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Abstract: The blue petrel (*Halobaena caerulea*) is a small pelagic seabird breeding on just a few Southern Ocean islands. Although it is known that oceanographic and climatic variability affect mortality rates, individual body condition and reproductive success, very few data are available on the global population status. We assessed the status of blue petrels at Mayes Island, Iles Kerguelen, in 2002 by estimating burrow densities and burrow occupancy using acoustic playbacks and response probability. The mean and highest burrow densities recorded were respectively 0.136 ± 0.026 and 2.3 entrances per m^2. Burrow occupancy increased with burrow density but stabilized at *c.* 0.6 occupied burrows per m^2. Taking into account the response probability to playback (0.819) the mean burrow occupancy density was 0.037 ± 0.094 per m^2, giving an estimated 142 000 (95% CI around 106 000–179 000) or 148 000 breeding pairs (95% CI around 55 000–241 000) on Mayes Island, respectively with and without taking into account spatial autocorrelation in burrow densities. This suggests that the entire breeding population of blue petrels at Kerguelen is much higher than current estimates, and that Kerguelen and Diego Ramírez archipelagos are key breeding sites for this species.

Introduction

There is increasing evidence that the population dynamics of seabirds in the Southern Ocean are affected by climate fluctuations, fisheries, and introduced predators (Weimerskirch *et al.* 1997, Jenouvrier *et al.* 2005, Frenot *et al.* 2005). It is therefore particularly relevant to monitor these populations, and several studies have been developed on large seabird species of the Southern Ocean (particularly Spheniscidae and Diomedeidae) aiming at understanding their population dynamics. However, very little is known on the population dynamics and abundance of burrowing or crevice nesting petrels, which range from medium size (*c.* 1.5 kg) to small size (*c.* 20 g) and comprize between 80 and 90 species (Warham 1990).

The blue petrel, *Halobaena caerulea* (Gmelin), is a small petrel (*c.* 220 g) which is known to breed at only six locations: Macquarie, Kerguelen, Crozet, Marion and Prince Edward, South Georgia, and Diego Ramirez, Cape Horn and nearby islands (Warham 1990). Among these, Kerguelen, Diego Ramirez and South Georgia are thought to be major breeding locations (Marchant & Higgins 1990, Lawton *et al.* 2005). Although several studies have revealed the effects of climate fluctuations on some of the key demographic parameters (survival and reproduction) of blue petrels (Guinet *et al.* 1998, Barbraud & Weimerskirch 2003), no reliable population size estimates are available at Kerguelen. This study attempts to provide an indication of the importance of Mayes Island (Iles Kerguelen) for the species, and baseline data for future assessment and monitoring, by assessing nest-entrance density and the proportion of burrows occupied with breeding pairs.

Materials and methods

The Iles Kerguelen (48°28'–50°S, 68°28'–70°35'E) consists of a 6600 km^2 island partly covered by an ice cap, and over 300 secondary islands and islets giving a total surface of 7200 km^2. Fieldwork was carried out in the eastern part of the Iles Kerguelen on Mayes Island (49°28'S, 69°57'E) situated in the Golfe du Morbihan (Fig. 1), a large bay about 700 km^2, in which large populations of petrels breed (Weimerskirch *et al.* 1988). Mayes Island has an estimated surface area of 2 787 400 m^2 (the surface area of four lakes on the island was excluded since lakes were not sampled). The main topographical features of the island are dry, rocky plateaus separated by vegetated valleys were the petrels breed.

Mayes Island has dry soils and is densely vegetated (mainly Kerguelen cabbage *Pringlea antiscorbutica* R. Br ex Hook f., *Azorella selago* Hook f., and *Acaena magellanica* (Lam.) Vahl.), providing diverse and highly suitable breeding sites for burrow-dwelling petrels. Twelve petrel species breed on the island. Three species are particularly abundant: the blue petrel, the thin-billed prion, *Pachyptila belcheri* (Matthews) and the common diving petrel, *Pelecanoides urinatrix* (Gmelin) (Weimerskirch *et al.* 1988, Mougeot *et al.* 1998). Thin-billed prions and blue petrels use similar sized burrows, but in general have
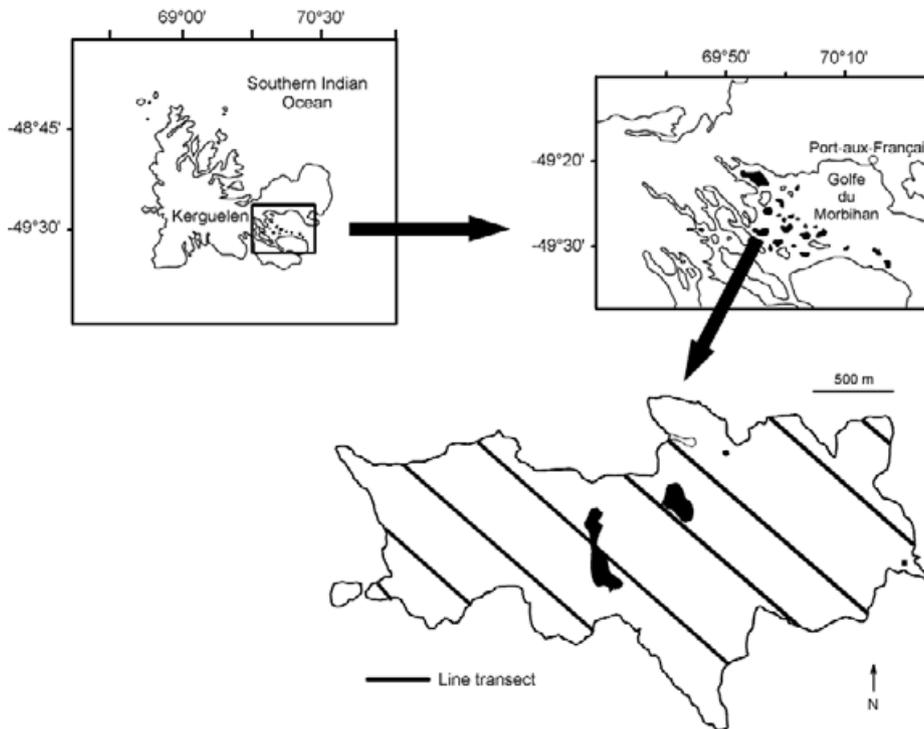
Fig. 1. Iles Kerguelen, the location of the Golfe du Morbihan with islands where blue petrels are know to breed (black shading), and Mayes Island with location of transects used for the census.

different habitat requirements in terms of vegetation cover and soil substrate (Genevois & Buffard 1994). Except for the house mouse *Mus musculus* L., there are no introduced vertebrates on the island.

Census work

Fieldwork was conducted between 20 and 28 November 2002 during mid incubation. Following the Catry *et al.* (2003) census of a closely related species, the thin-billed prion *Pachyptila belcheri* on the Falkland Islands, we used a systematic sampling approach to estimate blue petrel density. We ran eight transects crossing the whole island from south-east to north-west. The first transect location was chosen randomly, and the following transects paralleled the first one. The distance between successive transects was *c.* 300 m. In the field, each transect starting point was located with a GPS and plotted on a map. Along each transect, we stopped at counting points every 50 m (measured approximately using a 10 m rope). The application of these procedures resulted in all plots (a total of 149) being pseudo-randomly located in relation to habitat features and burrow entrance abundance. Although a truly random sampling approach would have resulted in all plots being randomly located in relation to habitat features, it was not feasible due to the time constraints in the field. At each location, one fieldworker stood at the centre of the plot holding the tip of a 5 m rope, while a second observer held the other end and walked describing a circle and counting all burrow entrances with centres that fell within the 78.5 m^2 plot. We only counted burrows with small entrances

typically used by either blue petrels or eventually by thin-billed prions (Genevois & Buffard 1994). We counted burrows with a clear entrance. Burrow entrances overgrown by the vegetation were not counted. Non-surveyed areas (lakes, steep cliffs) represent 2.2% of Mayes Island surface.

To assess burrow occupancy we used acoustic playbacks, a valuable technique used for censusing nocturnal burrowing seabirds (see for example James & Robertson 1985, Ratcliffe *et al.* 1998, Smith *et al.* 2001). Since calls are sex-specific in the blue petrel (Bretagnolle 1990), calls of both males and females were recorded on an endless tape by placing the microphone within the entrance of a burrow. Calls of males and females were successively played during the day at all burrow entrances found inside each 5 m radius plots, since in the thin-billed prion breeding birds respond far more to the calls of their own sex (Bretagnolle *et al.* 1998), and we recorded whether or not a bird responded. Because it is known that in Procellariiformes a proportion of birds present in burrows might not respond to the taped calls (Ratcliffe *et al.* 1998, Berrow 2000), we calculated a response probability to correct our occupancy estimate. This was estimated from a study colony of blue petrels as part of a long-term capture-recapture program. Since the occupancy of all nests in this colony was known exactly as birds were captured by hand in burrows for individual identification, we played the calls of males and females at all burrow entrances and recorded the number of responses. The response probability was then calculated as the number of burrows for which a bird responded to the playback divided by the number of burrows occupied by a bird.

Although the detailed habitat requirements for blue

petrels were previously studied on Mayes Island (Genevois & Buffard 1994), we described habitat type in each plot using four broad categories:

1) natural (NAT, includes plots covered with *P. antiscorbutica*, *A. selago*, *A. magellanica* in varying proportions),

2) mixed (MIX, includes plots with bare soils partly covered with vegetation of the previous species),

3) rocky (ROC, rocks and/or gravels), and

4) exotic (EXO, includes plots covered with introduced plant species such as *Poa annua* L. and *Taraxacum officinale* Weber ex Wiggers).

When more than one category occurred in a plot, the dominant type was chosen to describe it, although in the vast majority of plots only one type of habitat was present.

Data analysis

First we estimated burrow and blue petrel abundances, and the influence of habitat on blue petrel responses assuming there was no spatial autocorrelation in the blue petrel responses. To estimate burrow and blue petrel abundances we used estimators for simple random sampling, since they are similar to estimators for single systematic sampling (the sampling method used in this study; Thompson *et al.* 1998). Abundance was estimated as:

$$\bar{N} = \frac{\sum_{i=1}^{u} N_i}{u},$$

$$\hat{N} = U \times \bar{N},$$

$$\text{with } V\hat{a}r(\hat{N}) = U^2 \left[\left(1 - \frac{u}{U}\right) \frac{\hat{S}_{N_i}^2}{u} \right]$$

where $\hat{N}$ is the estimator of abundance, $\bar{N}$ is the sample mean number of burrows or responses from complete counts on points, $\hat{S}_{N_i}^2$ is the sample variance (N_i denotes a complete count on the *i*th selected plot), $V\hat{a}r(\hat{N})$ is the estimator of variance of total number of burrows or responses among sampling units, u is the number of sampling plots within the sample, and U is the number of sampling plots within the sampling frame. Using these estimators, the abundances of burrows and of responses were directly estimated. To obtain an estimate of breeding blue petrels we corrected the estimated abundance of responses by the response probability.

Using plots for which at least one burrow was detected we examined the influence of habitat (HAB) and abundance of burrows (BUR) on the number of responses of blue petrels (PET). The inclusion of the abundance of burrows in this analysis was motivated by the fact that *a priori* there was no reason to suppose that the number of responses increased linearly with the number of burrows. For example, density dependence mechanisms may act as limiting factors on the number of burrows occupied by blue petrels. Thus, this analysis tested whether the proportion of occupied burrows varied as a function of the number of burrows. We built generalized linear models (GLM) using the Genmod procedure with a negative binomial distribution and a log link function (SAS Institute Inc. 1999–2000). We started with the general models PET = HAB + BUR + BUR² + HAB*BUR and PET = HAB + Ln(BUR) + HAB*BUR, where the number of responses was respectively modelled as a quadratic and logarithmic function of the number of burrows, and tested for the effect of each variable and their interaction. Model selection was performed by selecting the model with the lowest Akaïke's Information Criterion adjusted for small sample size (AICc; Burnham & Anderson 2002). The goodness-of-fit of each model fitted was assessed using the value of the computed deviance divided by its number of degrees of freedom, and we used a deviance scale adjustment when the fit was poor.

In a second step, we took into account spatial autocorrelation in our analyses since for the thin-billed prion Catry *et al.* (2003) clearly showed the presence of spatial autocorrelation. We explored the spatial distribution of blue petrels responses by adjusting omnidirectional semi-variograms (Cressie 1993) using the Software Variowin version 2.21 (Pannatier 1996). An interactive procedure was used to model the geometry of the semi-variogram and get an estimate of the distance between points at which autocorrelation became negligible for blue petrel responses. Four covariance structures were assessed (spherical, exponential, gaussian and power). This modelling allowed us to explore the existence of spatial autocorrelation (Cliff & Ord 1998) between counts of blue petrel responses. Spatial autocorrelation may affect our estimates of abundance computed from a single systematic sample (Thompson *et al.* 1998). Thompson *et al.* (1998) recommend conducting a repeated systematic sample to obtain unbiased estimates of abundance and variance in any situation. Using the distance between points at which autocorrelation became negligible, we derived sub-samples of non-autocorrelated observations from the original data matrix, and considered these sub-samples as repeated systematic samples. Abundance was estimated as:

$$\bar{N}^* = \frac{\sum_{j=1}^{n_s} \bar{N}_j}{n_s},$$

$$\hat{N} = U \times \bar{N}^*,$$

$$\text{with } V\hat{a}r(\hat{N}) = U^2 \left(1 - \frac{u}{U}\right) \frac{\sum_{j=1}^{n_s} (\bar{N}_j - \bar{N}^*)^2}{n_s(n_s - 1)},$$
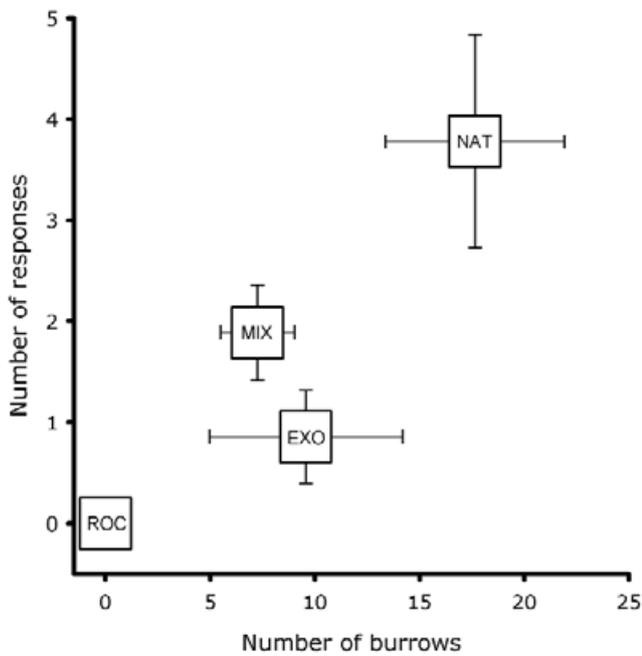
Fig. 2. Mean number of blue petrel responses and mean number of burrows for each habitat type at Mayes Island, Iles Kerguelen. Error bars indicate standard errors. Habitat type categories are: NAT for plots covered with *P. antiscorbutica*, *A. selago*, *A. magellanica* in varying proportions, MIX for plots with bare soils partly covered with vegetation of the previous species, ROC for rocks and/or gravels, and EXO for plots covered with introduced plant species such as *Poa annua* and *Taraxacum officinale*.

where $\bar{N}_j$ is the arithmetic mean of the *j*th systematic sample, n_s is the number of systematic samples chosen, and $\bar{N}^*$ is the overall mean across all systematic samples chosen, all other terms are defined as before.

Because the sample sizes in the sub-samples without autocorrelation were very small, we did not adjust GLM to these sub-samples.

Results

Burrow entrances were found in 54.4% of the 149 study plots, and blue petrel responses to playback were detected in 40.3% of the study plots. Mean (± SD) numbers of 10.7 ± 24.6 (min: 0; max: 182) burrow entrances, and of 2.3 ± 6.1 (min: 0; max: 40) responses per plot were recorded. Burrow entrances and responses were aggregated (variance/mean ratio of 56.6 and 15.9 respectively), but isolated burrow entrances and areas with very low densities were also found. The mean and highest raw densities recorded were respectively 0.136 ± 0.026 and 2.317 entrances m^{-2}, and 0.030 ± 0.077 and 0.509 responses m^{-2}.

Given that each plot had an area of $\pi \times 5^2$ m^2, the value of *U* was 35 490, and the total number of burrow entrances can
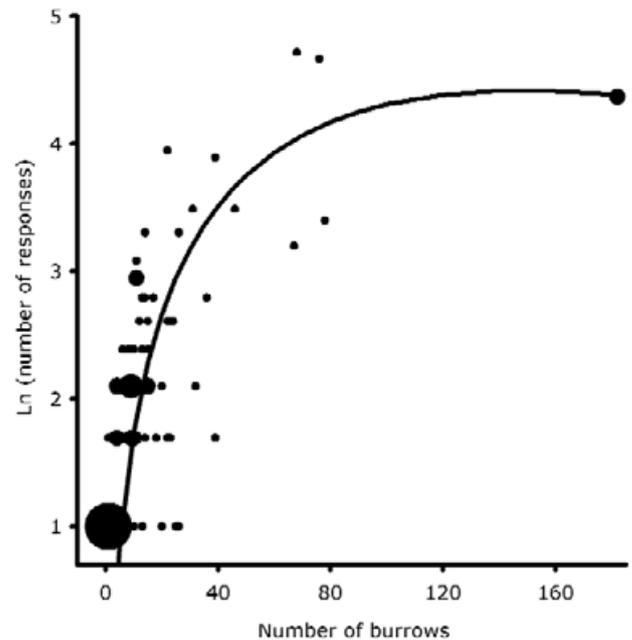

Fig. 3. The number of blue petrel responses plotted as a function of the number of burrows for each sampling point where at least one burrow was detected (i.e. proportion of occupied burrows as a function of the number of burrows) at Mayes Island, Iles Kerguelen. Different symbol sizes indicate the number of statistical units (6, 4, 2 and 1 from largest to smallest).

be estimated at 459 000 ± 87 000 (95% CI (Confidence Interval): 290 000–629 000). Similarly, the total number of raw responses can be estimated at 87 000 ± 27 000 (95% CI: 34 000–139 000).

Using the entire dataset, the goodness-of-fit tests for the models tested were relatively poor (deviance/df ratio between 0.59 and 0.80) and we used a deviance scale adjustment for model selection. The lowest AICc model was a model where the number of blue petrel responses was affected by the number of burrows on a natural logarithmic scale, but not by habitat, although the highest density of responses was found in the NAT habitat (Fig. 2). No response was detected in the ROC habitat. This model suggested that the number of responses increased sharply to a density of burrows of *c.* 0.60 burrows per m^2 and then stabilized (Fig. 3).

The best fit obtained for the semi-variogram that models the variability in blue petrel responses had a gaussian covariance structure, and a range value (i.e. the distance at which the variance reaches an asymptotic value) of ≈130 m. Therefore we used this distance to derive 18 sub-samples of non-autocorrelated observations comprising between 24 to 50 points from the original data matrix. Using these 18 sub-samples as repeated systematic samplings, the total number of burrow entrances can be estimated at 378 000 ± 27 000 (95% CI: 324 000–431 000), and the total number of raw responses at 83 000 ± 7900 (95% CI: 68 000–99 000).

The response probability was estimated on six sub-

samples of nests from the study colony and from a total of 167 nests. The response probability was 0.819 ± 0.075. This gives an estimate of the number of occupied burrows of $106\,000 \pm 34\,000$ (95% CI: 39 000–172 000) and $102\,000 \pm 13\,000$ (95% CI: 75 000–128 000) without and with taking into account spatial autocorrelation, respectively. Taking into account the response probability, the mean density of responses per m^2 was 0.037 ± 0.094.

Discussion

Apart from the blue petrel, some burrow entrances we counted belonged to the thin-billed prion (we obtained 16 responses from thin-billed prions for the 149 plots). Consequently, the estimated number of burrows comprises those used by blue petrels and some, but not all (since they nest in different habitats), of those used by thin-billed prions. In addition, although we estimated the number of burrow entrances, it is known that each entrance does not necessarily correspond to one nest chamber and one nesting pair (Genevois & Buffard 1994, Lawton *et al.* 2005). One entrance may lead to two or more chambers where eggs are laid, or two or more burrow openings may be linked to one single nest. This suggests that on islands with several similar sized petrel species for which burrow entrances might be difficult to differentiate (typically blue petrels and *Pachyptila* sp.), burrow densities are probably poor indicators of population sizes, and burrow occupancy needs to be estimated.

Burrow densities estimated in this study are within the range of those found on other sub-Antarctic islands for blue petrels (Marion: 0.0105–0.0189 mean entrances m^2, and up to 0.230 [Schramm 1986]; South Georgia: 0.720 mean entrance per m^2 [Croxall & Prince 1980]; Macquarie Island: up to 2 entrances per m^2 [Brothers 1984]; Diego Ramirez: from 1.11–2.03 burrows per m^2 [Lawton *et al.* 2005]), or prions (Marion: 0.008–0.014 mean entrances per m^2 for Salvin's prions *Pachyptila salvini* (Matthews) [Schramm 1986]; Ile aux Cochons: 0.104 mean entrances per m^2 for Salvin's prions [Derenne & Mougin 1976]; New Island, Falkland: 0.206 mean entrances m^2 for thin-billed prions [Catry *et al.* 2003]). At Mayes Island, Chaurand (1992) estimated density of blue petrels as 1.63 ± 0.12 burrows per m^2 in favourable areas (i.e. areas with native vegetation), which falls within the range of our estimates. Although we did not measure the slope at each point count, all burrow entrances and occupied burrows were situated in sloping areas, regardless of habitat, as found at other breeding localities (Schramm 1986, Catry *et al.* 2003).

For habitat plots where at least one burrow was detected, there was no evidence of an influence of habitat and of the interaction between habitat and the number of burrows entrances on the number of occupied burrows. Our samples sizes may have been insufficient to distinguish densities between habitats. Interestingly, the numbers of occupied burrows increased as a logarithmic function of the number of burrows, stabilising when burrow densities reached $c.0.6$ burrows per m^2. This suggests the existence of a limiting factor other than burrow availability to burrow occupation.

The spatial scale at which the autocorrelation in the number of occupied burrows became negligible (≈ 130 m) corresponds approximately to the size of the vegetation patches where blue petrels breed (Barbraud & Delord, personal observation). Thus, the spatial autocorrelation in the number of occupied burrows probably originated from transects crossing vegetation patches in which birds were breeding.

The effect of spatial autocorrelation on the estimated total number of occupied burrows on the island was relatively small. Indeed, not taking into account spatial autocorrelation only overestimated the number of occupied burrows by 4%. Because our survey was conducted half way through the incubation period it is a minimum estimate since birds that lost their egg before the survey were missed. Based on previous studies on blue petrels at Mayes Island (Chaurand & Weimerskirch 1994, Chastel *et al.* 1995), we assumed that egg failure was constant until hatching. Since hatching success (the proportion of eggs laid that hatched) is measured annually on Mayes Island as part of a long-term study, and was 43% in 2002, we therefore estimate the blue petrel breeding population on Mayes Island in 2002 to be around 142 000 (95% CI around 106 000–179 000) or 148 000 breeding pairs (95% CI around 55 000–241 000), respectively with or without taking into account spatial autocorrelation.

Blue petrels are found breeding throughout Iles Kerguelen, but are now very scarce on the main island because of introduced mammalian predators including cats *Felis catus* Linn. and ship rats *Rattus rattus* (Linn.). Most of the population of blue petrels now breeds on smaller islands where no predators were introduced. Although we have no precise estimate of breeding densities on other islands of the archipelago, field observations within the Golfe du Morbihan indicate that blue petrels breed on at least 18 other islands representing a surface area of about eight times that of Mayes Island (Fig. 1), with breeding densities on Mayes Island about twice to four times those on other islands (Barbraud unpublished data). Assuming such densities on other islands, the Golfe du Morbihan has a breeding population that may be situated between 400 000 and 800 000 pairs. This estimate is much higher than the 100 000–200 000 pairs estimated by Weimerskirch *et al.* (1988) for the Golfe du Morbihan. This difference between these two censuses does not reflect a trend but rather an artefact of differences in survey methods. The estimate from Weimerskrich *et al.* (1989) was obtained from extra-polations of densities measured on just a few numbers of quadrats. More census work on other breeding localities at Kerguelen (other islands in the Golfe du Morbihan, north and west of the mainland) will permit to obtain a more

robust estimate of the blue petrel population of the Iles Kerguelen. In the light of these estimates, it is likely that Kerguelen (this study) and Diego Ramírez (Lawton *et al.* 2005) are key breeding sites for the blue petrel, although more precise population size estimates are needed at other breeding localities.

Acknowledgements

References

BARBRAUD, C. & WEIMERSKIRCH, H. 2003. Climate and density shape population dynamics of a marine top predator. *Proceedings of the Royal Society London*, **B270**, 2111–2116.

BERROW, S.D. 2000. Using acoustics to monitor burrow-nesting white-chinned petrels *Procellaria aecquinoctialis* at Bird Island, South Georgia. *Polar Biology*, **23**, 575–579.

BRETAGNOLLE, V. 1990. Behavioural affinities of the blue petrel *Halobaena caerulea*. *Ibis*, **132**, 102–105.

BRETAGNOLLE, V., GENEVOIS, F. & MOUGEOT, F. 1998. Intra- and intersexual functions in the call of a non-passerine bird. *Behaviour*, **135**, 1161–1184.

BROTHERS, N.P. 1984. Breeding, distribution and status of burrow-nesting petrels at Macquarie Island. *Australian Wildlife Research*, **11**, 113–131.

BURNHAM, K.P. & ANDERSON, D.R. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd ed. New York: Springer, 488 pp.

CATRY, P., CAMPOS, A., SEGURADO, P., SILVA, M. & STRANGE, I. 2003. Population census and nesting habitat selection of thin-billed prion *Pachyptila belcheri* on New Island, Falkland Islands. *Polar Biology*, **26**, 202–207.

CHASTEL, O., WEIMERSKIRCH, H. & JOUVENTIN, P. 1995. Influence of body condition on reproductive decision and reproductive success in the blue petrel. *Auk*, **112**, 964–972.

CHAURAND, T. 1992. *Reproduction et stratégie d'approvisionnement chez un oiseau pélagique: le pétrel bleu (Halobaena caerulea)*. Thèse vétérinaire, Faculté de Médecine de Créteil, 137 pp.

CHAURAND, T. & WEIMERSKIRCH, H. 1994. Incubation routine, body mass regulation and egg neglect in the blue petrel *Halobaena caerulea*. *Ibis*, **136**, 285–290.

CLIFF, A.D. & ORD, J.K. 1998. *Spatial autocorrelation*. London: Prion, 318 pp.

CRESSIE, N.A.C. 1993. *Statistics for spatial data*. New York: John Wiley, 928 pp.

CROXALL, J.P. & PRINCE, P.A. 1980. Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biological Journal of the Linnean Society*, **14**, 103–131.

DERENNE, P. & MOUGIN, J.-L. 1976. Les Procellariiformes à nidification hypogée de l'île aux Cochons (archipel Crozet, 46°06'S, 50°14'E). *Comité National Français pour les Recherches Antarctiques*, **40**, 149–175.

FRENOT, Y., CHOWN, S.L., WHINAM, J., SELKIRK, P.M., CONVEY, P., SKOTNICKI, M. & BERGSTROM, D.M. 2005. Biological invasions in the Antarctic: extent, impacts and implications. *Biological Review*, **80**, 45–72.

GENEVOIS, F. & BUFFARD, E. 1994. Sites de nidification et caractéristiques des terriers chez deux espèces de petrels sympatriques aux îles Kerguelen: le Pétrel bleu *Halobaena caerulea* et le Prion de Belcher *Pachyptila belcheri*. *Alauda*, **62**, 123–134.

GUINET, C., CHASTEL, O., KOUDIL, M., DURBEC, J.P. & JOUVENTIN, P. 1998. Effects of warm sea-surface temperature anomalies on the blue petrel at the Kerguelen Islands. *Proceedings of the Royal Society London*, **B265**, 1001–1006.

JAMES, P.C. & ROBERTSON, H.A. 1985. The use of playback recordings to detect and census nocturnal burrowing seabirds. *Seabird*, **8**, 18–20.

JENOUVRIER, S., WEIMERSKIRCH, H., BARBRAUD, C., PARK, Y.H. & CAZELLES, B. 2005. Evidence of a shift in cyclicity of Antarctic seabirds dynamics link to climate. *Proceedings of the Royal Society, London*, **B272**, 887–895.

LAWTON, K., ROBERTSON, G., KIRKWOOD, R., VALENCIA, J., SCHLATTER, R. & SMITH D. 2005. An estimate of population sizes of burrowing seabirds at the Diego Ramirez archipelago, Chile, using distance sampling and burrow-scoping. *Polar Biology*, *Online First*, doi: 10.1007/s00300-005-0043-z.

MARCHANT, S. & HIGGINS, P.J. 1990. *Handbook of Australian, New Zealand, and Antarctic birds*. Melbourne: Oxford University Press, 735 pp.

MOUGEOT, F., GENEVOIS, F. & BRETAGNOLLE, V. 1998. Predation on burrowing petrels by the brown skua (*Catharacta skua lönnbergi*) at Mayes Island, Kerguelen. *Journal of Zoology*, **244**, 429–438.

PANNATIER, Y. 1996. *VARIOWIN: Software for spatial data analysis in 2D*. Berlin: Springer.

RATCLIFFE, N., VAUGHAN, D., WHYTE, C. & SHEPHERD, M. 1998. Development of playback census methods for storm petrels *Hydrobates pelagicus*. *Bird Study*, **45**, 302–312.

SAS INSTITUTE. 2001. *SAS/STAT User's Guide*. Cary, NC: SAS Institute Inc.

SCHRAMM, M. 1986. Burrow densities and nest site preferences of petrels (Procellariidae) at the Prince Edward Islands. *Polar Biology*, **6**, 63–70.

SMITH, S., THOMPSON, G. & PERRINS, C.M. 2001. A census of the Manx shearwater *Puffinus puffinus* on Skomer, Skokholm and Middleholm, west Wales. *Bird Study*, **48**, 330–340.

THOMPSON, W.L., WHITE, G.C. & GOWAN, C. 1998. *Monitoring vertebrate populations*. London: Academic Press, 388 pp.

WARHAM, J. 1990. *The petrels: their ecology and breeding systems*. London: Academic Press, 440 pp.

WEIMERSKIRCH, H., ZOTIER, R. & JOUVENTIN, P. 1988. The avifauna of the Kerguelen Islands. *Emu*, **89**, 15–29.

WEIMERSKIRCH, H., BROTHERS, N. & JOUVENTIN, P. 1997. Population dynamics of wandering albatross *Diomedea exulans* and Amsterdam albatross *D. amsterdamensis* in the Indian Ocean and their relationships with long-line fisheries: conservation implications. *Biological Conservation*, **79**, 257–270.