mapping had shown them to nest (Fig. 1). The plots sampled for Wedge-tailed and Audubon's Shearwaters represented 5.2% and 4.6%, respectively, of the colony areas. Wedged-tailed Shearwater plots took, on average, 30 min (SD = 19 min) to survey, including playback tests, ranging from 2 min for a plot on open flat rock to 86 min for a plot containing very large boulders, many nests and complex topography. Audubon's Shearwater plots were not timed because other species were counted at the same time, but if counted alone would likely take a similar time to the Wedge-tailed plots.

Classifying nest cavities

In common with most seabird censuses we used the number of apparently occupied nest cavities (K_{occ}) as the measure of the breeding population (Walsh *et al.* 1995). In this paper a potential nest cavity refers to a burrow, rock cavity, cave, rock overhang, crevice or other space in which a shearwater might nest. Since a few Wedge-tailed Shearwaters nested among boulders with minimal cover, suitability was difficult to judge, but any space with some sign of previous occupancy (feathers, faeces, eggshells, evidence of digging or trampling) was categorized as a potential nest cavity. A powerful torch was used to look into cavities by day and at night. Prior to call-playback testing the potential cavities were classified as follows (Table 1): K_{vis}: known to be occupied by seeing (or in a few cases feeling with a short stick) an adult or chick; K_u: cavity with unknown contents (too deep or twisted to see or feel the contents); K_{mort}: cavity containing a deserted or broken egg or dead chick; and K_{emp}: cavity known to be empty (definitely no adults, chicks, failed eggs or dead chicks, but with some evidence of previous occupancy). The call-playback tests were used to determine the proportion of unknown cavities (K_u) which were occupied.

Call-playback tests

A Sony TC-D5 ProII recorder, Sennheizer MZS16 directional microphone and Electrosound pre-amplifier were used to record calls. Wedge-tailed Shearwaters were recorded early in the breeding season (July) when there were many birds ashore establishing nest sites and calling frequently. Audubon's Shearwater calls were recorded in August. A series of calls, including both single birds and duets, was then copied on to a test tape. We found that Wedge-tailed Shearwaters usually responded while taped calls were being broadcast, whereas Audubon's Shearwaters usually responded during pauses between calls. The optimal test tape for Wedge-tailed Shearwaters comprised repeated sequences of 30 s of multiple calls separated by 5 s of silence, and for Audubon's Shearwaters was repeated sequences of a single 10–15 s call separated by 5 s of silence.

To test cavity occupancy the taped calls were played within 0.5 m of the cavity entrance at near-maximum volume, similar to a loud bird. The time taken for a shearwater in the cavity to respond after the playback started was recorded and the type of response was noted as calling only, emergence of the bird to the mouth of the cavity, or both. The test ended as soon as a bird responded, or 150 s after the start of playback if there was no response. Tests for Audubon's Shearwaters were reduced to 90 s after we found that they responded more quickly (see below).

Tests were made during the day (07h00–16h00) and at night starting 1.5 h after sunset (19h30–22h30). Each cavity was used for only one day and one night test. Cavities known to be occupied and those with unknown contents were marked as such with

TABLE 1

Definitions, numbers within plots, and densities of each type of nest cavity used in counting Wedge-tailed (50 plots) and Audubon's (70 plots) Shearwaters on Cousin Island, Seychelles

Code	Definition	Wedge-tailed Shearwater		Audubon's Shearwater	
		No. of cavities	Density per ha (mean ± SD)	No. of cavities	Density per ha (mean ± SD)
K_{vis}	Cavities known to be occupied from visual/tactile inspection	556	1112 ± 1277	46	42.9 ± 87.3
K_u	Cavities with unknown contents prior to playback tests	533	1066 ± 940	649	637.9 ± 618
K_{mort}	Cavities containing only broken eggs or dead chicks	74	148 ± 219	1	0.7 ± 6.0
K_{emp}	Cavities known to be empty after visual/tactile inspection	81	162 ± 179	–	–
K_{pot}	All potential cavities ($K_{vis} + K_u + K_{mort} + K_{emp}$)	1244	2488 ± 2247	696	681.4 ± 637.4
K_{occ}	Occupied cavities estimated after playback tests (see text)	673.3	1347 ± 1416	194.2	188.9 ± 177.8

reflective tape during daytime visits. This minimized the time and amount of trampling needed to relocate the cavities for night tests. Taped calls played at night elicited responses from a few shearwaters of both species whose cryptic cavities had been overlooked during daylight searches, and the call-playbacks therefore reduced the error from these omissions.

We did call-playback tests on samples of cavities with both known and unknown occupancy, and calculated the proportion of each cavity type that responded (proportions coded as R_o and R_u, respectively). We could not use R_u alone to estimate the number of unknown cavities likely to be occupied because some of the unknown cavities contained birds that would not respond. Accordingly, we used the ratio R_u/R_o to estimate the proportion of unknown cavities likely to be occupied.

Calculating the density of occupied cavities and total population

During the daylight visits we determined the number of cavities known to be occupied after visual and tactile inspection (K_{vis}) and the number of potential cavities with contents unknown (K_u) per plot. We applied the following formula to calculate the number of occupied cavities per plot (K_{occ}):

$$K_{occ} = K_{vis} + K_u(R_u/R_o)$$

Playback tests were not done at 17 Wedge-tailed and 13 Audubon's Shearwater plots which were too isolated or hazardous to visit at night. For these plots the formula reduced to:

$$K_{occ} = K_u(R_u/R_o)$$

We applied the appropriate formula to each census plot, and then calculated the mean density of apparently occupied cavities/ha. The total number of apparently occupied cavities was calculated by multiplying this density by the area of habitat in which nests were found (9.7 ha in Wedge-tailed and 27.0 ha in Audubon's Shearwaters; Fig. 1). We estimated the colony area from a 1:3000 topographic map, and did not include the effect of slope, which was too complex to include as a simple cosine function. To some extent the increased surface area produced by rough terrain was incorporated into our plots because in plots containing very large boulders the circle of 100 m^2 actually covered a much larger planar area in which the birds could nest.

Statistical treatment

Data were analysed using SPSS 10.0. Means are given ± one standard deviation (SD) except where 95% confidence limits are given. Non-parametric Mann-Whitney tests were used when the data did not meet the requirements for parametric tests.

RESULTS

Nest contents

Wedge-tailed Shearwater

During daytime visits, prior to playback tests, we found 556 cavities known to be occupied, 533 with unknown occupancy and 74 with failed eggs (we found no dead chicks), and 81 empty potential cavities (Table 1). Among 409 nests known to be occupied, 93.4% had an egg, 1.2% a chick, 4.4% a single adult only and 1.0% a pair only. Out of a sample of 22 empty potential cavities found in daylight, only one (4.3%) had a Wedge-tailed Shearwater when re-checked at night. This low level of nocturnal reoccupancy of potential sites, and the low proportion of cavities with adults but no egg or chick suggests that most laying was completed by the time of the count and that adults which had lost eggs were not returning every night to nest cavities.

Audubon's Shearwater

Occupancy and nest contents were difficult to establish in Audubon's Shearwater cavities, due to the narrow, twisted structure of most nest cavities. For the same reason it was impossible to estimate the number of potential empty cavities. During daylight checks we found 46 occupied cavities and one with a broken egg, but could not determine the occupancy of 649 cavities (Table 1). In a sample of 123 cavities known to be occupied after playback tests at night, the contents were identified in 58 (47.2%). These included 22 (38%) with an egg, 19 (33%) a chick, 13 (22%) a single adult only (no egg or chick) and 4 (7%) a pair only. The chicks included two small newly-hatched, five mid-sized, six fully-feathered and near fledging, and a further six which could be heard but not seen and hence were not aged.

Responses to call-playback

For Wedge-tailed Shearwater cavities known to be occupied, the proportion responding at night (0.774, n = 62) was significantly higher than in daylight (0.403, n = 62; Chi-squared test, χ^2 = 17.62, $P < 0.001$) but for cavities with unknown contents there was no significant difference between night (0.170, n = 159) and day (0.132, n = 88; χ^2 = 0.67, $P > 0.05$). Cavities with unknown contents were more likely than occupied cavities to be empty so less change was expected. Similarly, in Audubon's Shearwater cavities known to be occupied a higher proportion responded at night (0.714, n = 42) than by day (0.243, n = 70; χ^2 = 23.95, $P < 0.001$). The night response from Audubon's Shearwater cavities with unknown contents was low (0.164, n = 470), and we did not test unknown cavities by day. The night-time response coefficients (R_u/R_o) were almost identical for Wedge-tailed (0.220) and Audubon's (0.229). In other words 22.0% of Wedge-tailed and 22.9% of Audubon's Shearwater cavities with unknown contents were likely to be occupied at the time of our census. All census estimates were made using night-time response coefficients.

Most birds responded by calling, or less often emerging at the cavity entrance (Table 2). Only one (1.5%) of the 66 Wedge-tailed Shearwaters and two (1.6%) of the 122 Audubon's Shearwaters that responded emerged silently at the cavity entrance. Despite this, cavities in census plots were always checked to see if silent birds had emerged.

Audubon's Shearwaters responded more quickly than did Wedge-tailed Shearwaters to taped calls (Fig. 2). For both species we found no significant difference in the time to respond at night or by day, and between cavities with known and unknown occupancy (Table 2). Among Audubon's Shearwaters, a faster response was obtained at cavities containing a pair than those with a single bird, but the sample of Wedge-tailed Shearwater pairs was too small for statistical testing (Table 2). Nearly all the Wedge-tailed Shearwater cavities contained incubating birds, so we could not test the effects of nest contents. Among Audubon's Shearwaters, adults with an egg (11.8 ± 13.1 s, n = 14) responded in a similar time to those with a chick (13.3 ± 6.0 s, n = 11; Mann-Whitney test, Z = 1.62, P = 0.11). At six Audubon's Shearwaters cavities with a large chick but no adult, there was no response in two cavities, an exceptionally long delay in responding in four (35, 56 and 95 s) and only one rapid response (5 s). For future testing, a playback and listening period of 120 s after starting the tape was deemed sufficient for Wedge-tailed, and 80 s for Audubon's Shearwaters. These times included 100% and 98%, respectively, of the night responses (Fig. 2).

Cavity density and estimated populations

Wedge-tailed Shearwater

Occupied cavities were found in 78.0% of the 50 plots. The mean density of occupied cavities (1347/ha; Table 1) was multiplied by the area of the colony (9.7 ha; Fig. 1) to give a total estimate of 13 066 (95% confidence limits 9259–16 873) occupied cavities at the time of the census. Adding cavities with broken eggs, the total of cavities likely occupied through the season was 14 501 (95% confidence limits 10 175–18 819). The total number of potential cavities in the colony was 24 134 (95% confidence limits 18 092–30 175).

Audubon's Shearwater

Occupied cavities were found in 75.7% of the 70 plots. The mean density of occupied cavities was 188.9/ha (Table 1). Audubon's Shearwaters were found throughout the island (27 ha) and the total population was calculated to be 5101 occupied cavities (95% confidence limits 3770–6432). Including the cavity with a broken egg raised the estimate to 5120 occupied cavities (95% confidence limits 3792–6448). Since this species breeds year-round the overall population breeding on Cousin is much higher and likely double these figures, but at this stage we have no way of estimating the year-round breeding population from censuses.

DISCUSSION

Application and improvement of the call-playback method

Occupancy of a nest cavity can be assessed directly by seeing or feeling an adult or chick, or indirectly from evidence of eggshells, faeces, digging, or trampled vegetation. Temperature and carbon dioxide levels can also indicate occupancy (Birchard *et al*. 1984), but require specialised equipment and in the tropics occupied and unoccupied burrows are likely to have similar temperatures. Mark-recapture techniques have been used to estimate the densities of fledglings of burrowing shearwaters (Alexander & Perrins 1980, Walsh *et al*. 1995), but the method is extremely time and labour demanding and can cause disturbance in the colony. Tests with Manx Shearwaters *Puffinus puffinus* showed that the call-playback method gave similar results but was far quicker, safer and less disturbing to the birds than either the mark-recapture method (Gibbons & Vaughan 1998) or excavating burrows to check contents (James & Robertson 1985).

Playback tests are an effective method for determining occupancy when seeing and feeling are not sufficient. Our tests showed that

TABLE 2

Summary of responses by Wedge-tailed and Audubon's Shearwaters to call-playback. Numbers of responses in parentheses

	Wedge-tailed Shearwater		Audubon's Shearwater	
Proportion of responses of each type				
Call only	0.818		0.877	
Call and emerge	0.167		0.107	
Emerge silently	0.015		0.016	
	(66)		(122)	
Mean time (± SD) to respond (s)				
Cavity known to be occupied	33.5 ± 24.1	(72)	20.7 ± 23.0	(35)
Cavity with unknown contents	41.1 ± 33.1	(41)	12.0 ± 7.7	(82)
Mann-Whitney test	Z = 1.28, P > 0.05		Z = 1.34, P > 0.05	
Day	41.4 ± 32.6	(47)	16.8 ± 18.1	(17)
Night	32.6 ± 23.3	(66)	14.6 ± 14.6	(117)
Mann-Whitney test	Z = 1.47, P > 0.05		Z = 0.01, P > 0.05	
Single bird	37.6 ± 28.7	(103)	16.3 ± 16.5	(76)
Pair	23.3 ± 12.7	(4)	10.6 ± 8.8	(34)
Mann-Whitney test	Too few to test		Z = 2.22, P = 0.03	

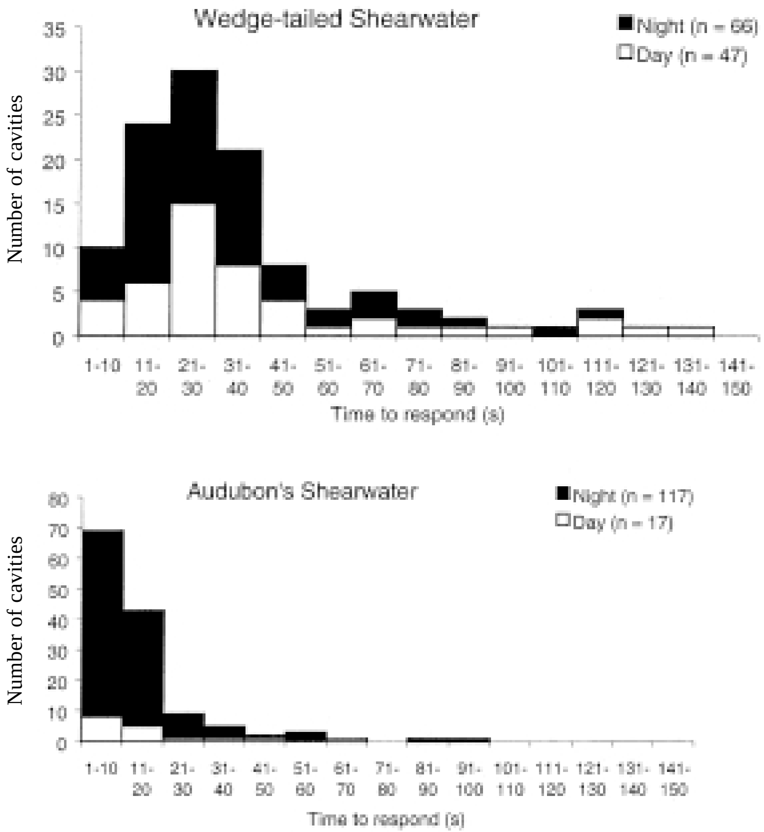


Fig. 2. *Frequency distribution of the time taken by Wedge-tailed and Audubon's Shearwaters to respond to playbacks of taped calls at night and by day.*

call-playback worked well for Wedge-tailed and Audubon's Shearwaters and significantly improved estimates of occupancy derived from simply looking and feeling into cavities. Our study also provides several refinements over previous applications of call-playback, which are applicable to many other burrowing seabirds.

The usual application of call-playback for counting cavity-nesting seabirds is to test all cavities in the census plot and apply a correction factor to account for the proportion of birds likely to call back (James & Robertson 1985, Gibbons & Vaughan 1998, Vaughan & Gibbons 1998). The correction factor is the inverse of the proportion of birds calling back in tests made with cavities known to be occupied, and can be expressed as K_{vis}/C_o, where K_{vis} is the sample of occupied cavities and C_o is the number from which birds called back. The total number of occupied cavities (K_{occ}) is then estimated as $K_{occ} = C_t * K_{vis}/C_o$, where C_t is the total number of birds calling back in the census plot. This procedure is simpler than our application of the R_u/R_o ratio, but cannot be applied to census plots in which some or all of the cavities are not tested. The R_u/R_o ratio can be applied to plots where the number of cavities is known (i.e., K_u), regardless of their contents or whether they were tested, but this should be done only if time, accessibility or risk to personnel constrain testing.

Our method requires testing both cavities known to be occupied and those with unknown contents to derive a R_u/R_o ratio. If R_u equals or exceeds R_o (i.e. R_u/R_o =1.0) then this method will overestimate the number of occupied cavities, and should not be applied. This is unlikely to happen because cavities with unknown contents can include empty cavities whereas the sample of occupied cavities cannot. Care should be taken not to disturb birds near cavity entrances and thus affect their response to the tapes, which will affect R_o.

There are always some birds that do not respond to taped calls and testing every cavity is time consuming. In some studies occupancy was determined solely by playback tests (Gibbons & Vaughan 1998, Vaughan & Gibbons 1998), but we applied the playback response coefficient (R_u/R_o) only to those cavities whose contents were unknown. This should greatly improve the accuracy of the census, because a significant portion of the occupancy (83% in Wedge-tailed and 24% of Audubon's Shearwaters; estimated as K_{vis}/K_{occ} from Table 1) was determined directly by sight or feel and the remainder from call-playback tests. Any inaccuracies in the playback method would thus have less effect on the population estimate than if occupancy was determined entirely from playback. A similar mixed method, involving playback only where occupancy could not be visually determined, was used to count Audubon's Shearwaters on Aride Island, Seychelles (Betts 1998).

Responses to call-playback vary considerably among species, between sexes and at different times of day (Table 3). In some species, including the Manx Shearwater, responses to taped calls of males come only or predominantly from other males, and playback methods are adjusted for this (James & Robertson 1985, Gibbons & Vaughan 1998). Females might respond to calls by other females (Warham 1996). James & Robertson (1985) found that males were in 55% of the burrows at the time of their tests. This proportion might vary significantly from 50% depending on the sequences and duration of incubation shifts by the two sexes. We obtained responses at night from 77% of Wedge-tailed and 71% of Audubon's Shearwater cavities known to be occupied. On nearby Aride Island, Betts (1998) obtained responses from 90% (n = 20) and 59% (n = 198), respectively, for these species. These results indicate that in these species both sexes respond, although we cannot rule out a greater response from one sex. By including duets in our playback tape we ensured that calls of both sexes would be heard, in case the shearwaters responded only to calls from the same sex. We considered it unnecessary, therefore, to make any adjustments to the playback responses because of a gender effect.

Our study showed that 120 s was an appropriate playback and listening time for Wedge-tailed Shearwaters during incubation, and 80 s for Audubon's Shearwaters. In other studies of procellariiforms the duration of the tape playback varied from 10 to 20 s and the listening time was usually not given (Table 3). It is important to test the time of response in each census, because the responses are likely to vary among species, sexes, adults and chicks, stages of breeding and nest types. If the playback or listening time is too short the population would be underestimated.

Cavity-nesting procellariiforms are generally counted at night, although tape playback has been used in daylight to count some species (James & Robertson 1985, Ratcliffe *et al*. 1998, Berrow 2000). Our study was unusual in that we combined daytime counts of cavities and occupancy checks with night-time playback responses. By checking cavities by day we were able to sample plots which were difficult or dangerous to reach at night. We found it far easier to locate and check cavities in daylight than at night. A powerful torch was needed to check cavity contents, even in daylight. Observers were far less likely to step on fragile burrows in daylight. Daytime visits do not disrupt adults changing incubation shifts or feeding chicks, because these events happen at night.

Vaughan & Gibbons (1998) found that British Storm Petrels *Hydrobates pelagicus* showed greater responses to taped calls at night than by day (Table 3). We found the same with Wedge-tailed and Audubon's Shearwaters. Lower responses by day do not necessarily lead to underestimates of occupancy, provided daytime ratios are applied to occupied and unknown cavities, but the low response in daylight might lead to more variable estimates of occupancy. Cavities with chicks are more likely to show occupancy at night when adults return to feed the chicks. We therefore used night playback tests. Night visits to a sub-sample of the plots were needed to obtain mean response proportions to apply to cavities of unknown occupancy, but every plot need not be visited at night. By marking the cavities with reflective tape during the day visit, we minimized our time and trampling in the plots while doing playback tests at night.

Our method provided a broader range of population estimates than usually given for cavity-nesting seabirds, by considering several categories of cavity occupancy (Table 1). For example, by combining the number of currently occupied cavities (K_{occ}) with those containing failed eggs or dead chicks (K_{mort}) we were able to make an estimate of the total number of cavities that were likely occupied through the season for Wedge-tailed Shearwaters. This was less effective for Audubon's Shearwaters which were non-seasonal and whose cavities were generally too narrow for us to see the contents. Classifying empty potential cavities was a rather subjective process and was not possible for the small, cryptic Audubon's Shearwater cavities. For Wedge-tailed Shearwaters, however, this allowed a crude estimate of the total (likely minimum) number of potentially available cavities and thus gave some information on the colony's carrying capacity.

Population status and trends on Cousin Island

Wedge-tailed Shearwater

Using a mark-recapture technique Diamond (1975, pers. comm.) estimated the population of Wedge-tailed Shearwaters on Cousin Island in 1973/74 to be 30 000–35 000 pairs. This estimate has been widely quoted in general reviews (Feare 1984, Stoddart 1984, Diamond 1994), but few details are available on the sample size and method. The total number of potential cavities in our study, 24 134 (95% confidence interval 18 092–30 175) was less than Diamond's estimate of breeding pairs, which suggests that Diamond might have over-estimated the breeding population.

A more rigorous comparison can be made with census data collected by Rocamora (1997) between 31 October 1996 and 15 March 1997. He determined occupancy at night by looking and feeling into cavities and applied a correction factor to estimate the total of apparently occupied burrows. He underestimated the area of the Wedge-tailed Shearwater colony and so his total population estimate is low, but his combined density of known or apparently occupied cavities (1283 ± 1162/ha, n = 12 plots of 100 m^2) was not significantly different from our 1999 estimate (1347 ± 1416/ha, n = 50; two-tailed t-test, $t = 0.143$, df = 60, $P = 0.887$). If Rocamora's density was correctly applied to 9.7 ha, the total number of occupied cavities would have been 12 445 (95% confidence limits 9321–15 569), which is very similar to our 1999 estimate of 13 066 (9259–16 873).

The close agreement between the 1996/97 and 1999 censuses, despite some differences in methods, gives confidence that the population of Wedge-tailed Shearwaters on Cousin Island in the late 1990s was about 13 000 pairs and certainly within the range of 9000–17 000 pairs. If Diamond's (1975) estimate for 1973/74 is correct, then this population has declined dramatically during

TABLE 3

Summary of call-playback tests on procellariiform seabirds in other studies

Species	Time tape played (s)	Time listening (s)	Day or night	Occupancy status of cavities tested	Proportion of cavities with a response	Reference
British Storm Petrels	10	30	Day	Unknown	0.25	Ratcliffe *et al*. (1998)
British Storm Petrels	10–15	–	Day	Unknown	0.34	Vaughan & Gibbons (1998)
British Storm Petrels	10–15	–	Night	Unknown	0.60	Vaughan & Gibbons (1998)
White-chinned Petrel	5–10	–	Day	Unknown	0.74–0.90*	Berrow (2000)
Manx Shearwater	'Several seconds'	–	Day?	Occupied – males only	0.98	James & Robertson (1985)
Manx Shearwater	c 15	–	Day	Unknown	0.21–0.39**	Gibbons & Vaughan (1998)
Audubon's Shearwater	15–20	–	Night	Occupied	0.59	Betts (1998)
Audubon's Shearwater	15–20	–	Night	Unknown	Not given	Betts (1998)
Wedge-tailed Shearwater	15–20	–	Night	Occupied	0.90	Betts (1998)

* Responses varied according to the type of call and were highest when both call types played sequentially.

** The response was 0.21 at low nest densities and 0.39 at high densities.

the past 25 years, but this seems unlikely. Over this period the nesting habitat of this species remained similar in size and character, there were no introductions of alien predators, and there was adequate protection against poaching. Conditions on the island are therefore unlikely to have caused such a decline. It is more difficult to reach any conclusions about changes that might have happened at sea. There have been periods with exceptionally warm seas, especially in 1997/98, which might have caused declines in prey abundance or created deeper thermoclines, making prey less accessible. The shearwaters might have been affected by declines in stocks of tuna, which drive food to the surface to facilitate feeding by the birds. Neither of these events seems likely to have had such a large impact on the shearwater population. The alternative is that Diamond (1975) overestimated the size of the Cousin population. No other population of shearwaters in Seychelles has been monitored over this period and most other seabirds on Cousin Island have either increased or remained stable since the 1970s (A.E.B. & A.D.L. unpubl. data). Clearly further monitoring is required to determine the population trends, and if a decrease has in fact taken place, then intensive studies are needed on the breeding success, diet, and other factors likely to affect the populations.

Audubon's Shearwater

There have been no previous reliable estimates of the Cousin Island population of this species. Rocamora (1997) concluded that his sample of 18 plots was inadequate to estimate the population. Audubon's Shearwaters breed all year round in Seychelles, and there is no known method to extrapolate from a census to estimate the year-round breeding population. There was a relatively high proportion (29%) of occupied cavities with no obvious egg or chick, suggesting that breeding adults were visiting cavities regularly at night in between breeding events. Population estimates, like ours, based on apparently occupied cavities would thus overestimate the currently active breeding population (those with eggs or chicks). Methods for converting census estimates into year-round breeding populations, and repeated censuses at intervals through the year to determine the spread of the breeding effort (Betts 1998) are needed to allow an overall population estimate.

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