

The importance of land-based prey for sympatrically breeding giant petrels at sub-Antarctic Marion Island

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Abstract: Northern (*Macronectes halli*) and southern (*M. giganteus*) giant petrels breed at different times at sub-Antarctic Marion Island. Long-term census and breeding success data are used to test for competitive overlap between the two species by correlating population trends with those of land-based prey/carrion species. No parameter was singularly important in population regulation of either giant petrel species and the assumed dependence of breeding northern giant petrels on southern elephant seal *Mirounga leonina* carrion is not entirely supported.

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Introduction

Northern giant petrels *Macronectes halli* (Mathews) commence breeding *c.* six weeks before southern giant petrels *M. giganteus* (Gmelin) at Marion Island, thought to be due to competition avoidance due to similar diets and foraging areas (Hunter 1987, Cooper *et al.* 2001). Seasonally abundant seal and penguin carrion predominate in the diet of breeding male giant petrels at Marion Island (Hunter & Brooke 1992). Observations at seal carcasses have suggested southern giant petrel dominance over northern giant petrels (Johnstone 1979, Hunter 1987, de Bruyn & Cooper 2005). Such dominance may have contributed to northern giant petrels breeding early, so as to utilize carrion during the energetically demanding time of early chick-rearing, when southern giant petrels are still incubating and presumably have lower energetic demands (Cooper *et al.* 2001).

Marion Island supports breeding populations of three seal species and four penguin species, which provide seasonal land-based food resources for giant petrels (Hunter & Brooke 1992, Cooper *et al.* 2001, Fig. 1). Condy (1979), Hunter & Brooke (1992) and Cooper *et al.* (2001) hypothesized an important link between the concurrent southern elephant seal *Mirounga leonina* L. pupping and northern giant petrel hatching periods (a time when other terrestrial prey resources are limited) with the latter species' breeding success being affected by the availability of pup mortalities and placentas. Connell (1983) describes the study of niche overlap of sympatric species as one of the leading ways of investigating the nature and likelihood of interspecific competition. For example, Lynnes *et al.* (2002) found that chinstrap penguins *Pygoscelis antarctica* (Forster) competitively excluded sympatric Adélie penguins *P. adeliae* (Hombron & Jacquinot) from their usual foraging grounds in the Scotia Arc during years of poorer resource

availability, giving rise to changes in the breeding success of both penguins. Conversely, Dieckmann & Doebeli (1999) described sympatric speciation as a likely outcome of competition for resources. The study of resource overlap and competition between closely related species could thus illuminate plausible speciation hypotheses and clarify the role that competition plays in life history parameters.

In this paper long-term monitoring studies on Marion Island are used to test the influence of land-based resource availability on giant petrel egg production and breeding success.

Data collection

Long-term monitoring data (1982–2003), from sub-Antarctic Marion Island (46°52'S, 37°51'E) were used for northern and southern giant petrels (Cooper *et al.* 2001, Crawford *et al.* 2003a, 2004), southern elephant seals (Wilkinson 1991, Pistorius *et al.* 2001, M.N. Bester unpublished data), Antarctic (*Arctocephalus gazella* (Peters)) and sub-Antarctic (*A. tropicalis* (Gray)) fur seals (Hofmeyr *et al.* 2006), rockhopper (*Eudyptes chrysocome* (Forster)), macaroni (*E. chrysolophus* (Brandt)), king (*Aptenodytes patagonicus* (Miller)) and gentoo (*Pygoscelis papua* (Forster)) penguins (Crawford *et al.* 2003a, 2003b, 2003c, 2003d, 2004).

Northern giant petrels

Annual data on egg laying, hatching, fledging and overall breeding success were collected in the east coast study colony between 1986–2003 (excluding 1995 and 2001) (Cooper *et al.* 2001, R.J.M. Crawford unpublished data). Nests were individually marked shortly after egg-laying and breeding status recorded at *c.* two week intervals. Hatching

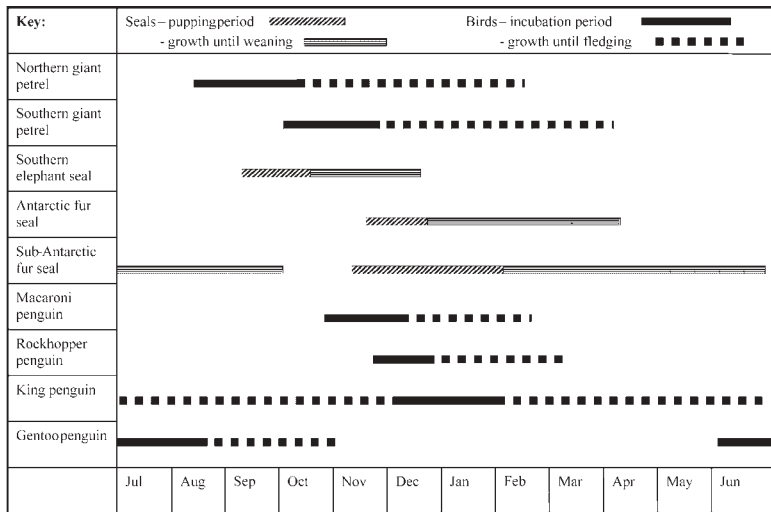


Fig. 1. Annual breeding cycles of northern and southern giant petrels (Hunter 1991), southern elephant seal (Condy 1979), Antarctic and sub-Antarctic fur seals (Kerley 1983), and gentoo, king, macaroni and rockhopper penguins at Marion Island (Hunter 1991, Crawford *et al.* 2003a, 2003b, 2003c, 2003d).

success (number of eggs hatched as a percentage of total laid), fledging success (number of chicks fledged as a percentage of eggs hatched) and overall breeding success (number of successfully fledged chicks as a percentage of eggs laid) were calculated. Complete island censuses of active nests during mid-incubation were carried out annually between 1984–2003 (excluding 1985, 1987 and 1995) (Crawford *et al.* 2003a, 2004).

Southern giant petrels

Annual data on egg laying, hatching, fledging and breeding parameters were collected in the Duiker’s Point study colony from 1986–1994 (Cooper *et al.* 2001). Complete island censuses of active nests were carried out annually during mid-incubation (1984–2003; excluding 1985, 1987 and 1995) and shortly before fledging (1998–2003) (Crawford *et al.* 2003a, 2004). Two separate measures of breeding success are thus available for non-overlapping times (initially for the monitored colony, followed by whole-island data).

Other species

Numbers of southern elephant seal pups born and pre- and post-weaning pup mortality (number and percentage) were determined for the whole island from 1986–2003 (Wilkinson 1991, Pistorius *et al.* 2001, M.N. Bester unpublished data). Antarctic and sub-Antarctic fur seal pups were counted between 1982–2003, during six and four seasons for the two species, respectively (Hofmeyr *et al.* 2006). Macaroni penguins were counted in colonies around the island during 1994–2002, using estimates of total numbers of breeding pairs for the island (Crawford *et al.* 2003c). Rockhopper penguins were counted (as breeding pairs) in colonies along the eastern coast between 1987 and 2003 (excluding 1988–1993, 1995) and these local estimates rather than total island estimates were used (Crawford *et al.* 2003b). Estimates for the total number of king penguin chicks surviving to the end of winter were available from 1987 to 2002 (excluding 1988, 1989 and 1995) (Crawford *et al.* 2003a). Estimates of the overall breeding population of gentoo penguins at Marion Island were available for 1994 to 2003 (Crawford *et al.* 2003d).

Table I. Spearman’s rank order correlations for northern (NGP) and southern (SGP) giant petrels vs counts of terrestrial potential prey species on Marion Island. The number of usable sample years for each species is given in parentheses.

	NGP eggs laid (n = 19)	% NGP breeding success (n = 18)	SGP eggs laid (study colony) (n = 12)	SGP eggs laid (whole island) (n = 8)	% SGP breeding success (study colony) (n = 10)	% SGP breeding success (whole island) (n = 6)
No. elephant seal pups (n = 18)	0.74*	0.52	-0.12	0.33	0.21	0.23
% elephant seal pup mortality (n = 18)	0.12	-0.35	0.78	-0.22	-0.02	-0.09
Macaroni penguin counts (n = 9)	0.83	0.32	-	0.60	-	-0.70
Rockhopper penguin counts (n = 10)	0.16	0.67	-	0.07	-	-0.43
King penguin chick counts (n = 12)	0.10	-0.28	-0.10	-0.07	0.90	-0.40
Gentoo penguin counts (n = 10)	0.05	0.62	-	0.00	-	-0.20
<i>A. gazella</i> counts (n = 6)	0.70	-0.90	1.00	-0.80	-	1.00
<i>A. tropicalis</i> counts (n = 4)	1.00	-1.00	1.00	-0.50	-	-

*significant at the $P \leq 0.0063$ level (Bonferroni adjusted)

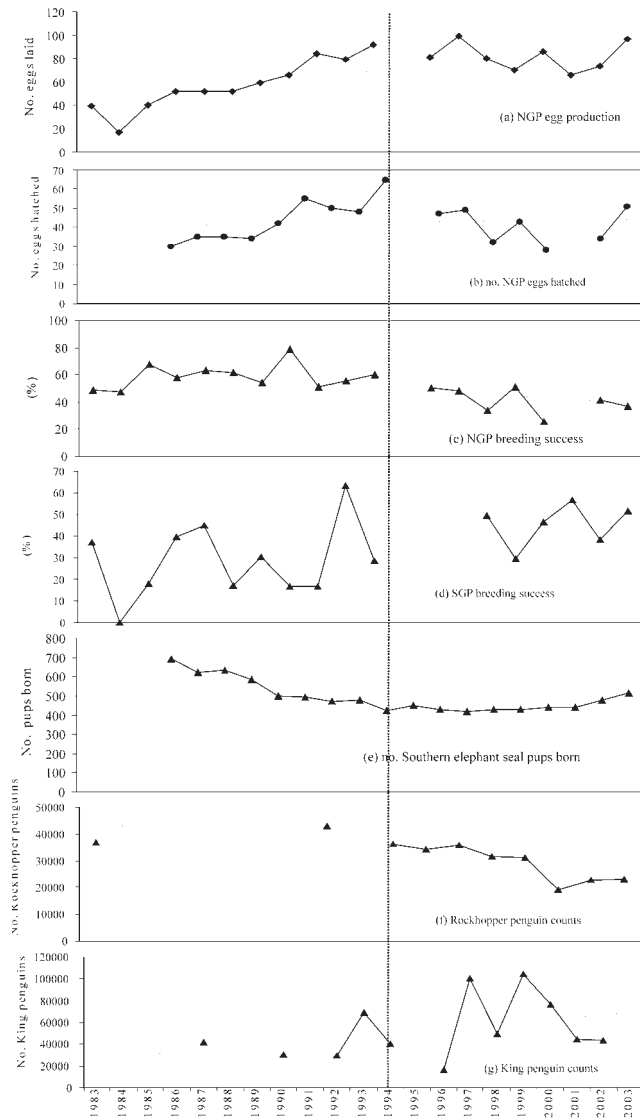


Fig. 2. Trend lines showing the number of **a.** northern giant petrel (NGP) eggs produced, **b.** number of NGP eggs hatched, **c.** NGP breeding success, **d.** southern giant petrel (SGP) breeding success, **e.** number of southern elephant seal pups born, **f.** rockhopper penguin counts and **g.** king penguin counts from (1983–2003). The dashed vertical line indicates the separation between the periods of decline and stability for southern elephant seals at Marion Island.

Table II. Mann Whitney U test for northern giant petrel breeding parameters between the period of southern elephant seal decline (1983–1994) and period of stability (1994–2003) on Marion Island.

	Z-value (adjusted)
No. eggs laid	-2.44*
No. eggs hatched	0.64
No. chicks fledged	0.05
% eggs hatched	3.12*
% chicks fledged	1.22
% NGP breeding success	2.94*

* significant at the $P = 0.01$ level

Data analysis

The software programme Statistica v.6 (Statsoft Inc, USA) was used for all analyses. Northern and southern giant petrel breeding parameters were tested for intra-specific relationships to assess which parameters (number of eggs laid, hatching success or fledging success) influenced breeding success. Using Spearman-R non-parametric correlations, northern and southern giant petrel breeding parameters were related to southern elephant seal pup numbers and pup mortality, macaroni, rockhopper and gentoo penguin counts, and Antarctic and sub-Antarctic fur seal counts. Non-parametric statistics were used because the data were not normally distributed and had small sample sizes that varied between datasets. To exclude type-1 error in our hypothesis testing we used standard Bonferroni adjustments as described by Rice (1989). When analysing correlation matrices it is useful to look at the R^2 values to describe the amount of variation that is explained in the correlation. We also tested for differences in northern giant petrel breeding parameters over the periods of elephant seal population decline (1986–94) and stability (1994–2003) on Marion Island (Pistorius *et al.* 2004) using Mann-Whitney U non-parametric tests. Southern giant petrel breeding data did not extend beyond 1994 and thus similar tests could not be performed.

Results

Northern giant petrel fledging success was significantly correlated with the number of eggs that hatched ($r = 0.94$, $P \leq 0.0083$) and breeding success within the study colony was significantly correlated with the percentage of eggs that hatched ($r = 0.92$, $P \leq 0.017$). All other breeding parameters showed no significant correlations. Southern giant petrel breeding success was significantly correlated with the number of chicks that fledged ($r = 0.89$, $P \leq 0.0083$). All other breeding parameters showed no significant correlations.

Northern and southern giant petrel breeding parameters varied in their relationships with the various potential prey species counts (Table I). Northern giant petrel breeding success was positively correlated with the number of southern elephant seal pups born ($r = 0.52$, $P \leq 0.05$, Fig. 2a & e), as well as with the number of rockhopper penguins ($r = 0.67$, $P \leq 0.05$, Fig. 2a & f). Southern giant petrel breeding success within the study colony was correlated to the number of king penguin chicks that survived the winter ($r = 0.9$, $P \leq 0.05$, Fig. 2d & g).

The number of eggs laid, hatching success and breeding success of northern giant petrels showed significant differences between the periods of decline (1983–1994) and stability (1994–2003) for elephant seals (Table II). The number of eggs laid by northern giant petrels increased during the period of elephant seal decline (1983–1994) and

levelled out during the period of stability (1994–2003) (Fig. 2a & e). Breeding success decreased concurrently with decreasing elephant seal numbers and appeared to stabilise when elephant seal numbers stabilised (Fig. 2c & e). Hatching success of the petrel seemed to be stable during the period of decline (1983–1994) but then started declining during the period of stability of the seal (1994–2003) (Fig. 2b & e).

Discussion

Food availability can affect life history traits, community structure (through competition) and can regulate population sizes (Martin 1987). Breeding seabirds are relatively restricted since they need to undertake incubation and chick feeding duties (e.g. González-Solís *et al.* 2000a, Phillips *et al.* 2006). Giant petrels feed on both marine and land-based prey and carrion (Hunter 1985, González-Solís *et al.* 2000a, 2000b). At Marion Island, diets of giant petrels varied considerably between sexes (especially for northern giant petrels), but less between species (Hunter & Brooke 1992). Males of both species, but especially northern giant petrels, consumed significantly greater proportions of seal and penguin carrion than did females, fed chicks more often than females, and northern giant petrel males guarded chicks for significantly more time than did females (Hunter & Brooke 1992, Cooper *et al.* 2001). These findings suggest that males are able to return more frequently with food and remain longer with the chick due to their greater use of nearby land-based carrion/prey. Successful chick rearing thus depends heavily on the ability of males to feed the chick regularly while females are foraging at sea. Giant petrel egg survival is considerably lower than is chick survival (Cooper *et al.* 2001, this study) and chick dietary samples (Hunter & Brooke 1992) indicate the importance of carrion to male parents and therefore their chicks; thus breeding success should conceivably be correlated in part to land-based resource availability.

Northern giant petrel numbers at South Georgia and Marion Island increased due to the increasing fur seal population, according to González-Solís *et al.* (2000a) and Nel *et al.* (2002). However, egg laying in both giant petrel species commences more than a month later at South Georgia (Hunter 1987) whereas the pupping seasons for southern elephant seals and Antarctic fur seals commence only approximately a week later than at Marion Island (Laws 1956, Condy 1979, Kerley 1983, Doidge & Croxall 1989). The availability of these land-based food resources are therefore temporally different for the two populations. Hunter & Brooke (1992) and Cooper *et al.* (2001) thus supposed a relationship between northern giant petrels and southern elephant seals at Marion Island (rather than with fur seals, as for South Georgia).

Northern giant petrel breeding success at Marion Island was correlated with the numbers of southern elephant seal

pups born annually over an 18 year period. However, the correlation is too weak to support unequivocally the hypothesis that southern elephant seal births are important to northern giant petrel chick survival. Giant petrels are not known to prey upon healthy pups, but each birth is accompanied by a placenta. Overall breeding success is probably not correlated with the number of placentas available, because they are often consumed by sub-Antarctic skuas *Catharacta antarctica* and lesser sheathbills *Chionis minor* before the arrival of giant petrels (P.J.N. de Bruyn personal observation). The suggestion that pup carcasses are an important factor in determining chick survival at Marion Island (Hunter & Brooke 1992, Cooper *et al.* 2001) is unlikely due to the absence of a strong correlation between northern giant petrel breeding parameters and southern elephant seal pup mortality. The argument is also weakened because the post-hatching period of northern giant petrels, when male participation is highest, coincides with the pre-weaning period of southern elephant seals when placentas are unavailable (Fig. 1).

Although we did find a significant difference in breeding success (but not in egg production) in the study colony of northern giant petrels between the period of rapid decline in elephant seal numbers from 1986–1994 and the period of stability from 1994–present (Pistorius *et al.* 2004), we cannot assume this to be a ‘cause and effect’ relationship. The possibility that similar environmental/climatic factors have acted upon the common resources of these top predators and in this way resulted in a similar trend over time, is more likely. Giant petrels (especially northern giant petrel females) and southern elephant seals consume relatively large proportions of the same prey species (e.g. the squid *Kondakovia longimana* constitutes 35% and 24% of the consumed biomass of the two species, respectively; Hunter & Brooke 1992, Rodhouse *et al.* 1992). Neither southern giant petrel numbers nor breeding success correlated with elephant seal population parameters or that of the two fur seal species at Marion Island. Dietary studies show that fur seals are a food source for southern giant petrels at Marion Island (Hunter & Brooke 1992), and elsewhere (Johnstone 1977, Hunter 1983, 1987, González-Solís *et al.* 2000a). However, this study finds no conclusive support for seals being more important than other prey items to either giant petrel species at Marion Island.

No correlation was found between penguin breeding numbers and northern giant petrel breeding success in the monitoring colony, although northern giant petrel breeding success correlated with the number of breeding rockhopper penguins. Rockhopper penguin carcasses are available from late November through March, but especially between late December and March when dead (and alive) penguin chicks can be preyed upon (Fig. 2c & f). Penguin chicks presumably constitute the major portion of penguin prey to giant petrels, since giant petrels rarely capture healthy adult penguins of any species at Bird Island, South Georgia

(Bonner & Hunter 1982). Although rockhopper penguins are not prevalent at Bird Island, they are at Marion Island, and their small size presumably makes them easy to subdue. This food source is available to northern giant petrel chicks until they fledge at Marion Island.

Although a correlation between southern giant petrel breeding success (in the study colony) with numbers of king penguins was found, the difficulty in estimating numbers of king penguins and the limited southern giant petrel breeding data for the study colony reduce confidence in this statistic. However, Fig. 2d & g, indicates a closely tied trend for both species' parameters during 1987–1994, when the southern giant petrel study colony was monitored. Hunter (1991) highlights the importance of southern giant petrel predation on king penguin chicks at Marion Island, particularly in winter. Descamps *et al.* (2005) shows that > 40% of king penguin chick failures are attributed to giant petrel predation by giant petrels at Iles Crozet, particularly during September and May (coinciding with the incubating and pre-winter periods, respectively).

Our data suggest that elephant seal carrion may not be the only or the most important factor in the success of northern giant petrel chicks. For southern giant petrels, no single land-based prey item appears to be critical to their survival at Marion Island, although king penguin population trends lend some support for a relationship between these two species. Although southern and northern giant petrels utilize similar prey they appear to avoid competition through differing breeding times (Cooper *et al.* 2001). Our data suggest no appreciable overlap whereby the same land-based resource singularly regulates either giant petrel's population. A complex suite of factors related to diet and foraging (both marine and land-based), and other factors, such as the availability of appropriate nest sites, most likely interplay to regulate populations of these sibling species.

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References

- BONNER, W.N. & HUNTER, S. 1982. Predatory interactions between Antarctic fur seals, macaroni penguins and giant petrels. *British Antarctic Survey Bulletin*, No. 56, 75–79.
- CONDY, P.R. 1979. Annual cycle of the southern elephant seal *Mirounga leonina* (Linn.) at Marion Island. *South African Journal of Zoology*, **14**, 95–102.
- CONNELL, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist*, **122**, 661–696.
- COOPER, J., BROOKE, M. DE. L., BURGER, A.E., CRAWFORD, R.J.M., HUNTER, S. & WILLIAMS, A.J. 2001. Aspects of the breeding biology of the northern giant petrel (*Macronectes halli*) and the southern giant petrel (*M. giganteus*) at sub-Antarctic Marion Island. *International Journal of Ornithology*, **4**, 53–68.
- CRAWFORD, R.J.M., COOPER, J., DYER, B.M., GREYLING, M.D., KLAGES, N.T.W., RYAN, P.G., PETERSEN, S.L., UNDERHILL, L.G., UPFOLD, L., WILKINSON, W., DE VILLIERS, M.S., DU PLESSIS, S., DU TOIT, M., LESHORO, T.M., MAKHADO, A.B., MASON, M.S., MERKLE, D., TSHINGANA, D., WARD, V.L. & WHITTINGTON, P.A. 2003a. Populations of surface-nesting seabirds at Marion Island, 1994/95–2002/03. *African Journal of Marine Science*, **25**, 427–440.
- CRAWFORD, R.J.M., COOPER, J., DYER, B.M., GREYLING, M.D., KLAGES, N.T.W., NEL, D.C., NEL, J.L., PETERSEN, S.L. & WOLFAARDT, A.C. 2003b. Decrease in numbers of the eastern rockhopper penguin *Eudyptes chrysocome filholi* at Marion Island, 1994/05–2002/03. *African Journal of Marine Science*, **25**, 487–498.
- CRAWFORD, R.J.M., COOPER, J. & DYER, B.M. 2003c. Population of the macaroni penguin *Eudyptes chrysolophus* at Marion Island, 1994/05–2002/03. *African Journal of Marine Science*, **25**, 475–486.
- CRAWFORD, R.J.M., COOPER, J., DU TOIT, M., GREYLING, M.D., HANISE, B., HOLNESS, C.L., KEITH, D.G., NEL, J.L., PETERSEN, S.L., SPENCER, K., TSHINGANA, D. & WOLFAARDT, A.C. 2003d. Population and breeding of the gentoo penguin *Pygoscelis papua* at Marion Island, 1994/95–2002/03. *African Journal of Marine Science*, **25**, 463–474.
- CRAWFORD, R.J.M., DE BRUYN, P.J.N., DYER, B.M., HANISE, B., KLAGES, N.T.W., RYAN, P.G., UNDERHILL, L.G. & UPFOLD, L. 2004. Counts of surface-breeding seabirds at Marion Island in 2003/2004. In *CCAMLR WG-EMM*, 04, 1–3.
- DE BRUYN, P.J.N. & COOPER, J. 2005. Who's the boss? Giant petrel arrival times and interspecific interactions at a seal carcass at sub-Antarctic Marion Island. *Polar Biology*, **28**, 571–573.
- DESCAMPS, S., GAUTHIER-CLERC, M., LE BOHEC, C., GENDNER, J.-P. & LE MAHO, Y. 2005. Impact of predation on king penguin *Aptenodytes patagonicus* in the Crozet Archipelago. *Polar Biology*, **28**, 303–310.
- DIECKMANN, U. & DOEBELI, M. 1999. On the origin of species by sympatric speciation. *Nature*, **400**, 354–357.
- DOIDGE, D.W. & CROXALL, J.P. 1989. Factors affecting weaning weight in Antarctic fur seals *Arctocephalus gazella* at South Georgia. *Polar Biology*, **9**, 155–160.
- GONZÁLEZ-SOLÍS, J., CROXALL, J.P. & WOOD, A.G. 2000a. Foraging partitioning between giant petrels *Macronectes* spp. and its relationship with breeding population changes at Bird Island, South Georgia. *Marine Ecology Progress Series*, **204**, 279–288.
- GONZÁLEZ-SOLÍS, J., CROXALL, J.P. & WOOD, A.G. 2000b. Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation. *Oikos*, **90**, 390–398.
- HUNTER, S. 1983. The food and feeding ecology of giant petrels *Macronectes halli* and *M. giganteus* at South Georgia. *Journal of Zoology*, **200**, 521–538.
- HUNTER, S. 1985. The role of giant petrels in the Southern Ocean ecosystem. In SIEGFRIED, W.R., CONDY, P.R. & LAWS, R.M., eds. *Antarctic nutrient cycles and food webs*. Berlin: Springer, 534–542.
- HUNTER, S. 1987. Species and sexual isolating mechanisms in sibling species of giant petrels *Macronectes*. *Polar Biology*, **7**, 295–301.
- HUNTER, S. 1991. The impact of avian predator-scavengers on king penguin *Aptenodytes patagonicus* chicks at Marion Island. *Ibis*, **133**, 343–350.

- HUNTER, S. & BROOKE, M. DE. L. 1992. The diet of giant petrels *Macronectes* spp. at Marion Island, southern Indian Ocean. *Colonial Waterbirds*, **15**, 56–65.
- HOFMEYR, G.J.G., BESTER, M.N., MAKHADO, A.B. & PISTORIUS, P.A. 2006. Population changes in Subantarctic and Antarctic fur seals at Marion Island. *South African Journal of Wildlife Research*, **36**, 55–68.
- JOHNSTONE, G.W. 1977. Comparative feeding ecology of the giant petrels *Macronectes giganteus* (Gmelin) and *M. halli* (Mathews). In LLANO, G.A., ed. *Adaptations within Antarctic ecosystems*. Washington, DC: Smithsonian Institution, 647–668.
- JOHNSTONE, G.W. 1979. Agonistic behaviour of the giant petrels *Macronectes giganteus* and *M. halli* feeding at seal carcasses. *Emu*, **79**, 129–132.
- KERLEY, G.I.H. 1983. Comparison of seasonal haul-out patterns of fur seal *Arctocephalus tropicalis* and *A. gazella* on subantarctic Marion Island. *South African Journal of Wildlife Research*, **13**, 71–77.
- LAWS, R.M. 1956. The elephant seal (*Mirounga leonina* Linn.). II. General, social and reproductive behaviour. *Scientific report of the Falkland Islands Dependencies Survey*, No. 13, 1–88.
- LYNNES, A.S., REID, K., CROXALL, J.P. & TRATHAN, P.N. 2002. Conflict or co-existence? Foraging distribution and competition for prey between Adélie and chinstrap penguins. *Marine Biology*, **141**, 1165–1174.
- MARTIN, T.E. 1987. Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecology and Systematics*, **18**, 453–487.
- NEL, D.C., RYAN, P.G., CRAWFORD, R.J.M., COOPER, J. & HUYSER, O.A.W. 2002. Population trends of albatrosses and petrels at sub-Antarctic Marion Island. *Polar Biology*, **25**, 81–89.
- PHILLIPS, R.A., SILK, J.R.D., CROXALL, J.P. & AFANASYEV, V. 2006. Year-round distribution of white-chinned petrels from South Georgia: relationships with oceanography and fisheries. *Biological Conservation*, **129**, 336–347.
- PISTORIUS, P.A., BESTER, M.N., KIRKMAN, S.P. & TAYLOR, F.E. 2001. Pup mortality in southern elephant seals at Marion Island. *Polar Biology*, **24**, 828–831.
- PISTORIUS, P.A., BESTER, M.N., LEWIS, M.N., TAYLOR, F.E., CAMPAGNA, C. & KIRKMAN, S.P. 2004. Adult female survival, population trend, and the implications of early primiparity in a capital breeder, the southern elephant seal (*Mirounga leonina*). *Journal of Zoology*, **263**, 107–119.
- RICE, W.R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.
- RODHOUSE, P.G., ARNBOM, T.R., FEDAK, M.A., YEATMAN, J. & MURRAY, A.W.A. 1992. Cephalopod prey of the southern elephant seal, *Mirounga leonina* L. *Canadian Journal of Zoology*, **70**, 1007–1015.
- WILKINSON, I.S. 1991. *Factors affecting reproductive success of southern elephant seals, Mirounga leonina, at Marion Island*. PhD thesis. University of Pretoria, Pretoria, South Africa, 185 pp. [Unpublished].