THE EFFECTS OF HUMAN DISTURBANCE ON THE SEABIRDS AND SEALS AT SUB-ANTARCTIC MARION ISLAND

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Dedicated to all past, present and future Marion Islanders

"Once an Islander, always an Islander"
GJG Hofmeyr

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Abstract

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Animals at Marion Island can be affected by logistic disturbance (especially helicopter noise), incidental pedestrian disturbance and research disturbance. The responses of wandering albatrosses (*Diomedea exulans*) and king penguins (*Aptenodytes patagonicus*) were investigated through standardised pedestrian approaches. Intensity of behavioural responses and levels of prolactin (females only) indicated that adult wandering albatrosses had become sensitised by high levels of chronic disturbance. Responses were greatest during the Prospecting and Early Incubation phases. Frequency of disturbance did not influence behavioural responses, but birds visited most often over three consecutive days had the lowest chick survival. Guarding king penguins were less likely to move away during disturbance than non-breeding groups. Visit duration and approach distance affected behavioural responses. There was evidence of habituation by king penguins to current levels of incidental disturbance. Grey-headed albatross (*Thalassarche chrysostoma*) adults and chicks showed short-term behavioural responses to research disturbance, and recovery times were variable. Level of chronic disturbance did not explain breeding success differences between colony sections. Instantaneous scans or counts of guarding and brooding gentoo penguins (*Pygoscelis papua*), incubating Crozet shags (*Phalacrocorax melanogenis*), pre-fledging grey-headed albatross chicks and non-breeding king penguins were made before and during helicopter operations. All species were more alert or responsive during flight operations and non-breeding birds left the area during disturbance. Birds were most responsive when the helicopter was close to colonies. Instantaneous scans and counts of non-breeding Subantarctic fur seals (*Arctocephalus tropicalis*) were made before and during helicopter operations and in the presence of pedestrian groups of different

sizes. Many seals left the beach during the first flights and those that remained were more likely t o be r esponsive and upr ight dur ing di sturbance t han be fore. Intensity of r esponse increased with increasing pedestrian group size. Monthly weighing did not influence the pre-weaning m ass o f pups , a m easure o f condition. Human ac tivities on the i sland ar e well managed but changes in t iming, frequency or i ntensity of ac tivities c ould be det rimental t o wildlife.

Layout and contributions of co-authors

This thesis consists of seven main chapters. These chapters are written as papers for submission to journals, so that the tables and figures follow the text. A reference list follows after each chapter. One of these chapters has been published and five have been submitted for publication (see below). The field work for this thesis was conducted at Marion Island from April 2004–April 2006. I was responsible for field work from April 2004 to the beginning of May 2005 as well as April–May 2006. I was responsible for all analyses and writing of each chapter. The contributions of the co-authors are stated below.

Chapter 1   Wheeler M, de Villiers M S, Majiedt P A The effect of history of chronic disturbance and phase of breeding cycle on the response behaviour of wandering albatrosses (*Diomedea exulans*) at sub-Antarctic Marion Island. Submitted to Mar Ornithol

Chapter 2   Wheeler M, de Villiers MS, Majiedt P A (2009) The effect of frequency and nature of pedestrian approaches on the behaviour of wandering albatrosses (*Diomedea exulans*) at sub-Antarctic Marion Island. Pol Biol 32: 32: 197–205

(in text referred to as Wheeler et al. 2009)

Chapter 3   Wheeler M, de Villiers MS, Underhill LG, Angelier F, Chastel O The influence of human disturbance on the behavioural responses and physiology of wandering albatrosses (*Diomedea exulans*) at sub-Antarctic Marion Island

(in text referred to as Wheeler et al. submitted)

Chapter 4   Wheeler M, de Villiers MS, Altweg R The effect of research disturbance on the behavioural responses and breeding success of grey-headed albatrosses

(*Thalassarche chrysostoma*) at sub-antarctic Marion Island. Submitted to Mar Ornithol

Chapter 5   Wheeler M, de Villiers MS, Underhill LG, Majiedt PA Responses to standardised pedestrian approaches by breeding and non-breeding groups of king penguins (*Aptenodytes patagonicus*) at sub-Antarctic Marion Island. Submitted to J Wildl Manage

Chapter 6   Wheeler M, de Villiers MS, Underhill LG, Majiedt PA The effect of helicopter flights on seabirds at sub-Antarctic Marion Island. Submitted to Pol Biol

Chapter 7   Wheeler M, Bester MN, Majiedt PA, Underhill LG The influence of helicopter, pedestrian and r esearch di sturbance on t he r esponse behav iour of Subantarctic f ur seals (*Arctocephalus tropicalis*) at M arion I sland. Submitted to J Wildl Manage

MSdV developed the research proposal which provided the financial support for this thesis, suggested methods of data anal ysis and c ommented on d rafts. P AM was r esponsible f or field w ork from M ay 20 05 t o M ay 2006. LGU suggested m ethods o f data anal ysis and commented on dr afts. MNB suggested field methods and c ommented on drafts. RA did the Capture-Mark-Recapture m odels and c ommented on a dr aft. Radioimmunoassays were conducted at the C entre d'Etudes B iologiques d e C hizé, Villiers-en-Bois, France by O C in collaboration with FA.

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At the end of my preprimary school year at Siembaba, I "graduated" with a cap on my head. When my photograph was taken, I decided that I will one day have the real university cap on my head. Eagerly I went to collect my graduation gear after I completed my BSc degree, but was told that much more work would be required if I wanted a cap on my head, seeing the university only provided caps for PhD graduates. So my journey continued and I had to keep on climbing the ladder. It has been a long journey filled with wonderful experiences, of which going to Marion Island was probably the best. However, there were some difficult times and here I wish to thank people who carried me through these times as well.

I am most grateful to my supervisor, Dr Marienne de Villiers, for all the advice and encouragement. During our first trip around the island together, I found it difficult to climb the steep hill at Azorellakop. She encouraged me when I reached the top by turning to me saying: "If it was easy to be at Marion Island, it would not have been such a special place. It will require dedication to make it through your time on the island". Now, after reaching the so-called top of the PhD study, I can only look back and see how we climbed together.

Three of my fellow Marion Island team members, became close friends at Marion Island and have been ever since. My deepest thanks to Ewald Ferreira, Elizabeth (Liz) Turner and Chris Swanepoel. "Only true friends leave footprints on the heart". Thanks also to Ewald Ferreira's family for all their support. Wanda Kaiser and I started to climb the scientific ladder together in first year and she has been a great friend.

I also wish to thank the Lord for strength throughout these years (Isaiah 40:31).

Introduction

<u>Human history at Marion Island</u>

The sub-Antarctic Prince Edward Island archipelago in the Southern Ocean (Figure 1) consists of Marion Island (290 km²; 46°54'S, 37°45'E) and Prince Edward Island (44 km²; 46°38'S, 37°57'E). Despite its remote position, Marion Island has a long history of human activity. It is believed that the island group was discovered in 1663, but the first recorded landing did not occur until 1803 or 1804 (Cooper 2008). Thereafter, many sealing vessels visited the islands and exploitation of the wildlife was severe. Fur seals (*Arctocephalus* spp.) were targeted for their skins and southern elephant seals (*Mirounga leonina*) were killed for their oil (Richards 1992). Sealers were routinely left on the islands for at least a year and after their food supplies were exhausted; they lived off seals, birds, eggs and fish. The skins of wandering albatrosses (*Diomedea exulans*) were cured and giant petrels (*Macronectes* spp.) were plucked for their feathers to make mattresses. Such high levels of exploitation probably caused severe population decreases of many species (Cooper 2008). The levels of all three pinniped species that breed at the islands decreased drastically during the early 1800s (Cooper and Headland 1991) and the sealing era was practically over by the 1850s (Cooper 2008). This allowed the fur seal populations to recover (Hofmeyr et al. 2006) – between 1951 and the late 1980s, Subantarctic fur seals (*Arctocephalus tropicalis*) increased at a rate of c. 10% per year (Wilkinson and Bester 1990) and the current rate of increase is 5.2% for Subantarctic fur seals and 14.8% for Antarctic fur seals (Hofmeyr et al. 2006). King penguins (*Aptenodytes patagonicus*) were among the birds that were impacted by the historic exploitation, but hunting ceased in the 1930s (Cooper and Headland 1991) and the numbers taken seem to have had little or no impact on the population (Crawford et al. 2003a).

Early scientific research at Marion Island included the collection of seabirds in 1830/31 and the collection of marine mammals in 1840 (Cooper 2008). Researchers visiting the island in

1873 commented on the mild responses of wandering albatrosses to pedestrians, noting that incubating birds were reluctant to stand up from their nests when approached (Moseley 1879 as quoted by Cooper 2008). Due to the dive-bombing behaviour of sub-Antarctic skuas (*Catharacta antarctica*), these birds were beaten off with sticks and gun barrels. These early scientists also made detailed observations of three of the four penguin species breeding at the island (Cooper 2008). Seabirds were intermittently studied during the first years after the annexation of the Prince Edward Islands by South Africa in 1947–1948 (e.g. Rand 1954, Van Zinderen Bakker 1971, Williams et al. 1975, Williams et al. 1979). Research effort intensified during the 1980s and 1990s, and has remained high ever since (e.g. Crawford et al. 2003a).

From the time of annexation by South Africa, there has been a permanent human presence at Marion Island. During the initial years after annexation, the main focus on Marion Island was weather data collection, but the conservation and research value of the islands' natural environment have increasingly been realised and since the 1970s there has been a strong emphasis on biological research (Chown and Froneman 2008). A permanent meteorological station was constructed on the northeast coast in 1948 and since then, 65 teams have stayed at the station for varying lengths of time. During this study, 15 personnel were station in 2004 and 13 in 2005; this number increased to c. 100 people during the annual resupply periods (April to May). The islands are currently managed by the South African Department of Environmental Affairs and Tourism. Construction of a new research station, adjacent to the station that is presently in use, commenced in 2003 and was still ongoing when this study was completed in 2009. This resulted in additional voyages each year, with greater numbers of personnel at the station and additional helicopter flights to transport personnel and equipment from the ship to the station. Some of these voyages coincided with the peak breeding seasons of seabird and seals at the island.

<u>Seabirds</u>

The Prince Edward Islands support 29 breeding species of birds (Crawford et al. 2003a). Surface-nesting species are monitored at selected long-term study colonies at Marion Island. Two demographic study colonies for wandering albatrosses were established in 1984 and a third in 1987 (Nel et al. 2003). The grey-headed albatross (*Thalassarche chrysostoma*) long-term studies began in 1997/98 (Ryan et al. 2006). Monitoring of Macaroni penguins (Cooper et al. 1997) started in the breeding season of 1979/1980 and the monitoring of other species followed with king penguins being monitored since 1987/88 (Crawford et al. 2003a) and gentoo penguins (*Pygoscelis papua*) being monitored since 1994/95 (Crawford et al. 2003b) Counts of birds at all breeding sites at Marion Island are conducted at least every five years and, for some species, every year (Nel et al. 2002, Crawford et al. 2003a). This monitoring has indicated that the Prince Edward Islands host a significant proportion of the global populations of several species: 44% of wandering albatrosses, 10% of grey-headed albatrosses (Tickell 2000, Crawford and Cooper 2003), 13% of king penguins and 0.5% of gentoo penguins (*Pygoscelis papua*) (Crawford and Cooper 2003). The Prince Edward Islands support one of only two breeding colonies of Crozet shags (*Phalacrocorax melanogenis*) in the world and host 33% of the entire population (Crawford and Cooper 2003). Research into the effects of human disturbance on these five seabird species is described in chapters 1-6 of this thesis.

Wandering albatrosses lay single-egg clutches and usually breed only in alternate years, although pairs with failed attempts during incubation or early chick-rearing can breed the following year (Tickell 1968). Although wandering albatrosses can breed at the age of seven years, the breeding success of birds younger than 10 years is 63% lower than it is for older birds. The breeding success of birds declines after 25 years of age, when it is 60% lower than that of birds between 10 and 25 years old (Nel et al. 2003). Wandering albatrosses are highly philopatric and usually breed with the same partner throughout their lives (Tickell 1968, Warham 1990). Mate changes were recorded for 5.3% of 3 984 breeding attempts at

Marion Island and in only 0.7% of these cases was the partner re-sighted alive (Nel et al. 2003). At Marion Island, this species breeds in loose colonies at densities of c. 5 nests.ha^{-1} around the island on the level coastal plains (Underhill et al. 2003). Prospecting for nest sites occurs in November and December, and eggs are laid in December or January and hatch in March (Ryan and Bester 2008). The brooding/guarding phase ends in late April or early May. Thereafter chicks are infrequently visited by their parents only for feeding, and must defend themselves (Mabille et al. 2004). Chicks fledge between December and February (Ryan and Bester 2008).

Grey-headed albatrosses are also generally biannual breeders, but at Marion Island 5.4% of successful breeders attempt to breed in successive years (but with 16.4% lower breeding success than the overall population mean) (Ryan et al. 2006). This species show a large degree of mate and nest-site fidelity. The same breeding partners were found in 96% of grey-headed albatrosses breeding in successive seasons. Once breeders were established in one colony, they rarely moved to adjacent colonies even if these colonies were only a few hundred metres apart (Prince et al. 1994). At Marion Island, grey-headed albatrosses breed in colonies on the steep cliffs on the south side of the island. Prospecting and nesting take place from August to September and incubation takes place from October until December. Chicks are brooded from December to January. Parents visit chicks infrequently from February to April, when chicks start to fledge (Marchant and Higgins 1990).

At Marion Island, king penguins breed in colonies on 15 sheltered beaches with gently-shelving slopes, mostly on the eastern side of the island (Hall and Williams 1981, van Heezik et al. 1995). They lay single eggs from mid-November to March (Williams 1995). Chicks are brooded for a month whereafter they congregate in crèches (Cherel et al. 1994) and have to survive on little or no food throughout the austral winter (van Heezik et al. 1993). Chick rearing lasts about 11 months (Cherel et al. 1994). Due to the prolonged breeding cycle, successful breeders can only lay again late in the following summer. However, late breeding

results in smaller breeding success, because at Marion Island only chicks from eggs laid early (before 7 February) in summer typically fledge (van Heezik et al. 1993). Successful breeders might therefore skip breeding in the following year (van Heezik et al. 1994), resulting in non-breeding individuals being present between breeding adults in a beach group. Due to the prolonged season, fledglings of one year can also be found during the following incubation period (Stonehouse 1960, Hughes et al. 2008). The adult moulting period is October to February (van Heezik et al. 1995).

Gentoo penguins are found throughout the year at Marion Island. They breed colonially on the grassy coastal plains and at Marion Island, colonies are distinct and small (<100 pairs) colonies (Williams 1980) and are mostly found on the eastern side of the island (Adams and Wilson 1987) Gentoo penguins lay two eggs and occasionally raise both chicks (Williams 1995). This is the only seabird species at Marion Island that breeds during the austral winter, with eggs being laid from June onwards. Females can relay if the first breeding attempt fails (Williams 1980) and laying can occur until November. Chicks can be found on the island until February (Cooper and Brown 1990). Adults moult from December to February (Williams 1995). Gentoo penguins on Marion Island seem to be especially sensitive to disturbance (van Zinderen Bakker 1971). Two breeding colonies close to the research station have been abandoned and this has been attributed to disturbance. The first was the colony adjacent to the station from which eggs were taken for human consumption (Rand 1994) and the second was at the Van den Boogaard River where diet samples were taken in 1994/95 (Crawford et al. 2003b). This intrusive sampling method has subsequently not been used for this species and the subsequent decline in numbers between 1995/95 and 2000/01 is not attributed to human disturbance (Crawford et al. 2003b).

Crozet Shags nest in colonies (Marchant and Higgins 1990) on coastal cliffs and offshore rocks and usually lay two or sometimes three eggs per clutch (Crawford et al. 2003c). Nest construction occurs in September (Marchant and Higgins 1990). Eggs are laid in October

and November, with 50% of eggs at Marion Island being laid by 11 November. Eggs found after November are considered to be replacement clutches (Crawford et al. 2003c, Williams and Burger 1979). The incubation and brooding periods last 28 and 18.5 days respectively. Chicks are attended to until they are 39.8 days old, although some chicks are fed until they fledge at 55.6 days old (Marchant and Higgins 1990).

Seals

Population trends of the three pinniped species at Marion Island have been followed from the 1970s and more intensively from the 1980s, by means of pup counts and long-term mark-recapture programmes (Wilkinson and Bester 1988, McMahon et al. 2003, Hofmeyr et al. 2006). Counts suggest that the Prince Edward Islands support total populations of c. 150 000 Subantarctic fur seals (33% of the world population) and 5 600 Antarctic fur seals (0.2% of the world population) (Hofmeyr et al. 2006, SCAR EGS 2004). Research into the effects of human disturbance on Subantarctic fur seals is described in chapter 7 of this thesis.

Subantarctic fur seals are found at Marion Island on beaches exposed to the prevailing westerly winds and covered with large, jumbled boulders (Condy 1978 in Hofmeyr *et al.* 2006). Pups are born between 16 to 20 December (Kerley 1985, Hofmeyr et al. 2007) and are attended by their mothers who alternate between foraging trips and visits ashore (Bester and Bartlett 1990). Maximum pre-weaning mass is attained at around 200 days of age in July (Kirkman et al. 2002) and pups are weaned in October (Kerley 1983, 1985).

Threats to the seabirds and seals

Current threats to seabirds and seals at the Prince Edward Islands include alterations of prey availability, mainly as a result of environmental change (McMahon et al. 2003, McMahon et al. 2005); introductions of alien species (e.g. Huyser et al. 2000); commercial fishing operations that result in high mortality rates of albatrosses and petrels (Nel et al. 2000, 2003); pollution and litter, especially the dangers these pose to wildlife through

entanglements and ingestion (Ryan 1987, Cooper and Condy 1988, Ryan 1996, Nel and Nel 1999, Hofmeyr et al. 2002); and human disturbance (de Villiers et al. 2005, de Villiers et al. 2006, de Villiers and Cooper 2008).

Human disturbance can have negative effects on the behaviour and physiology of wildlife (Weimerskirch et al. 2002, Engelhard et al. 2002, McClung et al. 2004, Ellenberg et al. 2007, van Polanen Petel et al. 2008), potentially influencing reproduction and survival (Bolduc and Guillemette 2003, Harris 2005). Characteristics of animals found in the sub-Antarctic and Antarctic make them especially vulnerable to disturbance (de Villiers 2008). Colonially breeding animals are vulnerable (Boersma et al. 2001) because large numbers of animals can be simultaneously affected. Animals live in a harsh environment with a limited breeding season and, because they are long-lived, slow to mature and slow to reproduce, have limited resilient to disturbance (de Villiers 2008). Animals on sub-Antarctic islands have not evolved appropriate antipredatory responses because they generally do not have natural land-based predators (Burger and Gochfeld 1999). At Marion Island, birds were exposed to the introduced domestic cat (*Felis catus*) in 1949, but cats were successfully eradicated from the island by 1991 (Bester et al. 2002).

Conservation management

Efforts to reduce disturbance on the Prince Edward Islands included the development in 1982 and adoption in 1988 of a "Code of Conduct for the Environmental Protection of the Prince Edward Islands" (de Villiers and Cooper 2008). The Prince Edward Islands archipelago was declared a Special Nature Reserve in 1995 in terms of the Environmental Conservation Act (Act No. 73 of 1989) and is managed according to the Prince Edward Island Management Plan (Prince Edward Island Management Plan Working Group 1996). This management plan has been reviewed and a new management plan (Chown et al. 2006) has been accepted by the Department of Environmental Affairs and Tourism, but had not yet been implemented at the beginning of 2009. No tourism is allowed at the islands under the

National Environmental Management: Protected Areas Act (Act No. 57 of 2003). However, wildlife can still be disturbed by logistic activities (especially helicopter flights), research activities and incidental disturbance by personnel passing by or approaching animals.

Recommendations to reduce potential disturbance by helicopter flights have been made based on qualitative observations during SAAFC-130 Hercules aircraft flights (Cooper et al. 1994). Recommendations for helicopter flights and a flight path plan for Marion Island have been incorporated into the new management plan (Chown et al. 2006). These recommendations have been made specifically to reduce potential disturbance to sensitive breeding colonies of wildlife at the island. Recommendations are that penguins, albatross and seal colonies should not be overflown lower than 600 m above ground level and landings closer than 250 m from colonies should be avoided. Research permits issued by the South African National Antarctic Programme (SANAP) are required before studies can be conducted at the island. These permits are only issued if approval has been obtained from the ethical committee of the institution to which the researcher belongs.

Marion Island has been zoned into four areas (Figure 2), partly to minimise disturbance to wildlife. Most logistic activities are performed at or near the station, in Zone 1 (the Service Zone). Zone 2 (the Natural Zone) forms a buffer between Zone 1 and the remainder of the island and areas surrounding the field huts are also in this zone. Personnel on the island are generally only provided with permits for these two zones. The remainder of the island, with the exception of Zone 4 areas, is a Wilderness Zone (Zone 3) where approved research activities are conducted. Zone 4 areas (the Protected Zone) are proclaimed for the extraordinary protection of especially sensitive species or sites. These areas include 100 m buffers around gentoo penguin and southern giant petrel (*Macronectes giganteus*) colonies, 200 m buffers around the three wandering albatross demographic study colonies (at Macaroni Bay, Sealer's Beach and Goney Plain) and a 200 m buffer around the grey-headed albatross demographic study section at Grey-headed Ridge (this buffer excludes a footpath

that crosses the ridge nearby the study section). Crozet Shag breeding colonies were recently awarded Zone 4 status, with a buffer of 100 m (M.S. de Villiers, personal communication). All sites with historical value also fall within this Zone (Prince Edward Island Management Plan Working Group 1996), as do the well-known lava tunnels at Fred's Hill. Prince Edward Island has been proclaimed a Zone 4 area in its entirety. This island has no permanent man-made structures. Only one visit per year by a maximum of six persons and for a maximum of four days is currently allowed (Prince Edward Islands Management Plan Working Group 1996), but visits to the island are even more infrequent than this. The new management plan will allow for one visit every second year by a maximum of 10 people and for a maximum of eight days (Chown et al. 2006).

Apart from the buffer areas set around the sensitive breeding colonies, a general minimum approach distance of 15 m to breeding birds and seals at Marion Island has been proposed (Hänel and Chown 1998). In the new management plan, this distance has been set for all species during all phases of the animals' breeding cycle, except for wandering albatrosses where a minimum approach distance of 50 m to courting birds has been recommended (Chown et al. 2006). The setting of a single approach distance for all species is unlikely to be effective, as responses to disturbance are species-specific (Ellenberg et al. 2006, Holmes 2007). Animals may perceive approaching pedestrians as potential predators; thus approaches may evoke anti-predatory responses (Frid and Dill 2002). Individuals might be more sensitive to disturbance during sensitive periods of the breeding cycle (Holmes et al. 2007, Frid and Dill 2002, Bolduc and Guillemette 2003) because nest defense behaviours of parents should be related to the reproductive value of their offspring (Trivers 1972). At Marion Island, the proposed distance of 15 m was based on *ad hoc* observations by personnel on the island rather than on quantitative evidence. Booth and Bio (2001) suggested that minimum approach distances will only be effective if based on empirical evidence of distance-related responses to disturbance.

The intensity of responses to disturbance can be influenced by various extrinsic and intrinsic factors (de Villiers 2008). It has been recommended that human disturbance studies should further investigate the effects of the following extrinsic factors: visitor group size; starting distances of approaches; frequency of visit; the distribution of visitors relative to animals; visitor access points and wildlife refuge areas; level of chronic disturbance; and different forms of transport. Species differences in susceptibility, and the effects of stage of breeding on responses to disturbance, also require further research (de Villiers 2008).

The aims of this thesis were to investigate some of these factors for different species of seabirds and seals at Marion Island. Specifically, this study focused on:

- The effects of history of disturbance and breeding phase of wandering albatross chicks and adults (Chapter 1)
- The effects of frequency of disturbance and human group size on the response behaviour and chick survival of wandering albatrosses (Chapter 2)
- The influence of different levels of chronic disturbance on the behavioural and hormone levels of wandering albatrosses (Chapter 3)
- The effects of research and incidental disturbance on the behaviour and breeding success of grey-headed albatrosses (Chapter 4)
- The effects of breeding phase, history of disturbance, visit duration, approach distance and weather on the behavioural responses of breeding and non-breeding groups of king penguins (Chapter 5)
- The effects of helicopter disturbance on brooding and guarding gentoo penguins, grey-headed albatross chicks close to fledging, incubating Crozet shags and non-breeding king penguins (Chapter 6)
- The effects of helicopter, pedestrian and research disturbance on the behavioural responses and pup condition of Subantarctic fur seals (Chapter 7)

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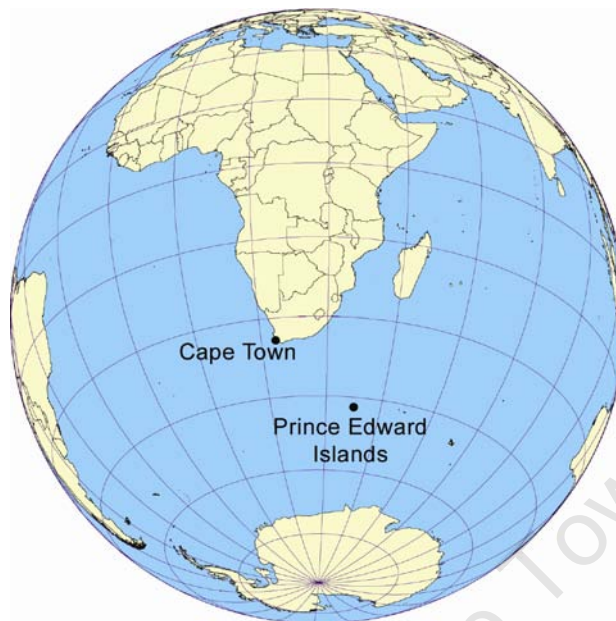
Figure 1 The position of the Prince Edward Islands in the Southern Ocean. Also indicated on the map is Cape Town, South Africa, from where voyages to the island are made.
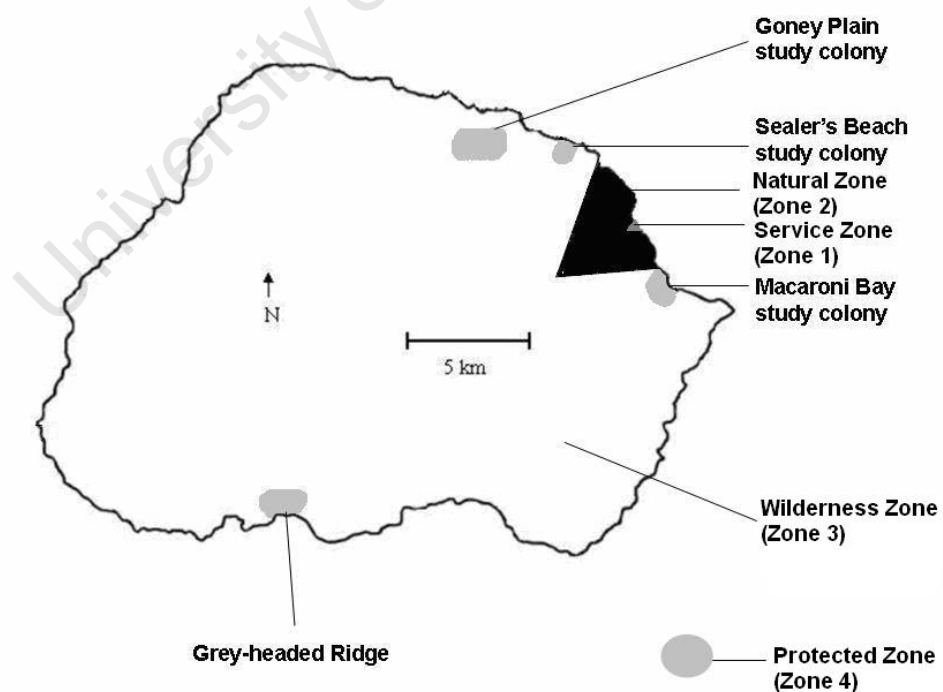
Figure 1 Management Zones on Marion Island. Crozet shag, gentoo penguin and southern giant petrel (*Macronectes giganteus*) colonies are also considered to be in the Protected Zones, but the locations of these colonies may vary over time.

The effect of history of chronic disturbance and phase of breeding cycle on the response behaviour of wandering albatrosses (*Diomedea exulans*) at sub-Antarctic Marion Island

Abstract

The effect of human disturbance was investigated through standardised single-person approaches to individual wandering albatross (*Diomedea exulans*) chicks in early May (n=27), late May (n=39), June (n=32) and November (close to Fledging) (n=98) 2005, as well as to adults during the Prospecting phase in December (n=72) 2005, Early Incubation in January (n=143), Late Incubation in February (n=139) and the Brooding phase in March (n=55) 2006. These birds were in four areas and were exposed to different levels of chronic disturbance: near Repetto's, a site far from the station (disturbance levels: research low; incidental low), close to the research station (disturbance levels: research medium; incidental high); Sealer's Beach study colony (disturbance levels: research high, incidental low); and Macaroni Bay study colony (disturbance levels: research high, incidental intermediate due to more pedestrians at boundaries). Behavioural responses were analysed according to Vocal Responses (VR), Non-vocal Responses (NVR) and Overall Responses (OR). In November chicks close to station tended to have smaller OR and fewer stood up than birds in other areas. All prospecting birds close to station stood up, compared to 67% far from station. The NVR and OR scores of birds far from station were smaller during Prospecting and Late Incubation than birds with higher disturbance levels. Over the breeding season, birds far from station had larger NVR during Early Incubation, and tended to have larger VR during Brooding, than during Prospecting. Chicks close to station and adults far from station responded least. The current zoning of the island seems to be effective in protecting the Prince Edward Island wandering albatross population from human disturbance.

Introduction

The Antarctic and sub-Antarctic regions, once seldom influenced by humans, are experiencing increases in human numbers and activities (Cool Antarctica 2008). These remote areas have become popular tourist destinations, for example the number of tourists to the Antarctic increased from 6 704 in the austral summer of 1992–93 to 29 530 in 2006–07 (IAATO 2008), an annual increase of 11.2%. Additionally, large numbers of people are stationed in the Antarctic as part of national programmes - 4 000 personnel were present in 2006–2007 (Cool Antarctica 2008). Permanent research stations have been established on the Antarctic continent and on many sub-Antarctic islands, and many colonies of seabirds in the region have been extensively studied over long periods (e.g. Prince et al. 1994, Crawford and Cooper 2003). Although research activities are essential to determine the breeding productivity of birds and the factors that can influence their breeding, human activities around stations and in study colonies can disturb animals and influence their behaviour (Knight and Cole 1995), potentially impacting their survival and productivity (O'Dwyer et al. 2006).

The intensity of response to disturbance is species-specific (Blumstein et al. 2003, Blumstein 2006, Ellenberg et al. 2006) and can depend on the history of disturbance experienced by animals (Walker et al. 2006). Timid species such as the southern giant petrel (*Macronectes giganteus*) are negatively impacted by human activities around stations, while scavenging species such as skuas may benefit (Jouventin and Weimerskirch 1991). The infrastructure of stations may also enhance predation opportunities (Descamps et al. 2005). Gentoo penguins (*Pygoscelis papua*) breeding at the station on sub-Antarctic Macquarie Island exhibited less intense behavioural responses to pedestrian approaches than birds breeding further away from the station, indicating habituation to daily disturbance at the station (Holmes et al. 2005). However, even where species seem to be able to habituate to human activities, habituation is rarely complete (Frid and Dill 2002).

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Individuals in different life stages can respond differently to disturbance (Müllner et al. 2004). The majority of studies on the effects of human disturbance on birds have focused on the responses of adults (Walker et al. 2005) and the responses of chicks are less frequently investigated (e.g. Lord et al. 1997, Giese and Riddle 1999, Müllner et al. 2004, Walker et al. 2005) but can be quite different. For example, adult Magellanic penguins (*Spheniscus magellanicus*) in a tourist-disturbed area had less intense behavioural responses and lower corticosterone levels than undisturbed adults (Walker et al. 2006), and breeding success was not influenced by tourist visitation. Chicks close to Fledging in visited areas could be approached to shorter distances than chicks in undisturbed areas. However, newly hatched chicks in visited areas had higher corticosterone levels than chicks in undisturbed areas and older chicks in both areas had similar corticosterone responses (Walker et al. 2005). Similarly, hoatzin (*Opisthocomus hoazin*) adults seemed to have habituated to disturbance, but juveniles in disturbed areas had reduced body masses and increased levels of corticosterone compared to juveniles in undisturbed areas. Chick survival was smaller at tourist-visited nests due to greater mortality of juveniles (Müllner et al. 2004).

The responses of adults can also differ over the phases of the breeding cycle (Frid and Dill 2002, Bolduc and Guillemette 2003). According to the Parental Investment Theory (Trivers 1972), nest defense behaviours of parents should be related to the reproductive value of the offspring. The intensity of responses should therefore increase throughout the breeding season. This has been found for many species, including long-eared owls (*Asio otus*) (Galeotti et al. 2000), Eurasian kestrel (*Falco tinnunculus*) (Carrillo and Aparicio 2001) and greylag geese (*Anser anser*) (Osiejuk and Kuczyński 2007).

The Prince Edward Islands archipelago, consisting of Marion Island (290 km²; 46°54'S, 37°45'E) and Prince Edward Island (44 km²; 46°38'S, 37°57'E), was declared a Special Nature Reserve in

1995 in terms of the Environmental Conservation Act (Act No. 73 of 1989) and no tourism is allowed under the National Environmental Management: Protected Areas Act (Act No. 57 of 2003). There has been a permanent research station on Marion Island since 1948. Construction of a new station, adjacent to the old station currently in use, commenced in 2003 and was still ongoing when the study was completed in 2006. Wandering albatrosses (*Diomedea exulans*) close to the station are frequently exposed to incidental disturbance. Although many of these birds have been ringed, they are not regularly monitored. Three demographic study colonies for wandering albatrosses (Macaroni Bay, Sealer's Beach and Goney Plain, Figure 1) were established in the mid 1980s. All chicks and adults breeding in these colonies have been ringed (Nel et al. 2003). The colonies are only entered by researchers with Limited Access Permits and they are buffered by exclusion zones of 200 m (Chown et al. 2006). Nests on the remainder of the island are counted twice annually (during Incubation and close to Fledging). Apart from these counts, these albatrosses are seldom disturbed.

The aims of this study were to investigate the behavioural responses of Marion Island wandering albatrosses to human disturbance and the effects of history of disturbance (albatrosses in areas with different levels of chronic disturbance) as well as age of chicks (early May, late May, June and close to Fledging) and breeding phase of adults (Prospecting, Early Incubation, Late Incubation and Brooding) on these responses.

Methods

Standardised single-person approaches were made to wandering albatross chicks and adults at Marion Island. Before field work was conducted, the approacher practiced to estimate distances in the field by placing a pole at 2 m to visualise the correct distance. Approaches were done during daylight hours and in relatively clear weather conditions. Standardised clothing was worn during all approaches. Before each approach, the investigator recorded the posture of the bird

(whether it was standing or sitting on or close to the nest). Approaches were made directly towards nests at one pace per second. During an approach, all vocal and non-vocal behaviours of a bird, and the distance between the approacher and the nest at which these were elicited, were recorded on dictaphone. The investigator stopped 2 m from the nest and remained stationary while recording aspects of the bird's behaviour for one minute on the dictaphone. Thereafter, a pole was used to gently shift adults on the nest so that nest contents could be determined.

Non-vocal reactions were classified as Head-Shake, Bow, Ritualised Preen, Flap and Tail-Shake, and Head-Turn (after Tickell 2000). A single Head-Turn was defined as a turn from centre to the side and back again. Vocalisations were classified as Bill Snap, Clappering, Shrill Clappering (after Tickell 2000), or Snapping (after de Villiers et al. 2005). Whether a bird stood up and / or resettled on its nest during the approach or during the minute that the researcher was at the nest, was also noted.

Analyses

Distances to nests where behaviours occurred were worked out through the steps counted on the dictaphone and using the average length of a pace of the approacher (0.65 m). The initial position of the bird before approach and data collected within 20 m of nests were used for the approach analyses. Responses were analysed according to a bird's Non-vocal Response (NVR), Vocal Response (VR), and Overall Response (OR). The frequency of Head-Turns during the approach was regarded as an index of vigilance and was used to determine a bird's NVR. The number of Head-Turns was also ranked. For adults, ranks were determined according to cutpoints set at the quartiles of the full range of head-turns and ranged from 0–4. Chicks turned their heads fewer times during approaches than adults; therefore Head-Turn ranks were determined by cutpoints set at the thirds and ranged from 0–3. Vocalisations were regarding as

an index of aggression and ranked according to intensity: No vocalisations (0); Bill Snap (least intense = 1); Snapping (2); Clappering (3); and Shrill-Clappering (most intense = 4) (de Villiers et al. 2005). The highest ranking vocalisation elicited during the disturbance was used as the VR score. The OR Index was the sum of VR and the ranked NVR and also incorporated whether or not birds stood and resettled during the disturbance. Standing/resettling behaviour of adults was considered to indicate the likeliness of a bird fleeing from its nest. Chicks might stand up from their nests in response to disturbance to appear larger. Birds that were already standing prior to the approach were excluded from this analysis. If a bird stood up during the last 20 m of the approach or during the minute at the nest a score of two was added to the OR rank, while one rank point was subtracted if a bird resettled on the nest during these periods. For each approach, OR was scored between 0 (no response) and 10 (high intensity response) for individual adults, and 0 (no response) and 9 (high intensity response) for individual chicks.

History of disturbance

The effect of history of disturbance was investigated by comparing the behavioural responses of birds in four areas (Figure 1) with different levels of chronic disturbance. Birds near Repetto's were far from the station (hereafter referred to as far-station birds) and were exposed to low levels of both research and incidental disturbance. Birds close to the station (hereafter referred to as close-station birds) were exposed to frequent incidental disturbance and intermediate levels of research disturbance. Many were ringed, although they were not regularly monitored. Birds at Macaroni Bay and at Sealer's Beach were exposed to high levels of research disturbance in the demographic study colonies. Nests were visited by researchers at weekly intervals during the Incubation and Brooding/Guarding stages and monthly thereafter (Nel et al. 2003). Birds in either one of these colonies will be referred to as study-colony birds. Macaroni Bay is closer to the station than Sealer's Beach and pedestrians used a foot path along the eastern boundary of the former colony. Birds at Macaroni Bay were thus exposed to

intermediate levels of incidental disturbance, while birds at Sealer's Beach were exposed to low levels of incidental disturbance.

Chicks were approached throughout the Nestling stages in early May (n=27), late May (n=39), June (n=32) and November (close to Fledging) (n=98) 2005. Approaches in early May, late May and June were made to birds close to the station and in the study colonies. In November, approaches were made to birds at these sites and to birds at Repetto's. Due to low sample sizes for chicks, responses of chicks in the two study colonies were combined for analyses.

Approaches to adults were made during the Prospecting phase in December (n=72), Early Incubation in January (n=143), Late Incubation in February (n=139) and the Brooding phase in March (n=55) 2006. During Prospecting, approaches were made to birds close to the station and at Repetto's, while approaches in subsequent months were made in all four areas. Results for Macaroni Bay and Sealer's Beach were analysed independently for adults. Results were not analysed independently for male and female adults, as no significant differences in any of the behavioural indices were found in previous studies at Marion Island (de Villiers et al. 2005, Wheeler et al. 2009).

Phase of the breeding cycle

Behavioural responses of birds within areas were compared to investigate whether birds were more susceptible to disturbance during certain phases of the breeding cycle. OR scores were not included in this analysis. Birds were expected to be more vigilant and likely to flee early in the season, but more aggressive later in the season, and these two types of responses were thus not combined into one index for comparisons of behaviour during different phases of the breeding cycle.

Nonparametric tests were performed using GenStat 9 (Lawes Agricultural Trust, Rothamsted Experimental Station). P values for Kruskal-Wallis tests and Mann-Whitney tests were adjusted for ties. Nonparametric multiple comparisons were used to give interpretations of results if Kruskal-Wallis tests indicated significance. Stand-and-Resettle responses for chicks in early May, late May and June and for adults during Prospecting were compared using Fisher's exact tests.

Results

History of disturbance

Chicks

A total of 196 approaches were made to chicks (Table 1). In early May, shortly after the Brooding/Guarding phase, no significant differences were found in any of the behavioural indices of close-station and study-colony chicks. In late May, study-colony chicks had larger NVR than close-station chicks (Mann-Whitney $U_{36}=67.0$, P =0.013). No other significant differences were found during this phase. In June, close-station chicks did not respond differently than study-colony chicks. In November, when chicks were close to Fledging, no differences were found in VR or NVR between chicks in different areas. A greater proportion of far-station chicks stood up during the disturbance than close-station or study-colony chicks ($\chi^2_2=9.16$, P =0.01). Fewer far-station chicks resettled than birds in other areas ($\chi^2_2,61=9.03$, P=0.011). Close-station chicks tended to have smaller OR (Kruskal-Wallis $H_{2,72}=5.49$, P=0.064) than far-station and study-colony chicks. A larger proportion of close-station chicks had mild responses (OR responses from 0 to 5), compared to chicks in other areas.

Adults

A total of 409 approaches were made to adults (Table 2). During Prospecting, far-station adults performed fewer Head-Turns than close-station adults (Mann-Whitney U_{72}=265.5, P=0.012). The VR of prospecting adults did not differ between the two areas. Fewer far-station birds than close-station birds stood up during the disturbance (Fisher's exact test v=1, n=70, P=0.006). The number of adults that resettled in different areas did not differ. Far-station adults had smaller OR than close-station birds (Mann-Whitney U_{70}=237.5, P=0.01). Fifty far-station adults (90.9%) had mild responses compared to ten close-station birds (66.7%).

During Early Incubation, no significant differences were found in any of the behavioural response indices between birds in different areas. During Late Incubation, the NVR of birds in different areas differed (Kruskal-Wallis $H_{3,139}$=14.3 P=0.003). Close-station adults turned their heads more frequently than far-station birds (Nonparametric multiple comparison, Q=3.05, k=4, P<0.05), while birds at Sealer's Beach tended to turn their heads more than far-station birds (Nonparametric multiple comparison, Q=2.57, k=4, P<0.10). There were no significant differences between birds in different areas in VR, the number of birds standing or the number of birds resettling. Birds in different areas differed in their OR (Kruskal-Wallis $H_{3,138}$=16.4, P<0.001). Far-station birds had smaller OR than close-station birds (Nonparametric multiple comparison, Q=2.84, k=4, P<0.05), birds at Sealer's Beach birds (Nonparametric multiple comparison, Q=3.04, k=4, P<0.05), and birds at Macaroni Bay (Nonparametric multiple comparison, Q=2.80, k=4, P<0.05).

During Brooding, no significant differences were found in any of the behavioural responses indices between birds in different areas. There were no significant differences in any of the behavioural indices in any phase between birds in the two study colonies.

Phase of breeding cycle

Chicks

The behavioural responses of close-station chicks did not differ significantly over the Nestling stage (n=45 approaches). Study-colony chicks (n=86 approaches) did not differ significantly in their VR, the number of birds standing or resettling. However, they differed over the Nestling stage in their NVR (Kruskal-Wallis $H_{3,80}$=9.99, P =0.019, with a smaller NVR in early May compared to late May (Nonparametric multiple comparison, Q =2.98, k=4, P<0.05) and June (Nonparametric multiple comparison, Q=2.68, k=4, P<0.05).

Adults

The responses of birds over the breeding cycle were first compared separately for each area. No significant differences were found for adults at Sealer's Beach (n=99 approaches) or Macaroni Bay (n=35 approaches) over the breeding season and the only difference for close-station birds (n=86 approaches) was in the number of birds standing, with all birds (n=15) standing during Prospecting compared to seven birds (23.3%), two birds (7.7%) and one bird (7.7%) standing during Early Incubation, Late Incubation and Brooding respectively (χ^2_3=45.1, P <0.001). As approaches were only made to close-station and far-station birds during Prospecting and no other differences were found within the three areas with high chronic levels of disturbance, the responses of close-station and study-colony birds were combined.

NVR and VR of disturbed birds did not differ significantly over the breeding season. More disturbed birds stood up during Prospecting (n=15, 100%) than during Early Incubation (n=19, 21.8%), Late Incubation (n=8, 11.0%) and Brooding (n=6, 14.6%) (χ^2_3=59.2, P<0.001). More disturbed birds tended to resettle during Late Incubation (n=7, 87.5%) and Brooding (n=6, 100%) than during Prospecting (n=7, 46.7%) and Early Incubation (n=12, 63.2%), with this result approaching significance (χ^2_3=7.37, P=0.061).

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For far-station birds (n=189 approaches), the number of Head-Turns differed with the phase of breeding (Kruskal-Wallis $H_{3,189}$=10.29 P=0.016); birds turned their heads more frequently during Early Incubation than during Prospecting (Nonparametric multiple comparison, Q=3.21, k=4, P<0.05). The VR of these birds also differed over the breeding cycle (Kruskal-Wallis $H_{3,189}$=10.18, P=0.017); VR tended to be larger during Brooding than during Prospecting (Nonparametric multiple comparison, Q=2.49, k=4, P<0.10). More far-station birds stood up during Prospecting than during Early Incubation, Late Incubation or Brooding (χ^2_3=72.7, P<0.001). The number of these far-station birds that resettled did not differ significantly over the breeding cycle.

Further analyses were done for far-station birds to determine whether birds reacted differently when there were eggs (Early Incubation and Late Incubation) or chicks (Brooding) in the nest. The intensity of NVR and the number of birds that resettled did not differ over these phases. The intensity of VR differed between the phases (Kruskal-Wallis $H_{2,133}$=6.44, P=0.040), because birds tended to have larger VR during Early Incubation than during Late Incubation, but this difference was not significant. More birds stood up during Early Incubation and Brooding than during Late Incubation; however, this difference was not significant.

Discussion

History of disturbance

Chicks

History of disturbance influenced the responses of chicks in this study. In summary, the behavioural responses of chicks close to the station indicated that they had habituated to frequent incidental disturbance. Close-station chicks were less vigilant than study-colony chicks in late May. They were also less likely to stand up and more likely to resettle than far-station

birds in November (close to Fledging). Close-station chicks also had smaller OR than birds with different disturbance histories in November.

Chicks close to the station were exposed to passing pedestrians almost daily. While pedestrians might have stood close to nests to take photographs, chicks were not handled. Chicks probably did not perceive the pedestrians as threatening and seemed to habituate to this type of disturbance. Chicks in the study colonies were visited monthly and although pedestrians infrequently passed along the boundaries of Macaroni Bay, only researchers approached these nests closely. During monthly nest monitoring, chicks were not handled (except in July, at five months of age, when they were ringed), but nests were closely approached to search for any nest pollutants. Study-colony chicks thus had less exposure to close pedestrian encounters and did not appear to habituate to these. Repetto's (far from station) was least frequently visited by pedestrians. Many of the nests were not near pedestrian routes and nests were seldom approached closely. Chicks therefore had little exposure to human disturbance. To these chicks, approaching pedestrians were unusual and unpredictable. Chicks probably perceived this as a potential threat (Frid and Dill 2002) and responded by standing up from the nests. This corresponds to the finding of Walker et al. (2005) that Magellanic Penguin chicks in undisturbed areas had a greater behavioural response to human approaches than birds in visited areas. Similarly, Burger and Gochfeld (1999) found that Laysan albatross (*Phoebastria immutabilis*) chicks with minimal human exposure reacted sooner and more severely than those that were more frequently disturbed.

Although Magellanic penguin chicks close to Fledging in the visited area had a lower behavioural response than chicks in unvisited areas, they had a similar corticosterone response (Walker et al. 2005), suggesting behavioural but not physiological habituation. Human disturbance can also affect breeding success. Yellow-eyed penguin (*Megadyptes antipodes*)

chicks in areas with high visitor numbers weighed significantly less than chicks in areas with few visitors (McClung et al. 2004, Ellenberg et al. 2007). An investigation of the hormone levels or fledging weights of wandering albatross chicks exposed to different levels of chronic disturbance might provide further insights into the habituation potential of chicks. Fledging weights of chicks can be obtained non-intrusively by using artificial nests incorporating automated systems to weigh chicks over time. This system has been used to determine the chick provisioning rate and growth of albatross chicks at South Georgia (Huin et al. 2000).

Adults

In contrast to the chicks, there were indications that adults at the station and in the study colonies had become sensitised to disturbance. In summary, during Prospecting, close-station birds were more vigilant than far-station birds, more close-station birds stood up and they had larger OR scores than far-station birds. During Late Incubation, far-station birds were the least vigilant and had smaller OR than birds in other areas.

These results support a similar finding by de Villiers et al. (2005) during the Brooding/Guarding phase. Lack of habituation to station-related disturbance is also suggested by the finding that the number of wandering albatross nests close to the station halved within the first two decades of human occupation of Marion Island (Watkins 1987). This reduction could be explained by an increased tendency among these birds towards heightened vigilance and flight upon disturbance. In the study colonies, birds were visited weekly by other researchers during the Incubation and Brooding phases. All adults were ringed and each week band numbers were read and nest contents were checked. In reaction, these birds might have perceived any approaching pedestrian as a threat to their offspring (Frid and Dill 2002). At Repetto's, nests were less frequently visited - adults on nests were only closely approached once during Incubation and very few adults or chicks were handled. Adults may thus not have felt as

threatened by an approaching pedestrian as did disturbed birds. This trend of birds reacting more to disturbance closer to the station than further away has been noticed on other sub-Antarctic islands (J. Croxall, H. Weimerskirch, personal communication). However, it is in contrast with the finding that Laysan albatross adults close to a station responded at shorter distances and less intensely than less-disturbed birds (Burger and Gochfeld 1999).

Phase of the breeding cycle

Chicks

Close-station chicks did not respond differently over the phases of the breeding cycle. These nests were not inspected monthly for pollutants and only a few nests were infrequently approached for photographs. Chicks, regardless of their age, seemed to have habituated to the presence of pedestrians in the area. However, the response of study-colony chicks differed according to phase of the breeding cycle.. Chicks were less vigilant in early May than later in the season. During approaches to brooding adults, small chicks did not respond to the approacher and lay on the feet of the adults. At the end of the Brooding/Guarding phase (Wheeler et al. 2009), chicks in nests where adults stood up, also stood up and Bill Snapped. The ability to recognise and respond to predators can develop with the age of offspring (Kullberg and Lind 2002), for example, older chinstrap penguin (*Pygoscelis antarctica*) chicks responded earlier during an approach than younger chicks (Martin et al. 2006).

Oil-spitting, or regurgitation, is a common antipredatory response among Procellariiformes' (albatrosses, fulmars, shearwaters and other petrels) chicks (Warham 1977).This behaviour has often been noted by researchers ringing wandering albatross chicks in the Marion Island study colonies (E.K. Turner, personal communication) but was seldom observed in response to approaches. Pedestrian approaches seemed to be less disturbing to chicks than handling.

Adults

In summary, the responses of adults differed between phases of the breeding cycle. All adults were more likely to stand up during Prospecting than later in the breeding cycle. Disturbed birds were more likely to resettle later in the breeding season (Late Incubation and Brooding) than during the earlier phases. When all phases were compared, far-station birds were more vigilant during Early Incubation than during Prospecting, and tended to be more aggressive during Brooding than during Prospecting. When the responses of far-station birds were compared over the phases with nest contents (Early Incubation, Late Incubation and Brooding), birds tended to be more responsive during Early Incubation than during Late Incubation and tended to stand up more during Early Incubation and Brooding than during Late Incubation.

Nest defense behaviour presents an interesting case of predator-prey interactions, as a predator can pose a threat to both the parent and to the nest contents (Osiejuk and Kuczyński 2007). Throughout a breeding season, parents should balance the costs and benefits of the present breeding attempt with potential future prospects (Trivers 1972, Andersson et al. 1980, Wallin 1987). Because the cost of replacing a clutch, and thus clutch-value, increases with time, parents can be expected to defend more and be less likely to abandon their nests later on in the season (Trivers 1972). Female greylag geese remained longer on their nests when approached during Late Incubation than during Early Incubation (Osiejuk and Kuczyński 2007). In this study, prospecting adults were more likely to rise up from their nests than later on in the breeding season. This is not surprising because prospectors have no nest contents to defend against predators or the elements. Exposing eggs or chicks to the cold sub-Antarctic environment might result in breeding failure through chilling (Catry et al. 2006). During Early Incubation, birds were also more likely to stand up from their nests than later in the season. Disturbed birds were less likely to resettle on their nests during Prospecting and Early Incubation. At the beginning of Incubation, birds were probably more nervous than during Prospecting and later on in the

breeding season, as they had eggs to defend but these were of relatively low value, compared to later in the season. Birds were least likely to stand up from their nests during Late Incubation. As expected, adults tended to be more aggressive during Brooding than during Prospecting, as they had small chicks with high reproductive value to defend.

Alternative hypotheses to the Parental Investment Theory (Trivers 1972) have been proposed for the temporal change of nest defense responses over the breeding cycle. According to the Renesting Potential Hypothesis, parents should defend their nests more later in the season - when they do not have relaying opportunities left - compared to earlier in the season (Barash 1975, Barash 1980, Weatherhead 1979). This theory does not apply to albatrosses as they lay only one egg in a season and do not relay if the nest fails (Tickell 2000). The Predation Risk Hypothesis or the Vulnerability Hypothesis (Harvey and Greenwood 1978, Greig-Smith 1980, Brunton 1990) states that parents need to defend their chicks more later in the season when they are more conspicuous or vulnerable to predators. This theory also does not apply to wandering albatrosses as parents leave chicks at the end of the Brooding/Guarding phase. Thereafter chicks stay at the nest for seven to eight months, during which they are visited by the parents only for feeding, and they have to defend themselves (Mabille et al. 2004).

Management implications

During and prior to this study, management regulations for the conservation of this vulnerable species (BirdLife International 2006) included the zoning of human activities on the island. Most human activities were limited to an area around the station (Hänel and Chown 1998, Wheeler et al. 2009) and this study indicated that adult wandering albatrosses in this area were sensitised by the high levels of incidental disturbance. Birds in the demographic study colonies were afforded the highest level of protection, with access to the areas being controlled through research permits (Prince Edward Islands Management Plan Working Group 1996). Although

incidental di sturbance was r educed, nests i n t hese colonies w ere c losely appr oached by researchers during monitoring and birds were handled. Study colony birds also showed signs of sensitisation to disturbance. However, only 5% of the annual breeding population on the Prince Edward I slands nests in t hese ar eas (Crawford and Cooper 2003). Long-term s tudies provide important information on population demographics and on breeding productivity and the factors that may influence this (Nel et al. 2003). For example, the effects of human disturbance on nest-site selection by northern royal albatrosses (*Diomedea epomophora sanfordi*) at the observatory at Taiaroa H ead, N ew Zeal and could onl y be detected t hrough l ong-term s tudies (Robertson 1998). It is im portant to continue l ong-term mo nitoring while m inimising di sturbance t hrough limited human access to s tudy c olonies. In t his s tudy, no s ignificant differences w ere found between birds at Sealer's Beach and Macaroni Bay. Although more pedestrians passed along the borders of Macaroni Bay, birds in this study colony were apparently not more affected by this higher l evel of incidental di sturbance than bi rds at S ealer's B each. The pat hway a long t he border is clearly defined in the vegetation and pedestrians stay it. Only a few of the study nests are close to the pathway. Use of this pathway improves the predictability of pedestrians in the vicinity of the colony, possibly reducing the effects of the incidental disturbance. If pedestrians strayed from the pathway, the level of incidental disturbance to birds in the study colony would increase as more birds would be closely approached. The boundary of 200 m around study colonies s hould be m aintained t o m inimise i ncidental di sturbance i n t hese ar eas. A z oning system w here bi rds ar e m ore frequently di sturbed i n s ome ar eas, but l ess frequently i n ot her areas, has al so been r ecommended for Lay san albatrosses at M idway A toll (Burger and Gochfeld 1999).

Incidental di sturbance t o bi rds c an al so be m inimised t hrough minimum approach di stances (Erwin 1989, Rodgers and Smith 1995). Birds are more s ensitive during c ertain stages t han others, so guidelines s hould be s et ac cording t o t he most v ulnerable phase o f t he en tire

breeding period (Müllner et al. 2004, Osiejuk and Kuczyński 2007). During this study, the recommended minimum approach distance to wandering albatrosses at Marion Island was 15 m (Hänel and Chown 1998), and a distance of 50 m to courting birds has been recommended (Chown et al. 2006). Although approaches were not made to courting birds, prospecting birds seemed more likely to flee as they were more likely to stand and less likely to resettle than during other phases of the breeding cycle. During this study, birds were more vigilant during Early Incubation and also tended to stand up more from nests than later in the season. It would thus be appropriate to extend the minimum approach distance during Prospecting and Early Incubation to avoid high levels of disturbance. Standardised approaches beginning at greater starting distances can be used to determine the appropriate minimum approach distance to birds during these phases.

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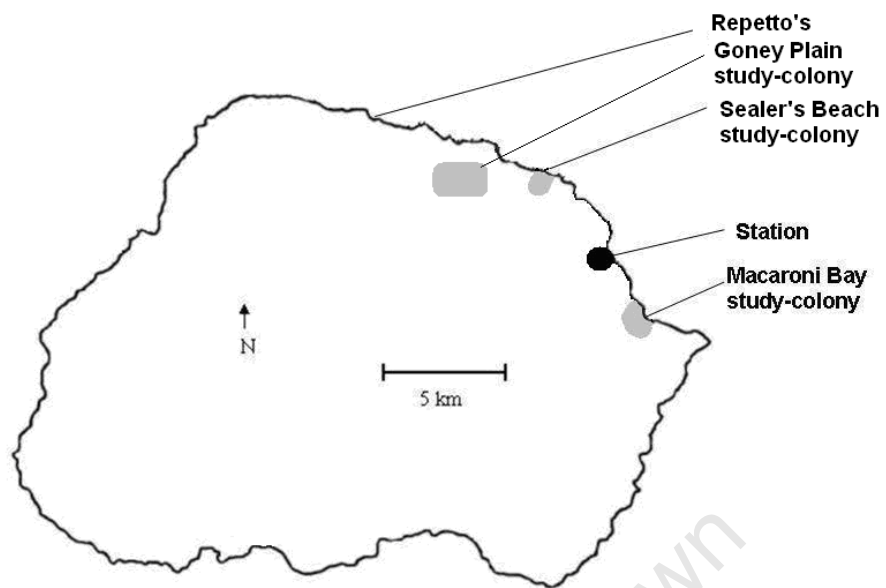
Figure 1 Outline of Marion Island indicating the positions of areas where wandering albatrosses were approached during this study. Also indicating the position of Goney Plain study-colony.

Table 1 Behavioural responses of wandering albatross chicks during standardised pedestrian approaches at Marion Island in Early May, Late May, June and November 2005. Birds were in areas with different disturbance histories: close to station (disturbance level: research intermediate, incidental high), in the two study colonies (disturbance level: high research disturbance, Macaroni Bay had intermediate levels of incidental disturbance and Sealer's Beach had low levels of incidental disturbance, but responses combined here for chicks) and far from the station (disturbance levels: research low, incidental low).

| Month | Area | Number of birds | Non-vocal Response (NVR) | | Vocal Response (VR) | | Stand | Resettle | Overall Response (OR) |
			median	range	no vocalisations (%)	VR of 3 or 4 (%)	(%)	(%)	mild response (OR of 0 to 5) (%)
Early May	Close to station	14	0.8	0–3.5	14	0	79	55	94
	Study colonies	13	1.0	0–3	15	0	100	80	100
Late May	Close to station	11	2.0	0.5–2.5	27	0	73	88	100
	Study colonies	28	3.0	0.5–5.5	29	0	78	57	83
June	Close to station	7	2.0	1–4	43	0	71	80	100
	Study colonies	25	3.0	0.5–5.5	20	0	83	37	76
November	Far from station	65	2.0	0–6	63	6	68	9	88
	Close to station	13	2.5	0–6.5	54	15	15	50	91
	Study colonies	20	2.5	0–7.5	55	20	17	36	75

Table 2 The behavioural responses of wandering albatross adults during standardised pedestrian approaches at Marion Island during Prospecting in 2005 and Early Incubation, Late Incubation and B rooding in 2006. Birds were in areas with different disturbance histories: far from t he s tation (disturbance l evel: r esearch l ow, i ncidental l ow), close t o s tation (disturbance l evel: r esearch i ntermediate, i ncidental l ow), Sealer's Beach (disturbance level: research high, incidental low) and Macaroni Bay (disturbance level: research high, incidental intermediate).

| Phase | Area | Number of birds | Non-vocal Response (NVR) | | Vocal Response (VR) | | Stand | Resettle | Overall Response (OR) mild response (OR of 0 to 5) |
			median	range	no vocalisations (%)	VR of 3 or 4 (%)	(%)	(%)	(%)
Prospecting	Far from station	56	1.0	0–5.5	75	11	67	57	91
	Close to station	16	3.0	0–6	63	31	100	47	67
Early Incubation	Far from station	56	2.5	0–8	52	21	13	57	89
	Close to station	30	2.3	0–6	53	20	23	71	93
	Sealer's Beach	47	3.0	0–10	49	36	23	55	83
	Macaroni Bay	10	1.5	0–4.5	50	50	10	100	90
Late Incubation	Far from station	65	1.5	0–5.5	71	12	3	100	100
	Close to station	27	3.0	0–5.5	52	19	8	100	92
	Sealer's Beach	30	2.8	0–8.5	53	30	10	67	87
	Macaroni Bay	17	2.5	0–7	59	41	18	100	82
Brooding	Far from station	12	1.5	0–3	50	42	18	100	91
	Close to station	13	2.5	0–3.5	54	38	8	100	77
	Sealer's Beach	22	2.0	0.5–8	68	18	20	100	95
	Macaroni Bay	8	2.3	0–4.5	63	38	13	100	100

The effect of frequency and nature of pedestrian approaches on the behaviour of wandering albatrosses at sub-Antarctic Marion Island

Abstract

The effects of disturbance frequency, pedestrian group size, history and approach distance were tested through standardised approaches to 148 brooding/guarding wandering albatrosses (*Diomedea exulans*) at Marion Island in 2006. Seldom-visited birds were approached at different frequencies over a three-day period and chick survival was monitored two weeks later. Two-person approaches were made to some seldom-visited birds and to birds that have recently been bled. Birds close to the station and in a long-term study colony were also approached. Non-vocal Response (NVR), Vocal Response (VR) and Overall Response (OR) of individuals were analysed. Frequency of approach did not influence short-term behavioural responses, but affected chick survival significantly - nests approached most often had the highest proportion of failures. Over the long-term, there was sensitisation to disturbance. Low OR ranks were found for 71.7% of seldom-disturbed birds, 41.7% of study colony birds and 28.6% of birds close to the station. Management regulations at the island are likely to be effective in protecting this species from human disturbance.

Introduction

Human disturbance influences the behaviour and physiology of nesting birds and this can result in long-term effects on the breeding success and survival of individuals (Knight and Cole 1995). The frequency and predictability (Pitman et al. 1988) of disturbance may influence the intensity of response of wildlife. Weddell seals (*Leptonychotes weddellii*) exposed repeatedly to predictable single-person approaches seemed to habituate to the disturbance within short periods of time, while seals that were exposed to irregular, unpredictable approaches did not (van Polanen Petel et al. 2008).

Animals can regard an approaching human as a potential predator (Frid and Dill 2002). Prey can respond more intensely to a larger predator group (Geist et al. 2005), because a larger number of predators decreases the chances of survival of prey (Abrams 1993). Holmes et al. (2007) found that breeding gentoo penguins (*Pygoscelis papua*) on sub-Antarctic Macquarie Island were significantly more vigilant when approached by five pedestrians than when approached by a single person. On the other hand, on the Antarctic peninsula, Nimon et al (1995) found that there was no difference in the behaviour or physiological responses of gentoo penguins to approaches by five persons or a single pedestrian. However, penguins were more likely to have elevated heart rates and increased levels of vigilance when approached by a group of minimum 15 people.

Closer pedestrian approaches are likely to provoke stronger responses than more distant approaches, because predation risk increases as a predator approaches (Beale and Monaghan 2004a, Holmes et al. 2005a, Ellenberg et al. 2006). A management tool to reduce the potential impact of human disturbance is to set minimum approach distances (Erwin 1989, Rodgers and Smith 1995). These distances are usually based on the distance at which an individual approached by a predator would initiate flight (Blumstein et al. 2003), but it has been suggested that these guidelines should rather be based on the distance at which an animal begins to exhibit alert behaviours (Rodgers and Smith 1997). Suggested minimum approach distances include 5–10 m for nesting seabirds (IAATO 2007), 25 m for traveling penguins (Burger and Gochfeld 2007), and 100 m for southern giant petrels (*Macronectes giganteus*) (Chown et al. 2006). However, these guidelines are often based on anecdotal information. Considering the species-specific nature of responses to disturbance (Blumstein et al. 2003), effective minimum distances should be informed by empirical evidence (Booth and Bio 2001).

Responses to disturbance are site- and species-specific (Göttmark 1992, Gill et al. 2001). Within a species, responses can vary according to the prior history of disturbance of individuals (Walker

et al. 2006). For example, at Midway Atoll, Burger and Gochfeld (1999) found that Laysan albatrosses (*Phoebastria immutabilis*) with minimal human exposure reacted sooner and more severely than those that were more frequently disturbed, suggesting habituation. In contrast, at Marion Island, de Villiers et al. (2005) found that wandering albatrosses with a history of frequent exposure to human activity (i.e. high levels of chronic disturbance), had more intense overall responses than those that were seldom disturbed.

The Prince Edward Islands archipelago, that consists of Marion Island (290 km²; 46°54'S, 37°45'E) and Prince Edward Island (44 km²; 46°38'S, 37°57'E), is the most important breeding ground of the wandering albatross (*Diomedea exulans*); 44% of the global population breeds there (Crawford and Cooper 2003). This species is Vulnerable (BirdLife International 2006) and fluctuations in the population size and proportion of birds attempting to breed there have been attributed to both natural effects (such as *El Niño* events) and anthropogenic effects (in the form of by-catch mortality (Gales et al. 1998, Ryan and Boix-Hinzen 1998)). Overall, however, breeding success is higher at the Prince Edward Islands than at other sub-Antarctic locations (Nel et al. 2003).

Under South African legislation, the Prince Edward Islands archipelago was declared a Special Nature Reserve in 1995 in terms of the Environmental Conservation Act (Act No. 73 of 1989) and no tourism is allowed under the National Environmental Management: Protected Areas Act (Act No. 57 of 2003). Albatrosses on Marion Island can be disturbed by biological research, by logistic activities and incidentally by island personnel. Types and frequency of human disturbance vary across Marion Island. There has been a permanent research station on the northeast coast of the island from 1948. Within the first two decades after the station was built, the number of breeding albatrosses around the station halved, possibly due to human disturbance (Watkins 1987). Construction of a new station, adjacent to the old one, started in 2003. The three wandering albatross demographic study colonies (Macaroni Bay, Sealer's

Beach and G oney P lain) hav e been af forded the hi ghest m anagement s tatus on t he i sland (Zone 4 status), with an exclusion zone of 200 m around colonies (Chown et al. 2006). Birds in these s tudy c olonies ar e v isited by r esearchers at w eekly i ntervals dur ing the i ncubation and brooding/guarding stages and chicks are visited monthly thereafter (Nel et al. 2003). According to the new Management Plan for the island (accepted but not yet implemented), outside of these areas breeding wandering albatrosses may be approached to 15 m, but courting birds may only be approached to 50 m (Chown et al. 2006).

This study investigated the short-term effects of frequency of human approach, pedestrian group size (one or t wo per sons), and long-term effects related to history of di sturbance, on the response behaviour of brooding/guarding wandering albatrosses at Marion Island. The suitability of the recommended minimum approach distance was also investigated.

Materials and methods

<u>Study site</u>

Marion Island is demarcated into management zones (Figure 1) allowing for additional protection of certain s pecies (Chown et al . 2006). Logistic activities ar e m ainly pe rformed at or near t he station, in Zone 1 (the Service Zone). Zone 2 (the Natural Zone) forms a buffer between Zone 1 and the remainder of the island. This zone also includes the areas around the field huts. Zone 2 areas near the station are visited by up to a hundred people during annual resupply voyages. The remainder of the i sland is Zone 3 (a Wilderness Zone), with the exception of Zone 4 ar eas (the Protected Zone), and permits must be obtained for research purposes within this zone. Swartkop (Figure 1), a l ocation on t he w estern side o f t he i sland, falls within t his z one and is intermittently visited by small num bers of island per sonnel when t raversing ar ound the i sland. Zone 4 ar eas hav e been a fforded the highest l evel of management p rotection, w ith L imited Access Permits being required for specified conservation and research purposes.

Pedestrian appr oaches were m ade t o wandering albatrosses at M arion I sland during t he resupply period in A pril 2006. This c oincided w ith t he end o f the br ooding/guarding pha se. Before field work was conducted, the approachers practiced to estimate distances in the field by placing a pol e at 2 m t o v isualise t he c orrect di stance. Adult al batrosses on nes ts w ere approached by one or t wo per sons to 2 m. Standardised c lothing was worn dur ing al l approaches. Approaches were made during daylight hours so that light conditions did not influence v isibility, and i n relatively clear conditions with no heavy pr ecipitation events. Each approach was performed directly to a bird on a nest at a constant rate of one pace per second. During an approach all Vocal- and Non-vocal reactions of the adult bird, and the distances from the nes t at w hich t hese oc curred, w ere r ecorded on di ctaphone. A t 2 m from the nes t, the approacher stood motionless and recorded the behaviour of the adult for one minute.

Non-vocal r eactions w ere c lassified as H ead-Shake, B ow, R itualised Preen, Fl ap and T ail-Shake, or Head-Turn (after Tickell 2000). A single head turn was defined as a turn from centre to the side and back again. Vocalisations were classified as Bill Snap, Clappering, Shrill Clappering (after Tickell 2000), or Snapping (after de Villiers et al. 2005). Whether a bird stood up and / or resettled on its nest during the approach or during the minute at the nest was also noted.

Factors tested

Frequency of approach

The effect of the frequency of short-term disturbance was tested by single-person approaches to seldom-visited bi rds at Swartkop. B irds t hat were not c lose t o the field hut at S wartkop were subdivided into three treatment groups to investigate the effect of frequency of approach: they were approached once on the first day and once on the third day of the study (two approaches, Treatment 101), four times on a s ingle day at i ntervals of abou t t wo hour s (four app roaches,

Treatment 400), or twice a day at intervals of between 3–5 hours between the two approaches, for three consecutive days (six approaches, Treatment 222). Approaches in Treatment 400 were done by M. Wheeler (1.71 m tall), while P.A. Majiedt (1.54 m tall) did the approaches to the other two treatment groups. Digital photographs were taken of these birds to detect change-overs by partners between approaches. Nests at Swartkop were monitored two weeks after the approaches when M.S. de Villiers was at Swartkop, to determine whether treatments had affected chick survival.

History of disturbance

The effect of long-term disturbance (three levels of chronic disturbance) was investigated by single-person approaches to birds at three locations: at Swartkop (seldom-visited); at Sealer's Beach study colony (see above); and close to the research station (birds exposed to frequent incidental disturbance and many were ringed, although they were not being monitored). At Swartkop, differentiation was made between birds close to a field hut (relatively high levels of incidental disturbance during the three days of approaches) and birds farther from the hut. The area is seldom visited and had last been visited 15 days prior to this study. Apart from the direct approaches performed and several hut restocking activities (including five helicopter flights to the hut), disturbance was kept to a minimum around the hut. The responses of birds close to the hut were compared to the responses of birds in Treatment 101 to first approaches, as this group was the furthest away from the hut (approximately 1.75 km to 2.25 km from the hut).

The effect of handling of birds was also investigated. The responses of recently handled birds that were approached by two persons (see below) were compared to the responses of the seldom-visited birds to two-person approaches.

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Pedestrian group size

Two-person approaches were made to seldom-visited birds on the western and northwestern sides of the island, and to birds that were handled and from which blood had been drawn one week previously as part of another research program (see Chapter 3). These approaches were similar to single-person approaches; both persons wore standardised clothing and approached at a constant rate of one pace per second, walking side-by-side. The responses of birds approached by two persons were compared to responses of birds at Swartkop to first approaches.

Analyses

Distances to nests where behaviours occurred were worked out through the steps counted on the dictaphone and using the average length of a pace of the approachers (0.65 m or 0.70 m respectively). For two-person approaches, the length of the pace was taken at 0.7 m. Although starting distance was on average 28 m away from the nest at Swartkop and seldom-visited areas, starting distances for approaches in the study colonies and close to the station were on average 20 m due to the topography or density of nests. Starting distances for birds close to the hut were on average 15 m. For analyses, responses were standardised to 15 m (proximity to hut), 20 m (areas, Swartkop treatments and research disturbance) and 28 m (pedestrian group size), and responses greater than these distances were not included in analyses.

Responses of birds in the three treatment groups were first compared to determine any initial differences in behaviour between the groups. At nests where change-overs occurred, photographs were used to determine the sex of each partner. Males tended to have whiter plumage, larger head to body ratios, as well as longer and thicker bills than females (Weimerskirch et al. 1989, Prince et al. 1997). The responses of these males and females were also compared for first approaches to determine any differences related to sex. The frequency of Head-Turns during the approach was regarded as indicating increased vigilance and was used

to determine a bird's Non-vocal Response (NVR). As repeated approaches were made to nests at Swartkop, a mixed effects model (using procedure lme in program R 2.5, R Development Core Team 2003) was used to determine differences in the NVR within and between treatments. Responses were analysed for individuals and not for nests, due to the change-overs of partners. We added individual identity as a random effect to control for consistent differences among individuals. Vocalisations were regarded as indicating increased aggression and were ranked according to intensity to obtain the Vocal Response (VR) Index: No vocalisations (0); Bill Snap (least intense = 1); Snapping (2); Clappering (3); and Shrill-Clappering (most intense = 4) (de Villiers et al. 2005). The Overall Response (OR) Index incorporated the VR, NVR rank and whether birds stood and resettled during the disturbance. The total number of Head-Turns over the 28 m, 20 m or 15 m approach distance was ranked according to quartiles (0–4) and added to the vocalisation score. Whether birds stood/resettled during the disturbance was considered to indicate the likeliness of the adult to flee from the nest. Birds that were already standing prior to the approach were excluded from this analysis. If a bird stood up during the approach or during the minute at the nest a score of two was added to the OR rank, while one rank point was subtracted if a bird resettled on the nest during these periods. The OR Index was scored between 0 (no response) and 10 (high intensity response) for individual birds for each approach.

The effect of approach distance on birds' behaviour was tested by comparing the NVR of birds close to the station and in the study colony for three distance intervals (5–10 m, 10–15 m and 15–20 m from bird). The NVRs observed during each of these distances intervals were compared for birds close to the station and at Sealer's Beach study colony.

Results

Frequency of approach

At Marion Island, undisturbed brooding/guarding adults at nests were generally inactive and displayed little vigilant behaviour. At Swartkop, a total of 88 individuals on 66 nests were

approached for the three treatments. Responses during first approaches were recorded for 30 individuals on 20 nests in Treatment 101, 14 individuals on 13 nests in Treatment 400 and 30 individuals on 19 nests in Treatment 222. During first approaches, the median number of Head-Turns was 2 (range 0–6.5) for Treatment 101, 3.25 times (range 1–6.5) in Treatment 400 and 1.5 times (range 0–4) for Treatment 222. This difference was significant (Kruskal-Wallis $H_{2,74}$=12.38, P=0.002). Birds in Treatment 400 turned their heads significantly more than birds in Treatment 101 (Nonparametric multiple comparison, Q=3.52, k=3, p<0.002) and Treatment 222 (Nonparametric multiple comparison, Q=2.49, k=3, p<0.05) (Zar 1999).

VR did not vary between treatments for the first approaches to birds (Table 1), with 21 birds (28.4% of all birds) vocalising during first approaches and 7 birds (9.5% of all birds) having VR ranks of 3 or 4. During first approaches, 10 birds (16.7% of all birds) stood up and of the birds that stood up, 5 (8.3%) resettled during the disturbance. There were no significant differences between treatments in the number of birds that stood up during first approaches or that resettled (Table 1). The OR of birds during first approaches did not vary significantly between treatments (Table 1), with most birds having low to mild OR ranks (56 birds, 93.3% in all treatments, had OR ranks from 0 to 5). No significant differences were found between males and females for any of the behavioural responses measured.

No other significant differences were found in N VR both within and between the three treatments. The model explained 43.1% of the variance. However, the treatment effects only explained 5.4% of the variance whereas the random effect (variation among individuals) explained 37.7% of the total variance. Sign tests revealed no significant differences in the VR or OR ranks for consecutive approaches within treatments.

Five of 63 nests in the treatments had failed within two weeks of the experimental approaches. Chick survival differed significantly ($X^2_{2,63}$=6.8, P=0.034) between the three treatment groups.

Treatment 101 (n=20 nests) had one nest failure, Treatment 400 (n=24 nests) had no failures and Treatment 222 (n=19 nests) had four nest failures. Chick survival of the treatment groups over these two weeks also differed significantly from chick survival in the three study colonies (4 failures from 170 nests, Percy Fitzpatrick Institute unpublished data) over the same time period ($X^2_{3,233}$=17.2, P<0.001). No nests close to the hut (n=10) failed during the two weeks.

History of disturbance

The median number of Head-Turns for birds close to the station was 2.3 (range 0–10, n=8) and for birds at Sealer's Beach was 2.5 (range 1–6.5, n=13). Birds in the three treatment groups at Swartkop a median number of 2.2 (range 0–6.5, n=74) times. In the three areas, 28 birds (29.5% of all birds) responded vocally, but only 10 birds (10.5%) had VR ranks of 3 or 4. Birds at sites with three levels of chronic disturbance did not differ significantly in the intensity of NVR or VR (Table 1). Eighteen birds (22.8% of all birds) stood up during the disturbance, with significantly more birds standing up in the study colony (six birds, 50.0%) and close to the station (two birds, 28.6%), than at Swartkop (10 birds, 16.7%) ($X^2_{2,79}$=6.7, P=0.040) (Table 1). Half of the birds (five birds) that stood up at Swartkop resettled during the disturbance, while no birds resettled close to the station and one bird (16.7%) resettled at Sealer's Beach, however this difference was not significant (Table 1). Birds at Swartkop had lower ORs than birds in the other two areas. OR ranks of 0 to 2 were found for 43 birds (71.7%) at Swartkop, two birds (28.6%) close to the station and five birds (41.7%) at Sealer's Beach (Figure 2). The OR of birds varied significantly between areas (Kruskal-Wallis $H_{2,79}$=9.32, P=0.009). The bird that reacted most severely during this study (VR=4, NVR=1.5, stood before approach and walked towards the approacher while Shrill Clappering) was a bird in close vicinity to the station and close to a path. Due to the increased number of people at the station during the annual resupply period, this bird was probably recently exposed to frequent disturbance.

Birds close to the hut had a median number of Head-Turns of 0.5 (range 0–3.5, n= 10), while birds farther away had a median of 1.5 (range 0–5, n = 30). Three birds (30%) close to the hut vocalised and one bird (10%) had a VR of 3 and no bird had a VR of 4. Of birds farther away, 10 birds (33.3%) vocalised and four birds (13.3%) had VR ranks of 3 to 4. While four birds (40.0%) close to the hut stood up and four birds (17.4%) farther away stood up, one bird (25.0%) that stood up in each area respectively resettled during the disturbance. All birds close to the hut had OR ranks from 0 to 5, while 22 birds (95.7%) farther away had OR ranks from 0 to 5. None of these differences were significant (Table 1).

Handled birds had a median number of Head-Turns of 3.5 (range 1–6.5, n = 11) and those not handled had a median of 2.5 (range 1.5–4, n = 19 at 20 m). Of the handled birds, five (45.5%) vocalised. Two handled birds (18.2%) had VR ranks of 3 or 4. Of the birds that were not handled, three birds (15.8%) vocalised, two birds (10.5%) had VR ranks of 3 and no bird had a VR of 4. While one handled bird (16.7%) stood up and resettled during the disturbance, four birds (25.0%) that were not handled stood up and only one (25.0%) of these resettled. One handled bird (16.7%) and no unhandled birds approached by two persons had OR higher than 5. None of these differences were significant (Table 1).

Pedestrian group size

Birds approached by a single person had a median number of Head-Turns of 2.25 (range 0–9, n = 66) and those approached by two persons had a median of 3 (range 1.5–4.5, n = 18 at 28 m). This difference was not significant (Table 1). During single-person approaches, 20 birds (30.3%) vocalised and seven birds (10.6%) had VR ranks of 3 or 4, while three birds (16.7%) vocalised during two-person approaches and two birds (11.1%) had ranks of 3 or 4. Differences were not significant (Table 1). While 11 birds (20.0%) approached by a single person stood up and five (45.5%) of these resettled during the disturbance, four birds (25.0%) stood up during two-person approaches and one of these (25.0%) resettled. During single-person approaches, 51 birds

(92.7%) of birds had OR ranks from 0 to 5, but no birds approached by two-persons had OR ranks higher than 5. These differences were not significant (Table 1).

The median numbers of head turns at nests close to the station in the three distance intervals (5–10 m, 10–15 m, 15–20 m away from nest) were 2 (range 0–4), 0 (range 0–6) and 1.5 (range 0–7) respectively. These differences were not significant (Friedman Test, T=0.36, based on 8 blocks of three treatments and adjusted for ties, P=0.834, based on a Chi-square approximation with two degrees of freedom). Birds in the study colony had median numbers of head turns of 4.0 (range 0–10), 4.0 (range 0–10) and 2.0 (range 0–6) respectively when the approacher was within each of the distance intervals. These differences were not significant (Friedman Test, T=4.79, based on 13 blocks of three treatments and adjusted for ties, P=0.091, based on a Chi-square approximation with two degrees of freedom).

Discussion

In summary, this study found that wandering albatrosses at Marion Island did not habituate to short-term disturbance - no significant differences in behavioural responses were found between seldom-visited birds approached at different frequencies. Instead birds approached most frequently (Treatment 222) had the highest percentage of nest failures. Birds seemed to become sensitised to disturbance – more birds close to the station and in the study colony stood up than birds at Swartkop. Birds close to the station had the highest OR ranks of all three areas, while birds in the study colonies also had higher OR than birds at Swartkop. Furthermore, birds close to a field hut did not show signs of habituation, as their behavioural responses were similar to birds farther away from the hut. Recent handling did not influence behavioural responses, as birds that were bled had similar responses than birds that were seldom-visited. Birds approached by two persons had similar responses to birds approached by a single person. The NVR of birds did not differ significantly over the three approach distance intervals tested.

Nests i n treatment groups at Swartkop w ere chosen to standardise appr oach conditions. However, one of t he appr oachers w as t aller t han t he other. During first appr oaches, b irds approached by t he t aller per son had s ignificantly hi gher N VR than bi rds appr oached by t he shorter person, but none of the other behavioural indices differed between the treatment groups and t he N VR di d not di ffer w ithin and bet ween g roups for consecutive appr oaches. As birds were more vigilant dur ing appr oaches by a tall person, disturbance might be r educed if researchers approach nests by bending their knees and stooping.

Animals that are exposed to repeated disturbances might respond less (Walker et al. 2006) and at closer distances, and might require less time to resume undisturbed behaviour patterns over time (Rees et al . 2005). Such habituated r esponses have been f ound for a v ariety of s pecies (e.g. v an H eezik an d S eddon 1990, Y orio and B oersma 1992, B urger and G ochfeld 199 9, Fowler 1999, Holmes et al. 2005b). But the capacity for habituation depends on the intensity and predictability of the disturbance (van Polanen Petel et al. 2008), and this response is not ubiquitous am ong al l s pecies (Conomy et al . 1 998, Blumstein 2006 , E llenberg et al . 2006). Some species apparently become sensitised to repeated exposure to disturbance and show stronger r esponses over time. Hoatzin (*Opisthocomus hoazin*) chicks (Müllner et al. 2004) and Magellanic penguin (*Spheniscus magellanicus*) newborn chicks (Walker et al. 2005a) in tourist areas showed stronger hormonal responses to disturbance than those in undisturbed areas, even though adul ts s eemed t o hav e habi tuated t o di sturbance. The be havioural r esponses of wandering albatrosses in this study did not differ over consecutive approaches, indicating lack of habituation ov er a s hort t ime i nterval. Furthermore, bi rds ex posed t o s hort-term i ncidental disturbance close to the field hut at Swartkop did not differ in behavioural response from those farther away.

In this study, wandering albatrosses exposed to high levels of disturbance seemed to become sensitised, supporting a s imilar finding by de V illiers et al . (2005). Although w andering

albatrosses with different levels of chronic disturbance did not differ in their VR or NVR to approaches by humans on foot, birds near the research station (exposed to frequent incidental disturbance) and to a lesser extent in a study colony (regularly monitored and occasionally handled) exhibited more intense OR than those at a seldom-visited location, as they were significantly more likely to stand up from nests. Adults standing up from nests might influence the corticosterone levels of chicks, as Walker et al. (2005a) speculated for Magellanic penguin chicks in areas visited by tourists. This action could also expose chicks to potential predators and to ambient environmental conditions (that might result in chilling of the chick (Catry et al. 2006)). The exposure of eggs during incubation could be especially harmful and it would be useful to investigate the effect of human approaches at this stage of breeding (see Chapter One). The greater responses of birds close to the station suggest that station-related activities negatively affect this species. This is also indicated by the reduced number of birds breeding in the vicinity of the station (Watkins 1987). Robertson (1998) found that northern royal albatrosses (*Diomedea epomophora sanfordi*) close to an observatory at Taiaroa Head, New Zealand, appeared to have habituated to human disturbance, but long-term studies indicated avoidance rather than habituation; over time, the albatrosses moved away from the observatory into areas less suitable for breeding. Study techniques involving handling and blood sampling can have negative effects on wildlife (Perkins et al. 2004). Some species exhibit larger stress responses when captured and restrained (Walker et al. 2006) or during band checks (Weimerskirch et al. 2002) than when merely visited. However, the heart rates of wandering albatrosses recovered to basal levels within 9–12 minutes after band checks and birds did not respond differently during a second band check 5–18 hours later (Weimerskirch et al. 2002). At Marion Island, birds were approached one week after they were handled and blood was drawn. Their behavioural responses were similar to birds that had not recently been handled, indicating some degree of recovery to short-term research disturbance. However, the high OR ranks of study-colony birds compared to birds in a remote area suggest that over the long term, this species can become sensitised to research disturbance.

The use of behavioural responses alone to determine the susceptibility of animals to disturbance has recently been questioned (Gill et al. 2001, Beale and Monaghan 2004b) and it has been proposed that that the fitness consequences of responses should also be quantified (Gill 2007). This study found that birds that were more disturbed might have suffered the highest fitness consequences, although they had similar responses to birds that were approached fewer times. Blackmer et al. (2004) and Arroyo and Razin (2006) showed that more-frequently disturbed birds experienced lower breeding success than others. Although the wandering albatrosses at Marion Island did not show extreme behavioural responses to human approach, they might have experienced physiological responses such as increased heart rates and increased corticosterone levels (see Chapter 3). Weimerskirch et al. (2002) indicated that the heart rates of wandering albatrosses increased in the presence of humans without overt behavioural responses. Increases in corticosterone levels may trigger self-maintenance behaviour such as feeding (Astheimer et al. 1992), resulting in reduced parental care to chicks. If a higher frequency of approaches results in higher levels of corticosterone, some individuals that were approached on consecutive days in this study might have left to feed, exposing their offspring to the elements or to potential predators. However, the available data are insufficient to draw definite conclusions on the cause of the chick mortality. Further studies on the nest attendance behaviour of adults would provide more insight into the causes of chick mortality.

The effect of the disturbance is likely to be greater when more pedestrians approach an animal (Beale and Monaghan 2004a, Burger and Gochfeld 2007, Holmes et al. 2007). This was found for crimson rosellas (*Platycerus elegans*), but pied currawongs (*Strepera graculina*) did not respond more when approached by two persons than by a single intruder (Geist et al. 2005). At Marion Island, birds approached by two persons tended to be more vigilant than those approached by a single pedestrian, but this difference in response was not significant. Larger human groups might elicit greater responses. This could be tested through the use of dummies

similar to those used by Schuster (2008) to determine the behaviour and heart rate of Adélie penguins (*Pygoscelis adeliae*) during pedestrian approaches.

Management considerations

In the Antarctic and sub-Antarctic minimum approach distances are usually set as voluntary guidelines. Visitors might be expected to identify key behavioural responses of wildlife and adjust their own behaviour accordingly, in order to reduce disturbance (Holmes 2007). However in Antarctica, visitor compliance with guidelines has been shown to be imperfect and inadvertent and deliberate infringements of guidelines occur, suggesting that guidelines may be inadequate to prevent negative impacts on wildlife (Davis 1995).

The minimum approach distance for wandering albatrosses on nests has been set at 10 m for visitors to Prion Island, South Georgia (Government of South Georgia and the South Sandwich Islands 2006). This species has been classified as Endangered in Australia and the minimum approach distance on Macquarie Island is 25 m (Tasmanian Parks and Wildlife Service 2003). At Marion Island, the behavioural responses of wandering albatrosses to human approaches are generally of low intensity, and the species is generally regarded as tolerant of this kind of disturbance. During this study, the minimum approach distance to breeding wandering albatrosses at Marion Island was 15 m (Prince Edward Islands Management Plan Working Group 1996). This guideline appears to be conservative as no significant differences in behaviour at closer distances were found. However, this study indicates that wandering albatrosses did not habituate to short- or long-term disturbance, and that repeated approaches influenced their chick survival. These birds are thus sensitive to disturbance and might be experiencing physiological changes that are not reflected in their behaviour. Because self-regulation of visits to these behaviourally conservative birds is unlikely to be effective, we recommend that the precautionary guideline be maintained. This approach might be especially

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important during sensitive stages of the breeding cycle when birds are likely to react more to disturbance (Côté 2000, Walker et al. 2005b) (see Chapter One).

Minimum approach distances on the island are currently voluntary guidelines and personnel tend to approach closer to animals. The effectiveness of the minimum approach guidelines can be improved if personnel are made aware of the potential negative effects of their approaches to these birds. Currently this is being done through providing copies of the introductory guide to Marion and Prince Edward Island (Hänel and Chown 1998) and the management plan (Prince Edward Island Management Plan Working Group 1996) to the overwintering team, resupply personnel and construction personnel and through talks by the conservation officer. However, it is recommended that the main results of this study also be made available to personnel by means of a brochure and displayed posters.

An additional management strategy to reduce the effects of disturbance is zoning, allowing for the regulation of the types and frequencies of human activities by area. By the start of the twenty-first century, tourism was permitted at most of the breeding locations of the wandering albatross. For example, South Georgia received 5 436 tourists during 49 visits in the 2005/06 season (Government of South Georgia and the South Sandwich Islands 2006), and 750 visitors were allowed per season at Macquarie Island (Tasmanian Parks and Wildlife Service 2003). Both locations have set areas aside for special protection of this species. For example, Albatross Island, South Georgia, previously open to tourists, has been closed to such visits since 2004 (Government of South Georgia and the South Sandwich Islands 2006). At Marion Island, there is no tourism and zoning ensures that disturbance away from the research station and study colonies is minimal. The combination of minimum approach guidelines and zoning of human activities is likely to be effective for conservation of wandering albatrosses at Marion Island.

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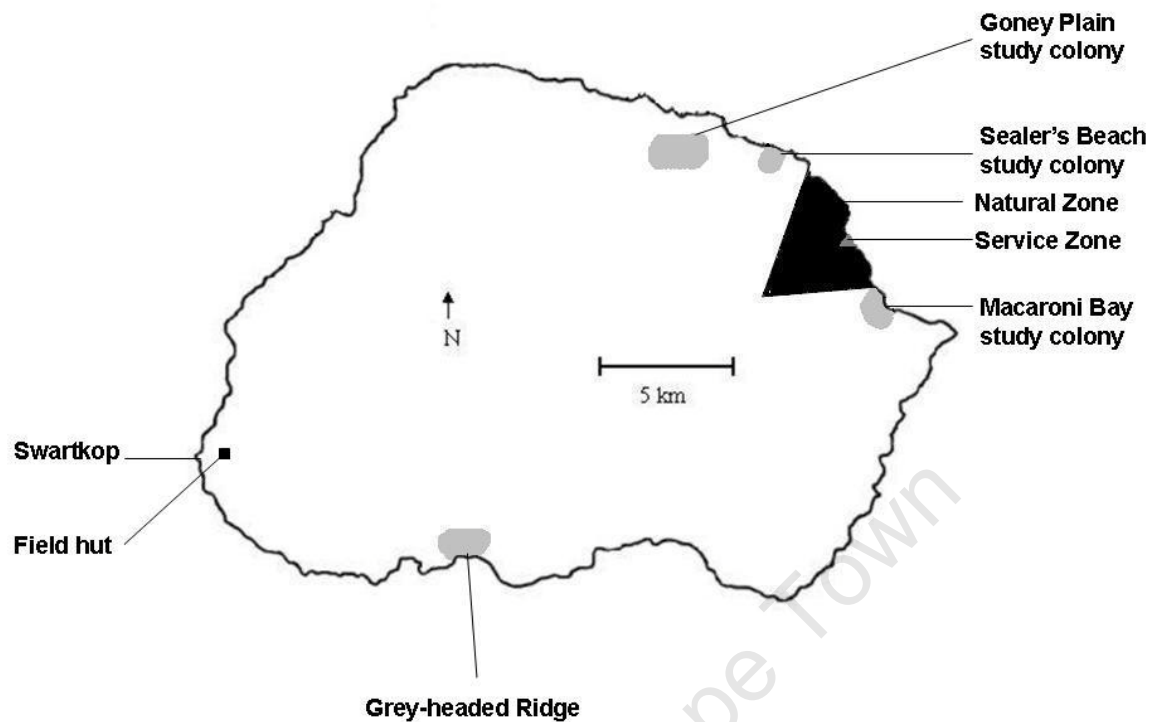
Figure 1 M ap of management z ones o f M arion I sland as s tipulated i n t he P rince E dward Island M anagement P lan (Prince E dward I sland M anagement P lan Working G roup 1996) . Also indicating the position of Swartkop, where repeated approaches w ere done t o wandering albatrosses, and the position of the field hut at Swartkop.

a
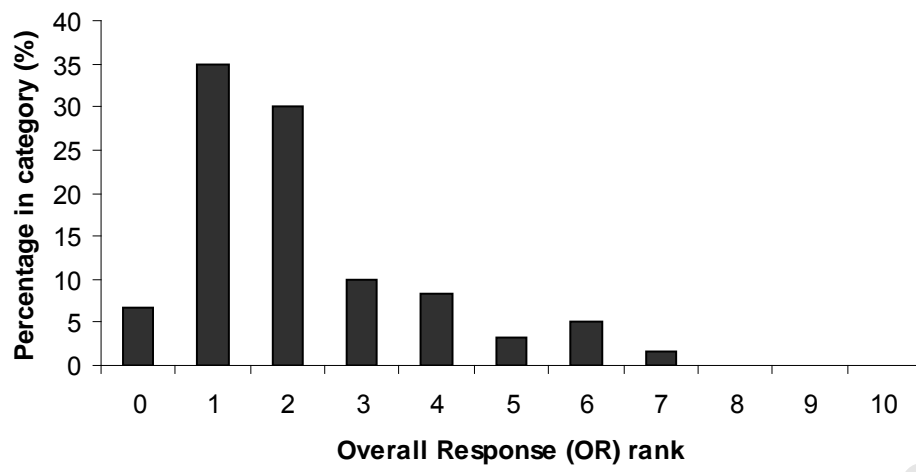
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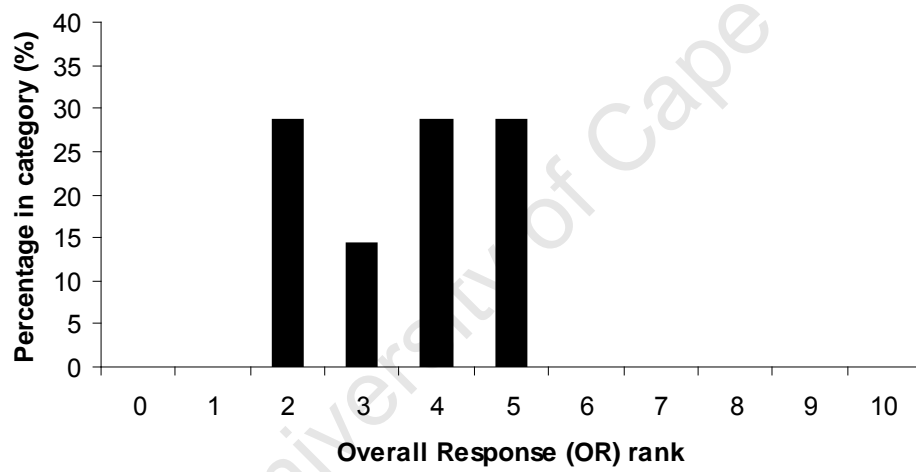
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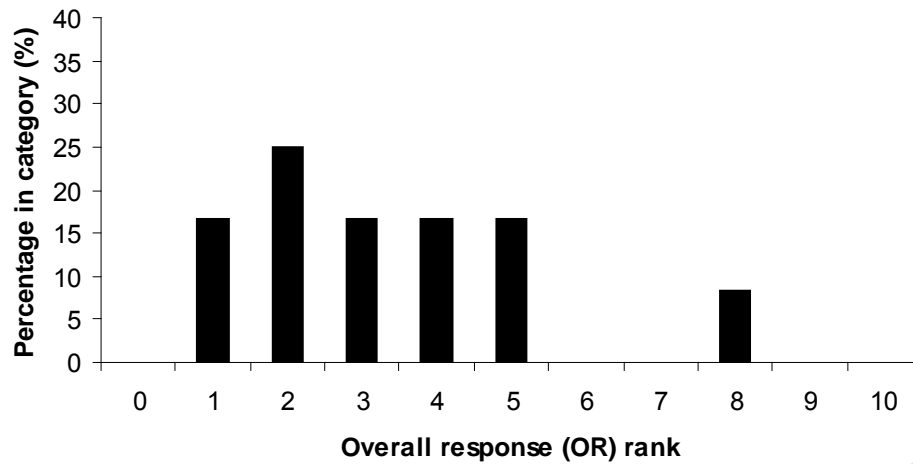
Figure 2 Proportion of wandering albatrosses at Marion Island per Overall Response (OR) Index rank (0–10) during standardised single-person approaches in 2006. Birds were in three areas with different levels of chronic disturbance a) Swartkop (disturbance level: research low, incidental low); b) close to the station (disturbance level: research intermediate, incidental high); and c) Sealer's Beach (disturbance level: research high, incidental low). Rank 0: No response. Rank 10: most intense response possible.

Table 1: Behavioural responses of wandering albatrosses exposed to levels of disturbance. Swartkop first approaches (first approaches to birds in treatment groups); Group size (single- versus two-person approaches); Areas (seldom-disturbed, frequent incidental disturbance, and regularly monitored and occasionally handled); Proximity to hut (birds close to hut versus birds farther away); Research disturbance (unhandled vs recently bled birds). Behavioural responses categorised as Non-vocal Response (NVR), Vocal Response (VR), Overall Response (OR), Stand (Rising from nest during disturbance) and Resettle (settling during disturbance) (see text).

Response	Swartkop treatments	Group size	Areas	Proximity to hut	Research disturbance
NVR	$H_{2,74}=12.38$, P=0.002	$U_{1,84}=434.5$, P=0.081	$H_{2,95}=3.38$, P=0.185	$U_{1,40}=108.5$, P=0.196	$U_{1,30}=70.0$, P=0.136
VR	$H_{2,74}=2.50$, P=0.287	$U_{1,84}=516.0$, P=0.293	$H_{2,95}=2.92$, P=0.233	$U_{1,40}=138.5$, P=0.678	$U_{1,30}=74.5$, P=0.138
OR	$H_{2,60}=3.54$, P=0.170	$U_{1,70}=361.0$, P=0.455	$H_{2,79}=9.32$, P=0.009	$U_{1,33}=108.5$, P=0.801	$U_{1,22}=39.5$, P=0.521
Stand	$\chi^2_{2,60}=1.00$, P=0.606	$v=1$, n=70, P=0.452	$\chi^2_{2,79}=6.46$, P=0.040	$v=1$, n=33, P=0.103	$v=1$, n=22, P=0.581
Resettle	$\chi^2_{2,13}=1.67$, P=0.435	$v=1$, n=15, P=0.462	$\chi^2_{2,18}=3.00$, P=0.223	$v=1$, n=8, P=1	$v=1$, n=5, P=0.400

H denotes the Kruskal-Wallis test, U denotes the Mann-Whitney test and χ^2 denotes the Chi-square test. P values for Kruskal-Wallis tests and Mann-Whitney tests have been adjusted for ties. The stand and resettle responses for Group size, Proximity to hut, and Research disturbance were done through Fisher's exact tests.

The influence of human disturbance on the behavioural responses and physiology of wandering albatrosses (*Diomedea exulans*) at sub-Antarctic Marion Island

Abstract

Wandering albatrosses (*Diomedea exulans*) at sub-Antarctic Marion Island are exposed to different levels of research and incidental disturbance. The relationships between level of disturbance, behavioural responses and hormone levels (corticosterone and prolactin) were investigated through standardised pedestrian approaches and blood sampling of birds in three areas. Birds near Repetto's, a site far from the station (disturbance levels: research low; incidental low) had less intense behavioural responses than birds close to the research station (disturbance levels: research medium; incidental high) and in a long-term study colony (disturbance levels: research high; incidental medium). Corticosterone levels were not correlated to gender of bird, area or behavioural indices. Prolactin levels of females were higher than for males. Far-station females had higher prolactin levels than disturbed females. Because birds that had the least intense behavioural responses to disturbance had the highest level of prolactin (indicating that they were less physiologically stressed), it is recommended that behaviours be used to assess the stress levels of individuals of this species.

Introduction

Animals have evolved behavioural and physiological strategies that interact to allow them to cope with changes (Wingfield 2001, Huey et al. 2003). Behavioural responses to human disturbance can range from short-term changes, such as increased vigilance (Walker et al. 2006, Holmes et al. 2005a, Van Polanen Petel 2008), to changes in essential behaviours such as feeding activity (Rees et al. 2005) and parental care (McClung et al. 2004), to highly stressed states such as flight (Wilson et al. 1991, Giese and Riddle 1999, Harris 2005). Such

changes in behaviour can be due to an immediate short-term (acute) stressor and can be influenced by the distance between the stressor and the animal, the size of the stressor and the speed at which it approaches, and the distance to shelter (Frid and Dill 2002). But behavioural responses to stressors can also be altered if an animal is chronically stressed. They may habituate (e.g. Holmes et al. 2005b, van Polanen Petel et al. 2008), or may become sensitised to the stimulus and respond more over time (e.g. Fowler 1999, van Polanen Petel et al. 2008). Behavioural responses can also be influenced by the condition of an animal and how it perceives its environment (Beale and Monaghan 2004). The intensity of behavioural responses has often been used to inform management recommendations on ways in which to reduce disturbance, such as the setting of minimum approach distances (e.g. Cooper et al. 1994, Holmes et al. 2005a, de Villiers et al. 2006, Burger and Gochfeld 2007) and the zoning of areas (Burger and Gochfeld 1999).

However, even when human disturbance has no or little overt influence on behaviour, physiological responses can occur. The importance of physiological measurements to determine the effects of human disturbance has increasingly been realised (Carey 2005, Walker et al. 2005a, de Villiers 2008). Physiological studies include measurements of heart rate (e.g. Wilson et al. 1991, Weimerskirch 2002, Holmes et al. 2005a, de Villiers et al. 2006, Ellenberg et al. 2006), blood chemistry parameters (Engelhard et al. 2002), stress proteins levels (de Villiers et al. submitted) and body condition (McClung et al. 2004, Ellenberg et al. 2007, Engelhard et al. 2001). Most physiological studies on the influence of human disturbance (e.g. Müllner et al. 2004, Walker et al. 2005b, 2006, Ellenberg et al. 2007) have focused on the use of hormones, specifically corticosterone.

Glucocorticosteroids (corticosterone in birds) are important for their role in gluconeogenesis (Sapolsky et al. 2000, Remage-Healey and Romero 2001). Stress results in an elevated response of the hypothalamic-pituitary-adrenal (HPA) axis that leads to increased levels of glucocorticosteroids and related hormones. This response allows animals to cope during

short-lived perturbations (Sapolsky et al. 2000), also called "emergency life-history stages" (Wingfield 2001). The levels of these hormones can also be elevated during energetically-demanding breeding stages (Romero 2002), because corticosterone levels increase with decreasing body reserves (Cherel et al. 1988). In the long term, elevated levels of corticosterone can result in compromised immune functioning, reduced growth rates, disease, reduced fertility, lower life expectancy (e.g. Siegel 1980, Wingfield 1985, Wingfield et al. 1995, Sapolsky et al. 2000) and even nest desertion (Angelier et al. 2006).

Prolactin is an important hormone that influences reproductive performance, affecting the behaviour, physiology and morphology of animals during parental stages (Sharp et al. 1988, Buntin 1996). Levels of this hormone increase during the pre-laying period or during incubation (Hector and Goldsmith 1985, Cherel et al. 1994, Delehanty et al. 1997, Vleck et al. 2000) and this ensures attendance behaviour patterns.

In contrast to poultry and ducks that require tactile contact between the brood patch and eggs or chicks for the maintenance of high prolactin levels (El Halawani et al. 1980, Richard-Yris et al. 1998), penguins and albatrosses maintain high levels of prolactin during feeding bouts away from breeding grounds, helping to ensure that parents return to their offspring (Cherel et al. 1994, Vleck et al. 2000, Hector and Goldsmith 1985). In albatrosses, prolactin levels finally decrease at the end of the brood/guard period (Hector and Goldsmith 1985). During stressful conditions, prolactin levels increase in mammals (de Vlaming 1979), but prolactin levels generally decrease in birds in response to stress (Manney et al. 1999, Chastel et al. 2005, Angelier et al. 2007a, Verreault et al. 2008, Angelier and Chastel 2009). Stressful environmental conditions resulted in decreased prolactin levels in incubating male Wilson's phalaropes (*Phalaropus tricolor*) (Delehanty et al. 1997) and male glaucous gulls (*Larus hyperboreus*) chronically exposed to organohalogen contaminants also had lower prolactin levels (Verreault et al. 2008). Under certain circumstances, such decreases could be adaptive in the long term, encouraging birds to desert the current breeding attempt and

thereby ensuring future survival and reproductive success (Delehanty et al. 1997). However, under stressful situations, birds can attenuate or suppress the prolactin response to stress to maximise the current reproductive effort (Chastel et al. 2005).

Marion Island, in the sub-Antarctic, has been zoned into management areas (Prince Edward Islands Management Plan Working Group 1996), partly to protect disturbance-sensitive seabird species. There have been indications that certain behavioural and physiological parameters differ for wandering albatrosses in the different zones (de Villiers et al. 2005, submitted, Wheeler et al. 2009, submitted). De Villiers et al. (submitted) found that levels of chronic disturbance influenced the physiology of birds. The aim of the present study was to investigate whether these zone-related differences were reflected by differences in levels of corticosterone and prolactin. Because the relevance of intensity of behavioural response to susceptibility to disturbance has been questioned (Gill et al. 2001), the relationship between behavioural responses and hormone levels was also investigated.

Methods

This study was conducted at Marion Island (290 km²; 46°54'S, 37°45'E) in April 2006, during the annual resupply period. Throughout the year, 10 to 15 personnel are stationed at the island's research station, but the number of people increases to approximately 100 people during April and May.

Standardised approaches were made to brooding birds at three sites: Repetto's, close to the research station and Macaroni Bay study colony (see Figure 1 of Chapter 1 for the locations of the study sites). Birds at these sites were exposed to different levels of chronic disturbance. Birds near Repetto's were far from the station (hereafter referred to as far-station birds) and experienced low levels of both incidental and research disturbance (annual nest checks during incubation and before fledging). Close to the station, birds were exposed to high levels of incidental disturbance (especially during the resupply period) and medium

levels of research disturbance (many were ringed, although these close-station birds were not regularly monitored). Birds in the Macaroni Bay demographic study colony (hereafter referred to as study-colony birds) were exposed to intermediate levels of incidental disturbance and high levels of research disturbance.

Standardised approaches to brooding wandering albatrosses were made (Chapters 1, Wheeler et al. 2009), except for this study they were made by three people and the behaviour of the bird at the nest was not recorded for a minute at 3.5 m from the nest. Instead, birds were captured on the nest. Blood (c. 0.8 ml) was drawn from the intertarsal vein of each bird within three minutes of capture. For all samples, plasma was separated from the cell fraction of the blood eight hours after collection. Samples were stored at –20°C until further analyses (de Villiers et al. submitted). Bill measurements were taken to determine gender, and feather lice were collected (de Villiers et al. submitted). Handling time was recorded. Behaviour was recorded as birds were released a few meters from the nest, towards the nest. Responses were recorded after Tickell (2000), de Villiers et al. (2005) and Wheeler et al. (2009).

Hormone analyses were conducted at the Centre d'Etudes Biologiques de Chizé, Villiers-en-Bois, France. A heterologous radioimmunoassay (Cherel et al. (1994) and used by Angelier et al. (2006) for wandering albatrosses) was first done to determine the plasma level of prolactin. A radioimmunoassay (Lormeé et al. 2003) was then performed to determine the plasma level of corticosterone. One assay was run for each hormone and the intra-assay variation was 6.9% for corticosterone and 8.4% for prolactin (five duplicates for both hormones).

Analysis of behaviour during approaches followed Wheeler et al. (2009). Data collected within 28 m of nests were used for the approach analyses. The most intense vocalisation during the approach was used as the Approach Vocal Response (AVR) and the frequency of

Head-Turns during the approach was used to determine a bird's Approach Non-vocal Response (ANVR). The most intense vocalisations during capture and release were used as a measure of the Capture Vocal Response (CVR) and Release Vocal Response (RVR), respectively. The position of the bird after release was considered to indicate the likeliness of the bird returning to its chick and ranked as 0: bird on nest, 1: next to nest and 2: a few metres from nest, following de Villiers et al. (submitted). Responses of birds in the three areas were compared using Kruskal-Wallis tests and the P-values were adjusted for ties.

The relationships between plasma hormone levels, gender of the bird, level of chronic disturbance and behavioural indices during approach and capture were investigated using multiple regression analyses. Further regression analyses were done to determine whether starting distance of approach and time of day influenced hormone levels and whether handling time influenced the RVR and the position relative to the nest after release.

Results

Twenty-four far-station, 19 close-station and nine study-colony birds were approached (Table 1). During approaches, the ANVR of birds in different areas differed (Kruskal-Wallis $H_{3,47}$ =11.9, P=0.003), with study-colony birds performing more Head-Turns than close-station birds (Nonparametric multiple comparison, Q=2.80, k=3, P<0.05) and far-station birds (Nonparametric multiple comparison, Q=3.38, k=3, P<0.05). There were also area differences in AVR (Kruskal-Wallis $H_{3,47}$ =7.8, P=0.020), with study-colony birds having more intense vocalisations than close-station (Nonparametric multiple comparison, Q=2.66, k=3, P<0.05) and far-station birds (Nonparametric multiple comparison, Q=2.44, k=3, P<0.05).

During capture, there were area differences in CVR (Kruskal-Wallis $H_{3,51}$ =8.3, P=0.016), with study-colony birds having more intense vocalisations than far-station birds (Nonparametric multiple comparison, Q=2.86, k=3, P<0.05). Birds were handled for an average time of 12.33 minutes (range 7 – c. 20 minutes). The RVR of birds in different areas did not differ significantly and handling time did not influence RVR or position of the bird relative to the

nest after release. However, position relative to the nest differed between areas (Kruskal-Wallis $H_{3,51}$ =11.2, P =0.004), with study-colony birds staying closer to the nest than far-station birds (Nonparametric multiple comparison, Q =3.16, k=3, P <0.05) and close-station birds (Nonparametric multiple comparison, Q=2.16, k=3, P<0.10). No significant behavioural differences were found between genders.

Corticosterone levels were determined for 51 birds (25 females and 26 males). There was much individual variation in baseline corticosterone level (mean 9.5 ng/ml, range 0.65–27.9 ng/ml). Corticosterone level did not differ between genders (mean $\pm$ sd: females 10.4 $\pm$ 5.8 ng/ml, males 8.7 $\pm$ 4.7 ng/ml) or areas (mean $\pm$ sd: far-station birds 8.9 $\pm$ 6.1, near-station birds 10.0 $\pm$ 5.2 ng/ml, study-colony birds 9.9 $\pm$ 3.2 ng/ml) (Figure 1). Regression analyses indicated no relationship between corticosterone level and gender, area or any of the behavioural indices. Time of day did not influence corticosterone level. There was a tendency for corticosterone levels to be higher when approaches were started from farther away (r=0.23, P=0.099).

Prolactin levels were determined for 48 birds (22 females and 26 males). There was much individual variation in this parameter (mean 35.9, range 7.2–76.5 ng/ml). Time of day did not influence baseline prolactin levels. There was a tendency for prolactin levels to be lower when approaches were started from farther away (r=-0.26, P=0.074). The level of prolactin in females was 41.4 ng/ml (sd= 41.4 $\pm$ 17.7 ng/ml) and in males 31.2 ng/ml (sd = 8.0 ng/ml). The difference in prolactin levels between genders was significant (Mann-Whitney U_{48}=187.0, P=0.041). Far-station females had higher levels of prolactin (mean $\pm$ sd: 54.7 $\pm$ 20.4 ng/ml, n=7) than study-colony females (39.4 $\pm$ 15.5 ng/ml, n=4) and close-station females (33.6 $\pm$ 11.9 ng/ml, n=11) (Figure 2), but not significantly so (Kruskal-Wallis $H_{3,22}$ =4.84, P=0.089). Close-station males had higher levels of prolactin (mean $\pm$ sd: 36.7 $\pm$ 23.7 ng/ml, n=6) than far-station males (mean $\pm$ sd: 32.9 $\pm$ 17.3 ng/ml, n=15) and study-colony males (mean $\pm$ sd: 19.5 $\pm$ 6.5 ng/ml, n= 5) (Figure 2), but not significantly so (Kruskal-Wallis $H_{3,26}$ =2.23,

P=0.251).   Because the prolactin levels of genders differed significantly, regression analyses were done separately for males and females. Close-station females and study-colony females had similar prolactin levels and birds in both areas were disturbed, therefore these birds were combined to determine the effect of chronic disturbance on females. The best model for females explained 24.3% of the variance in prolactin level and included level of chronic disturbance. Far-station birds had 1.6 times higher prolactin levels than disturbed birds (t_{20}=19.57, P=0.012). No relationship was found for males between level of chronic disturbance and prolactin level. No relationship between behaviour upon approach or capture and physiology was found for either gender.

Discussion

Wandering albatrosses in a study colony on Marion Island had more intense vocal and non-vocal responses during approaches than non-study birds close to or far from the research station. This is in partial agreement with previous studies which indicated that study-colony and close-station birds had more intense behavioural responses during pedestrian approaches than far-station birds (de Villiers et al. 2005, Wheeler et al. 2009, submitted). The elevated behavioral response to approaches of study colony birds relative to other birds indicates that wandering albatrosses exposed to high levels of disturbance can become sensitised to disturbance. During capture, study-colony birds had more intense vocal responses than far-station birds. More study-colony birds were on or close to their nests after they were released than far-study birds. The vocal responses upon capture and the position relative to the nest of close-station birds were more similar to study-colony birds than to far-station birds. Although close-station birds were not generally handled, this indicates that close-station birds also perceived handling as a threat and both study and close-station birds were more likely to return to their nests after release to protect their chicks against the threat. Far-station birds did not seem to perceive humans as a threat and responded therefore less upon capture and release. The finding that males and females had similar behavioural

responses to disturbance corresponds with the findings of de Villiers et al. (2005) and Wheeler et al. (2009).

Levels of corticosterone were not influenced by gender of the bird. This was as expected because in species where parental investment is equal for the sexes, males and females have similar levels of corticosterone. This has been shown to be the case for wandering albatrosses (Angelier et al. 2006). At Marion Island, the level of chronic disturbance did not influence corticosterone levels. This was also found for other species where individuals were exposed to different levels of chronic disturbance (e.g. Müllner et al. 2004, Walker et al. 2005b, 2006, Ellenberg et al. 2007).

During the capture stress protocol of Wingfield et al. (1983), birds are restrained for set intervals of time at which blood is drawn to determine changes in blood hormones (e.g. Müllner et al. 2004, Chastel et al. 2005, Walker et al. 2005b, Angelier et al. 2007a). Birds are kept in individual cloth bags between intervals. In this study, blood was drawn once during the first three minutes after capture. Thereafter birds were measured and searched for feather lice. Birds were not kept in bags. The time that a bird was handled did not influence behavioural responses (the RVR or the position of the bird relative to its nest upon release), although it could have influenced hormonal levels. A further blood sample during handling would provide information on the physiological responses to capture.

At Marion Island, females had significantly higher prolactin levels than males. In species where one parent plays a dominant role in attendance behaviour, individuals of this gender have higher prolactin levels than individuals of the other gender (Delehanty et al. 1997), but elevated levels of prolactin are expected to be similar for species with biparental care (Gratto-Trevor et al. 1990). Most seabird species share parental duties equally (Lack 1968, Tickell 1968, Weimerskirch 1995). However, prolactin levels have been found to be higher in females than males in several species (Cherel et al. 1994, Vleck et al. 2000, Angelier et al.

2007a, Angelier et al. 2007b, Angelier and Chastel 2009), including wandering albatrosses (Hector and Goldsmith 1985, Angelier et al. 2006). This pattern for seabirds of higher prolactin levels in females than in males is not yet understood (Lormée et al. 2000, Angelier et al. 2006).

Females that experienced low levels of human disturbance had significantly higher prolactin levels than disturbed birds. Prolactin levels have been found to decrease in response to stress in birds (Delehanty et al. 1997, Chastel et al. 2005, Angelier et al. 2007b, Verreault et al. 2008). This indicates that disturbed females responded physiologically to stress. This result supports the finding of de Villiers et al. (in press) that birds close to the station and in the Macaroni Bay study colony had higher stress protein levels than birds further away from the station and a disproportionate number of birds in the study colony had low plasma protein levels. Study colony males had the lowest prolactin levels, but not significantly so. Verreault et al. (2008) suggested that genders may differ in the sensitivity of their prolactin control mechanisms in response to acute or chronic stress.

Data on the breeding experience and age of birds outside the study colony were not available. In wandering albatrosses, corticosterone increases with breeding experience but decreases in old birds. Prolactin levels also increase with breeding experience in males and females that breed for the first time have lower prolactin levels than more experienced birds (Angelier et al. 2006). Older birds seem more able to resist stress as they had higher stress-induced prolactin levels than younger birds (Angelier et al. 2007a). Breeding success of wandering albatrosses increases with breeding experience (Weimerskirch 1992, Nel et al. 2003). More experienced birds at Marion Island were found to have less intense behavioural responses to standardised approaches (de Villiers et al. 2005). It would have been interesting to have investigated the effects of chronic levels of disturbance on the prolactin levels of birds with known breeding records.

To obtain baseline levels of hormones, blood needs to be taken before the levels change in response to the stressor. To obtain baseline corticosterone levels, blood must be drawn within three minutes of capture (Wingfield et al. 1982, Lormée et al. 2003). Thereafter, corticosterone levels increase and the acute stress response can be described by measuring changes in hormone levels over time (e.g Müllner et al. 2004, Chastel et al. 2005, Walker et al. 2005b). Blood drawn within three to five minutes after capture is considered to reflect baseline prolactin levels (Verreault et al. 2008). In this study, blood was drawn within three minutes. However, the baseline levels of these hormones might not have been obtained because the stressor that triggers changes in hormone levels might not be capture but rather the onset of the approach or even the first sight of people. There was a tendency for birds to have higher corticosterone levels and lower prolactin levels when approaches were started from further away. Birds would also have seen the pedestrians before the approach started and this time interval would have differed according to the surrounding terrain. Furthermore, some birds would have seen nearby birds being bled. These are shortfalls of the current study, but were difficult to control for due to the terrain. Angelier et al. (2006) sampled only one bird in a cluster of birds to reduce potential disturbance to neighbouring birds. However, only sampling birds that would not have seen humans in the area or other birds being bled would result in small sample sizes, especially for study-colony birds.

No relationships were found between the behaviour during approaches and upon capture and the level of corticosterone or prolactin. However, birds that were exposed to low levels of human disturbance had less intense behavioural responses and for females, these far-station birds also had the highest level of prolactin (indicating that they were not physiologically stressed). Blood measurements can in themselves be disturbing to birds. Therefore, other non-invasive methods of measuring hormone levels, such as faecal sampling (Koch et al. 2009) and sampling through the use of blood-sucking Triatomine bugs (Arnold et al. 2008) have been recommended. However, such methods are not practical at Marion Island, due to logistic difficulties and the restriction on the introduction of alien

organisms (Prince Edward Island Management Plan Working Group 1996). It is therefore recommended that behavioural responses of birds at Marion Island be used to determine stress levels. Holmes (2007) suggested that pedestrians should use alert, agonistic and threat behaviours as telltale signs of stress in penguins. For wandering albatrosses, vigilance and vocalisations are valuable telltales of stress and are easily noticeable by scientists and non-scientists. Visitors to the Marion Island should be advised to keep to the recommended minimum approach distance of 15 m to birds on nests, but to retreat if birds respond intensely.

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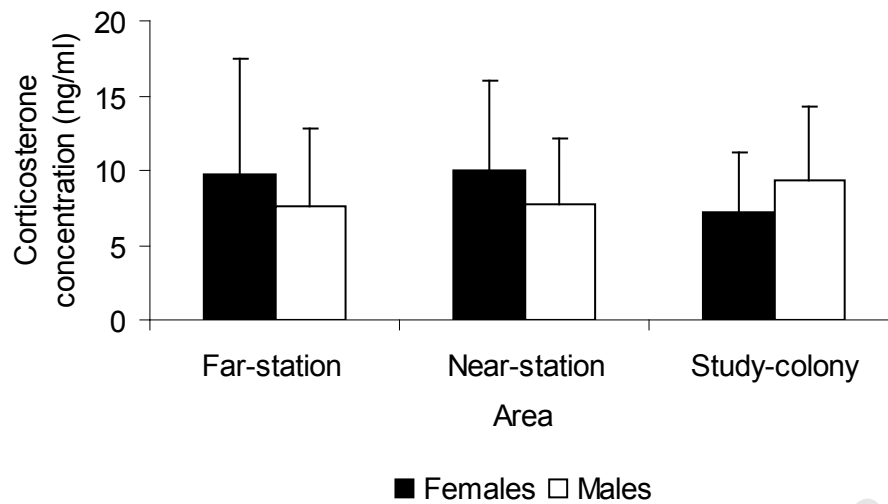
Figure 1 Mean (+1 sd) corticosterone levels (ng/ml) of wandering albatross females and males at three areas at Marion Island in 2006. Birds were in three areas with different levels of chronic disturbance: far-station (research: low; incidental: low), near station (research: medium; incidental: high) and in the study colony (research: high; incidental: medium).
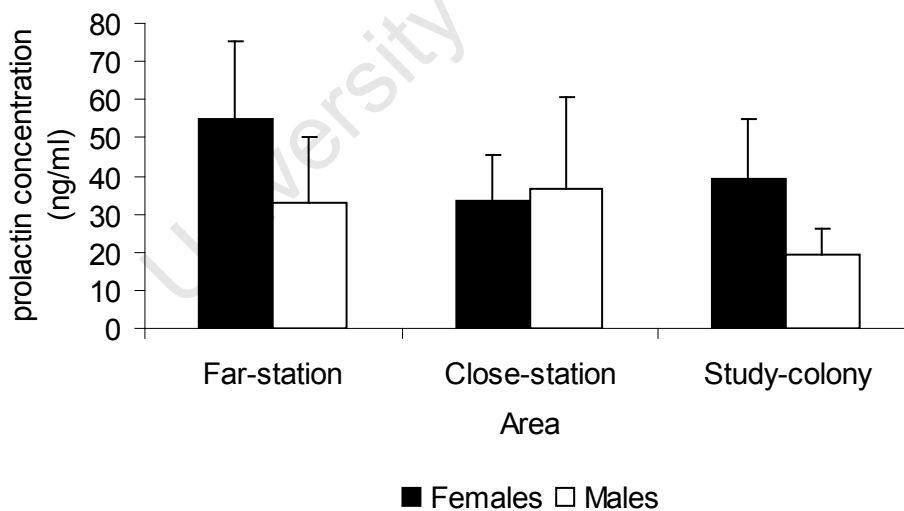
Figure 2 Mean (+1 sd) prolactin levels (ng/ml) of wandering albatross females and males at three areas at Marion Island in 2006. Birds were in three areas with different levels of chronic disturbance: far-station (research: low; incidental: low), near station (research: medium; incidental: high) and in the study colony (research: high; incidental: medium).

Table 1 Behavioural responses of brooding wandering albatrosses during standardised pedestrian approaches at Marion Island in 2006. Birds were in three areas with different levels of chronic disturbance: far-station (research: low; incidental: low)), near station (research: medium; incidental: high) and in the study colony (research: high; incidental: medium).

Responses		Far-station birds	Close-station birds	Study-colony birds
Number of birds		24	19	9
Approach Non-vocal Response (ANVR)	median number of Head-Turns	3.2	3.7	5.6
	range of Head-Turns	1–6	1–7	3–7
Approach Vocal Response (AVR)	no vocalisations (%)	90	94	56
	VR of 3 or 4 (%)	5	6	33
Catch Vocal Response (CVR)	no vocalisations (%)	61	37	0
	VR of 3 or 4 (%)	22	32	33
Release Vocal Response (RVR)	no vocalisations (%)	42	32	22
	VR of 3 or 4 (%)	42	58	56
Position after release	On nest (%)	17	53	44
	Next to nest (%)	48	47	56
	Away from nest (%)	35	0	0

The effect of research disturbance on the behavioural responses and breeding success of grey-headed albatrosses (*Thalassarche chrysostoma*) at sub-antarctic Marion Island

Abstract

Grey-headed albatrosses (*Thalassarche chrysostoma*) on G rey-headed Albatross Ridge at M arion Island have been afforded the highest level of management protection, but these birds can be affected by research and incidental human disturbance. Nine sections of the c olony with different levels o f chronic di sturbance w ere i dentified. One s ection was m onitored m onthly as par t o f a demographic study and another section was entered monthly to collect cephalopod beaks. The behaviour of chicks close to fledging and brooding adults in these sections was recorded prior to, during and after research disturbance events, and a section further along the ridge served as control. During disturbance, both chicks and adul ts in the study sections were significantly more likely to be s tanding and to be responsive than before disturbance. Rates of recovery to pre-disturbance levels of behaviour were variable. In 2004/ 05, breeding s uccess was determined by m arking nes ts i n six sections and these nests were checked twice during the breeding season. In 2005/06 and 2006/07, all sections were monitored through fixed point-photography. Breeding success was determined as the percentage o f marked or identified nes ts t hat w ere s till ac tive when nests w ere c hecked or a photograph was taken. In February of all three seasons, the calculated breeding success was 62.5%, 55.8% and 71. 8%. There w ere no significant di fferences in success between s ections. History o f disturbance and the s ize of section did not i nfluence breeding success. Fixed-point phot ography i s recommended as a non -intrusive m ethod t o c ompare the b reeding success at study and non -study sections.

Introduction

Human di sturbance o f wildlife c an c ause beha vioural c hanges t hat r ange from m inor, s hort-term changes such as i ncreased vigilance (Walker et al. 2006, Holmes et al. 2007, Van Polanen Petel

2007), to changes in essential behaviours such as feeding activity (Rees et al. 2005) and parental care (McClung et al. 2004), to long-term changes that can result in reduced survival or reproduction (Bolduc and Guillemette 2003, Harris 2005). Nest monitoring, to determine the breeding success of birds and the factors that influence success, is important for the assessment of the conservation status of threatened species. However, the study techniques used to obtain these data can themselves influence behaviour (Knight and Cole 1995), survival and breeding success (O'Dwyer et al. 2006).

The effects of disturbance can depend on the frequency of visits to nests by researchers. Leach's storm-petrel (*Oceanodroma leucorhoa*) had 50% and 56% reduced breeding success when handled weekly or daily compared to a control group that was handled once during incubation (Blackmer et al. 2004). In contrast, research disturbance had no effect on the hatching success or chick quality (growth rate and body mass) of Gould's petrels (*Pterodroma leucoptera*) at nests where adults were disturbed every 7–10 days during their 40-day incubation period (O'Dwyer et al. 2006).

The timing of disturbance can also be important. The cost of replacing a clutch, and thus clutch-value, increases with time and parents may be less likely to abandon their offspring later in the season (Trivers 1972). The first visit to common eider (*Somateria mollissima*) colonies resulted in 26–33% of breeding failures when nests were visited early in incubation, but 11% when nests where first visited later in the incubation period (Bolduc and Guillemette 2003).

Ground surveys can cause disturbance and are often difficult and expensive (Werschkul et al. 1976, Tremblay and Ellison 1979), therefore photography has been recommended as a non-intrusive monitoring method (Trathan 2004). Aerial photography from low altitudes has become a popular method to census bird colonies (Frederick et al. 1996, Trathan 2004). Photographic techniques can be especially useful in long-term studies that may involve a number of different observers. For example, photographic images were successfully used to obtain information on nest site selection, matings,

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divorces and other changes over time for rockhopper penguins (*Eudyptes chrysocome*) (Warham 1983). Photographic monitoring (Herranz et al. 2002, Anthony et al. 2004) and video identification (Stake et al. 2004) have been used to determine nesting success and to identify predators at nests. Changes that occur over time can be monitored through fixed-point photography, where photographs are taken at fixed locations, in the same directions and at the same height at set intervals. This technique was used to monitor the impact of recreational activities on the shoreline of the Maine Islands (Sea Grant 2004) and to monitor changes in vegetation cover over an 11-year period (Tyndall 2000).

The grey-headed albatross (*Thalassarche chrysostoma*) is listed as vulnerable (BirdLife International 2006), with large numbers being killed as bycatch in the long-line fishing industry (Nel et al. 2000, 2002, Ryan et al. 2006). Approximately 10% of the global annual breeding population breeds at the Prince Edward Islands in the sub-Antarctic (Crawford et al. 2003). Grey-headed albatrosses are bi-annual breeders with one-egg clutches. At Marion Island, prospecting and nesting occur from August to September and incubation takes place from October to December. Chicks are brooded from December to January. Parents visit chicks infrequently from February to April, when chicks start to fledge (Marchant and Higgins 1990).

At Bird Island, South Georgia, extensive long-term studies on this species started in 1975/76 (Prince et al. 1994). At Marion Island (46°54'S, 37°45'E), the larger of the two islands in the Prince Edward archipelago, colonies are found on cliffs on the southern side of the island. Annual counts commenced in 1984/85 (Nel et al. 2002) and long-term studies began in 1997/98 (Ryan et al. 2006). The main study area was on a section of Grey-headed Albatross Ridge on the southern side of the island, comprising between 92 and 123 (mean 107) nests annually. Here, nests were marked each season and monitored at monthly intervals, and pre-fledging chicks and breeding adults were ringed (Ryan et al. 2006). Censuses of active nests along the ridge were conducted bi-annually, once during

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incubation and again shortly before fledging. A field hut is situated c. 80 m from the bottom of the ridge and a pathway over the ridge is approximately 100 m from the study area.

The aims of this study were to determine whether the behaviour and breeding success of grey-headed albatrosses on Grey-headed Albatross Ridge were affected by research disturbance or incidental human disturbance associated with occupation of the field hut and crossing of the ridge.

Methods

Behaviour

The effect of research disturbance on the behaviour of grey-headed albatrosses at three sections on the ridge with different levels of disturbance was investigated. This was done from the field hut through Instantaneous Scan Sampling (Altmann 1974) of the behaviour of each bird at five-minute intervals. A scan of all visible birds took between two to three minutes. The demographic study section, Section 2, as well as Section 3 (hereafter called study sections) were visited by the researcher/s while the control section, Section 4, was further along the ridge (Figure 1).

In April 2004, the behaviour of chicks (n=49) in the study sections and chicks (n=32) in the control section was monitored. Before two researchers entered the study sections, 23 scans at five minute intervals were made over a period of 2.25 hours. Scans were made during a period of 2.75 hours while the researchers were on the ridge, and the part of the sections in which the researchers were active was noted. Scans were made for 0.25 hours after researchers had left the section. In January 2005, the behaviour of 91 brooding adults in the study sections and 38 adults in the control section was monitored. Before one researcher visited the ridge, 33 scans were made at five-minute intervals over a period of five hours. The researcher spent 1.5 hours on the ridge to monitor nests in Section 2 and to collect cephalopod beaks from Section 3. Nine scans were recorded during this period. Thirteen scans were made during the 1.25 hours after the researcher had left the ridge.

Behaviour was categorised into states (inactive (resting or sleeping), standing, walking) and events (Altmann 1974). Events for both chicks and adults included responsive behaviours (alert, aggressive, or threatening behaviour), comfort behaviours (preening, shaking or stretching body), nest attendance (i.e. pecking at nesting material), parent-chick interactions, partner interactions and wing movements (flapping or shaking wings) (Marchant and Higgins 1990). Walking, wing movements, nest attendance, parent-chick interactions and partner interactions occurred at low frequencies and were not modelled.

Fisher exact tests were done to compare the behaviour of the study sections with the control section before disturbance. Generalised Linear Models with the binomial logistic link function (Genstat 8.2 2005) were used to model the effect of disturbance on behaviour. Explanatory variables included were section of ridge (study or control) and level of research disturbance. In the model for chicks, disturbance level was recorded as 1: no disturbance (researchers absent from ridge), 2: researchers in section but not in chick's subsection, 3: researchers working in chick's subsection and 4: post-disturbance (researchers left ridge). In the model for adults, disturbance level was recorded as 1: no disturbance, 2: researcher on ridge, 3: post-disturbance.

Breeding success

Breeding success was determined as the percentage of marked or identified nests that were still active when nests were checked or a photograph was taken. Data were collected during three breeding seasons: 2004/05, 2005/06 and 2006/07.

2004/05

Sections along the ridge (Figure 1) were entered at different frequencies during the breeding season for various research activities (Table 1). In the demographic study colony section (Section 2), 110 nests were marked out in October and checked approximately monthly. Section 3 was entered

monthly to collect cephalopod beaks as part of a diet study (n=5 nests in middle October). In October, active nests (n=204) were marked out in Section 3 and five other sections. In November, all seven sections were entered as part of another study, and the contents of 20 nests in each subsection of a section were checked. For this study, Sections 1 and 3–7 were entered again in February for nest checks and the researcher remained an equal amount of time in each section. Nest contents were monitored again in these sections in April. Breeding success was calculated as the number of nests that were marked out that were active in February and April and success between sections was compared.

2005/06 and 2006/07

Sections 1 and 3 were entered during these breeding seasons for the same kinds of activities (Table 1). Breeding success of all sections was monitored monthly during the breeding season by means of fixed-point photography. Careful consideration was given to the location from where photographs were taken to ensure that identifying features (i.e. large rocks) could easily be seen on the photographs to assist in nest identification. In 2005/06, photographs were taken at subsections of six sections (including Section 2) at the beginning of October, and three more sections were added to the study during the second trip in October. Because eggs could not be seen on the photographs, and loafers (non-breeding adults in and around sections of the colony) and late breeders might have been sitting on empty nests, nests were assumed to be active during incubation if they were occupied in both of the first two photographs. Photographs were taken from November to April at subsections of these nine sections (n=584 nests).

In 2006/07 the level of research disturbance at Section 2 was greater than the previous two breeding seasons. Upon arrival at the nests, birds were measured and weighed and had a blood sample taken once. During incubation, birds were exposed to six weeks of daily checks and nests were checked monthly thereafter. Photographs were taken in six sections at the end of October and monthly from

December to April. Similar to above, nests were assumed to be active during incubation if they were occupied in both the October and December photograph. Photographs were taken in December, February and March in two more sections. As photographs were not taken in January in Sections 7 and 8, half of the nest failures that occurred between December and February were allocated to January. The total number of nests monitored over this breeding season was 586.

The progress of each breeding attempt was followed on the series of photographs. The absence of a nestling meant that it had died. This allowed monthly calculations of success that was determined as the percentage of identified nests that were still active when a photograph was taken. Because chicks might have fledged before photographs were taken in April, breeding success was only determined until March.

Statistical analyses to determine survival estimates were performed for each year by means of Capture-Mark-Recapture models (Lebreton et al. 1992), because they offer a flexible tool to study survival in relation to various factors. The median-$\hat{c}$ procedure in program MARK 5.0 (White and Burnham 1999) was used to assess goodness-of-fit (GOF) for the model with additive effects of section and time (month) on survival. Two further assumptions, instantaneous sampling and no misidentification of individuals, were met. It was assumed that sections would have had similar breeding success if no disturbance occurred at the ridge and that all individuals within sections had the same survival rate. Model selection was based on Akaike's Information Criterion, adjusted for overdispersion and sample size (QAICc, Burnham and Anderson 2002).

The effects of history of disturbance and section size on breeding success were determined. History of disturbance was categorised into three levels of chronic disturbance: high (close to the footpath and hut and entered monthly, Sections 2 and 3), medium (close to the footpath, Sections 1 and 4) and low (further along the ridge and not entered, Sections 5 –9). The sections were divided into three

categories according t o size (large, medium a nd s mall), based on t he r elative s ize of the e ntire section, not just the area photographed. Small sections had less than 34 nests that were monitored on the photographs, medium size sections had less than 85 nests that were monitored and the two large sections had 99 and 147 nests that were monitored. Size and disturbance were treated as linear covariates at the section level. Analysis of Deviance (ANODEV) was used to estimate the proportion of among-section variance in survival that was attributable to size of the section and disturbance level. ANODEV was used to further examine how much of the temporal variation in survival was explained by r ainfall. Rainfall da ta w ere av ailable f rom t he South African Weather S ervice. The av erage daily rainfall between the intervals at which photographs were taken was used in the analysis.

Results

Behaviour

No chicks left their nests during observations. Before disturbance, on average 20.2% of chicks in the study s ections were inactive, 39. 5% were responsive, 25. 5% were standing and 31 .0% were performing c omfort beh aviours. O n av erage 22. 4% o f c hicks i n t he c ontrol s ection were inactive, 38.9% were responsive, 32.7% were standing and 28.6% were performing comfort behaviours. More chicks i n the control section stood during observations before disturbance than in the study sections (v=1, n =1857, P <0.001). No o ther behav iours differed s ignificantly bet ween t he s ections be fore disturbance. When all observations were modelled (Table 2), chicks in the control section were more likely to be inactive and less likely to be responsive than birds in the study sections. When researchers were on t he ridge, chicks in the study sections were 42.4% more likely to be r esponsive, 25.4% more likely t o be s tanding a nd 40.9% less l ikely t o be per forming comfort behav iours t han be fore disturbance. Chicks stood up and started Bill Snapping (de Villiers et al. 2005) when researchers approached s ubsections. When researchers w ere i n a s ubsection, c hicks i n the s ubsection w ere 87.2% less likely to be inactive, 76.4% less likely to perform comfort behaviours, 121.6% more likely to be r esponsive and 141.7% more l ikely t o be s tanding than be fore di sturbance. The proportion o f

chicks i n s ubsections t hat w ere i nactive, r esponsive, s tanding or per forming c omfort behav iours remained v ariable af ter r esearchers had l eft t he s ubsection but were still on t he r idge. After th e researchers had l eft the ridge, chicks were 58.9% m ore likely t o be i nactive t han before disturbance and t he proportion of i nactive chicks did not r eturn to pre-disturbance l evels within the 15 m inutes of post-disturbance observations.

No adults were seen t o abandon their nests during this study. Before disturbance, on av erage 72.7% of adults in the study sections were inactive, 11.1% were responsive, 20.4% were standing and 7.3% were performing comfort behaviours. On average 75.0% of adults in the control se ction were inactive, 9.8% were responsive, 17.5% were standing an d 8.5% were performing c omfort behav iours. Fewer adults in the control section stood before disturbance than in the study sections (v=1, n=4210, P=0.017). More adults in the control section were inactive before disturbance than in the study sections (v=1, n=4199, P=0.066). When all observations were modelled (Table 3), adults in the control section w ere m ore l ikely t o be i nactive and t ended t o be l ess r esponsive t han bi rds i n t he s tudy sections. During disturbance, adults in the study sections were 38.4% more likely to be responsive, 20.5% more likely to be standing and 8.4% less likely to be inactive than before disturbance. After the disturbance, adults in the study sections were 3.8% more likely to be standing than before the disturbance. The proportion of adults that were i nactive returned t o pre-disturbance proportions af ter the di sturbance, the pr oportion o f adul ts t hat were r esponsive or per formed c omfort behav iours remained v ariable af ter t he di sturbance w hile t he pr oportion o f adul ts s tanding r emained hi gh af ter disturbance as compared to the pre-disturbance period. The proportion of adults performing comfort behaviours or standing did not return to pre-disturbance levels during the observations.

Breeding success

2004/05

When nests were checked in February, 4 of the 5 nests that were marked out in Section 3 in October had failed and the remaining nest failed by March (Figure 2). The proportion of active nests was not dependent of section in February (X^2=6.97, P=0.323) and in April (X^2=10.50, P=0.105). The overall breeding success was 62.5% and 57.0% in February and April respectively. During the nest check in February, chicks stood up from the nests when the researcher was in sight and upon closer approach most regurgitated. Fewer chicks regurgitated in April than in February.

Rainfall

More rain fell between October and April in 2005/06 than in 2006/07 with 1197.8 mm and 1043.8 mm respectively. Rainfall patterns differed interannually. In 2005/06, rainfall was smallest in the October-November interval and largest in the November-December interval. In 2006/07, rainfall was smallest in the November-December interval and largest in the December-January interval (Figure 3).

2005/06 and 2006/07

The GOF tests for the capture-mark-recapture analysis showed slight overdispersion (2005/06: $\hat{c}$=2.16, se=0.10 and 2006/07: $\hat{c}$=2.05, se=0.28). This was attributed to non-independence among nests because several nearby nests could be affected by the same event, e.g. flooding. The estimated $\hat{c}$ was used to adjust the confidence intervals of the survival estimates.

In 2005/06, the Capture-Mark-Recapture modelling showed that the best model, according to QAICc, was the one with time-dependent survival (Model 1, table 4A), whereas in 2006/07 the best model included rainfall effects on survival (Model 1, Table 4B). In 2005/06 the average monthly survival in different sections ranged from 74.7% (January-February) to 95.7% (February-March) (Figure 4). In 2006/07 monthly survival in different sections ranged from 79.3% (December-January) to 98.2%

(February-March). The overall chick survival in February in 2005/06 was 55.8% and in 2006/07 it was 71.8% (Figure 5).

Size of a section, disturbance level, and their interaction did not explain significant amounts of the among-section variances in either year (ANODEV using Models 1, 5, and 6 in Table 4A, and Models 2, 6, and 7 in Table 4B: 2005/06 explained deviance = 4%, $F_{3,5}$ = 0.08, P = 0.97; 2006/07 explained deviance = 31%, $F_{3,5}$ = 0.61, P = 0.64). Rainfall explained 0.2% of the temporal variance in survival in 2005/06 (ANODEV: 2005/06 using Models 1, 7, and 8 in table 1A: $F_{1,3}$ = 0.01, P = 0.94), but explained 99% of the temporal variance in 2006/07 (using Models 1, 2, and 8 in table 1B: $F_{1,1}$ = 749.77, P = 0.02). However, with only three time periods in that year, this result needs to be interpreted with care. The section (section 6) that had the most failures per month in 2006/07, was a section that had a 34% reduction in breeding success between December and January and no nest mounds of the failed nests were visible on the January photograph.

Discussion

Behaviour

Before the disturbance, more chicks in the control section stood than chicks in the study sections. In contrast, more adults in the study sections stood than in the control section and fewer adults in the study sections were inactive before disturbance than adults in the control section. Although no researcher had been on the ridge when the before-disturbance data were recorded, there was activity at the hut. The study sections were the closest sections to the hut. Because adults returned to their sections to breed, they had been handled when they were ringed and subsequently visited during ring and nest checks. They therefore seemed to have become sensitised to the presence of humans. Adult wandering albatross (*Diomedea exulans*) at Marion Island that were more exposed to human disturbance, also reacted more during disturbance than those that were seldom visited (Wheeler et al. 2009). Before the ringing event, chicks had been exposed to nest checks, but they had not been

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handled. Their responses seemed to indicate that they had habituated to the presence of humans, because they did not perceive the researchers as a threat. Magellanic penguin (*Spheniscus magellanicus*) chicks (Walker et al. 2005) and Laysan albatross (*Phoebastria immutabilis*) chicks (Burger and Gochfeld 1999) in undisturbed areas also had a greater behavioural response to human approaches than birds in visited areas.

When researchers were on the ridge, adults in the study sections and chicks in the subsections were less likely to be inactive than before the disturbance. Chicks and adults were more likely to be responsive and to be standing during than prior to disturbance. Birds may have regarded the approaching researcher as a predator (Frid and Dill 2002) and therefore have been more likely to be defensive. Because the risk of predation increases as the predator approaches a nest (Beale and Monaghan 2004), the intensity of response was greatest when the researcher was nearby. Adults brooding chicks stood up to defend their chicks. During incubation, adults were observed to be more aggressive than during brooding but to remain on their eggs, even when the researcher was at a nest (M. Wheeler, personal observation). Although brooding adults were more responsive during disturbance, the probability of being responsive was much lower than for the chicks during disturbance. Both chicks and adults in the control section were not visited by researchers; thus they were more inactive and less responsive than birds in the study sections when all observations were considered.

Because such a high proportion of chicks were responsive during disturbance, the probability of performing comfort behaviour was significantly less for chicks. Adults in the study sections that were not responsive were more likely to be performing comfort behaviours, but not significantly more. When disturbed, an animal needs to assess the costs of staying and fighting, or fleeing (Ydenberg and Dill 1986). This is especially important in the case of an animal on a nest, as both the parent and the offspring are threatened by the predator (Osiejuk and Kuczyński 2007). But even when a parent does

not flee from the nest, disturbances are likely to lead to trade-offs between avoidance behaviours and other fitness-enhancing activities (Frid and Dill 2002). Animals often respond to disturbance through irrelevant behaviours, called displacement behaviours (Kortmulder 1998). Such behaviours include comfort behaviours and maintenance activity. Royal penguins (*Eudyptes schlegeli*) were also more likely to perform comfort behaviours (during and after) and maintenance behaviour (after) human disturbance (Holmes et al. 2005).

Post-disturbance recovery by chicks and adults in the study sections was variable. Chicks in the study sections were more likely to be inactive after disturbance. Chicks were also more likely to be sitting inactive on their nests. After disturbance, the proportion of responsive adults remained variable, but high during observations. Adults were more likely to be standing at their nests after disturbance than before disturbance. They were also more likely to perform comfort behaviours than before, but not significantly so. They were therefore more likely to be performing displacement behaviours. Disturbance might have resulted in physiological as well as behavioural responses.

Breeding success

Incubation is a critical period for albatrosses. Birds need to accumulate sufficient reserves during foraging trips to sustain them during the next fast, while foraging trips need to be kept short enough to avoid returning to a nest already deserted by the incubating partner (Weimerskirch 1995). At Bird Island, South Georgia, almost two thirds of breeding failures occurred during the incubation period (Prince et al. 1994). Another critical period for survival is when the chicks are left alone at the nest for the first time. At South Georgia, the daily chick mortality rate was 18 times higher during the first 2–3 days when left alone than during the rest of the fledging period. Larger chicks have better thermoregulatory mechanisms and can defend themselves better against predators and therefore have a lower mortality rate (Catry et al. 2006a). Failures at Bird Island therefore usually occurred during the first half of the breeding season (Catry et al. 2006b). Similarly on Marion Island, fewer

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failures occurred from February to April than before February. In 2006/07, most failures occurred during incubation to early brooding (December-January interval). However in 2005/06, most failures occurred during late brooding and over the critical period when chicks were first left alone at the nest (January-February interval).

Although adults did not desert their nests during research disturbance (see above), they were more likely to stand up from their nests during and after disturbance. This action can expose eggs or chicks to potential predators and to ambient environmental conditions. The corticosterone levels of chicks can also be influenced by the response of adults, as speculated for Magellanic penguin chicks in areas visited by tourists (Walker et al. 2005). In this study, chicks were observed to regurgitate when closely approached. Regurgitation, or oil-spitting, is a common chemical defence/offence mechanism amongst surface-nesting procellariformes (albatrosses, fulmars, shearwaters and other petrels) (Warham 1977). Although this oil spitting can be effective in avoiding predation, it is energetically costly to the chick. The oil is produced by adults while foraging and thereby the energy content of the prey item at capture is concentrated between 5–35 fold. The oil of grey-headed albatrosses has a mean energy content of 39.7 kJ/g of stomach oil. This oil is fed to the chick and is used by the adult and chick for the maintenance of water and heat during fasting periods (Warham et al. 1976). The quantity of oil regurgitated differs according to the age of the chick in some species, with larger chicks spitting smaller quantities due to larger consumption rates of the oil (Warham et al. 1976). Our finding that fewer chicks regurgitated in April than in February supported this. Nest monitoring might therefore be less energetically costly to larger chicks.

The effects of research disturbance on breeding success can be influenced by the frequency at which breeding birds are disturbed, with birds that experience a higher frequency of researcher disturbance having lower success (Blackmer et al. 2004). For example, the breeding success of bearded vultures (*Gypaetus barbatus*) decreased with the frequency of incidental disturbance in the area (Arroyo and

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Razin 2006). At Marion Island, history of chronic disturbance did not explain breeding success differences between colony sections visited at different frequencies. History of disturbance also did not explain a significant amount of the variance among Section 2 and sections that were only monitored through fixed-point photography in 2005/06 or 2006/07. The level of research disturbance did not seem to influence the breeding success of grey-headed albatrosses. However, it could influence other factors that were not measured in the current study, such as the number of prospectors or first-time breeders.

While most seabirds breed colonially (Brown et al. 1990), there are costs and benefits to breeding in such aggregations (Danchin and Wagner 1997). Individuals can spend less time on vigilance and therefore more time on other fitness-enhancing activities (Terhune and Brilliant 1996). However, the breeding success of colonial animals can be influenced by characteristics of their colony such as colony size. Larger colonies can have greater breeding success than smaller colonies, because they have smaller proportions of peripheral nests which are expected to have lower breeding success than central nests (Becker 1995). The presence of close neighbours can aid in group defense (Becker 1995) or prevent avian predators from landing between nests (Anderson and Hodum 1993). However, larger colonies can be more conspicuous to predators, leading to larger colonies having lower success. Colony size has been found to be negatively related to predation rates in Cape petrels (Weidinger 1998) and negative relationships have been found between population or colony size and clutch size, growth rate, fledgling weight and breeding success (Hunt et al. 1986). Breeding success can also be optimum in intermediate size colonies (Brown et al. 1990). In other colonies, trade-offs between the benefits of transformation of foraging information and the costs of parasite load can result in size not having an influence on breeding success (Brown et al. 1990). The sections on Grey-headed Albatross Ridge investigated in this study all form part of one colony. Although differences in breeding success were possibly due to the differing geography of the sections, the size of the section did not have a significant effect on breeding success in either of the years modelled.

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Climatic factors, s uch as r ainfall, c an ne gatively af fect b reeding s uccess. Rain r esulted in hi gh reproductive failure in Humboldt penguins (*Spheniscus humboldti*)*,* because adults were more likely to abandon flooded nes ts than non -flooded nests and to l eave the section. Breeding ev ents were also delayed when nests were flooded (Simeone et al*.* 2002). In this study, rainfall explained almost all of the t emporal v ariation i n 2006/ 07. Grey-headed albatross nes ts c onsist o f pac ked s oil and gr ass (Marchant and Higgins 1990) and hav e been obs erved t o c ollapse a fter r ainy c onditions. Flooding probably al so ac counted f or t he non -independence am ong survival because s everal near by nests would have been flooded by the same event. This seemed to have occurred in the section (section 6) where most failures were recorded in 2006/07 between December and January.

Although research activities influenced the short-term behavioural responses of study birds, it did not seem to influence the breeding success of the study section. Section 2 did not have lower breeding success than sections that were monitored less frequently (2004/05) or those that were only monitored through f ixed-point pho tography. H owever, f ixed-point phot ography was a us eful, non -intrusive method to compare the breeding success at study and non-study sections, especially if future studies are conducted at higher levels of disturbance.

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Footpath across the ridge

1

1

1

Size: small
Disturbance: medium

2

Size: medium
Disturbance: high

4

Size: medium
Disturbance: medium

5

Size: small
Disturbance: low

6

Size: medium
Disturbance: low

7

Size: small
Disturbance: low

7

8

Size: large
Disturbance: low

3

Size: small
Disturbance: high

9

Size: large
Disturbance: low

Hut
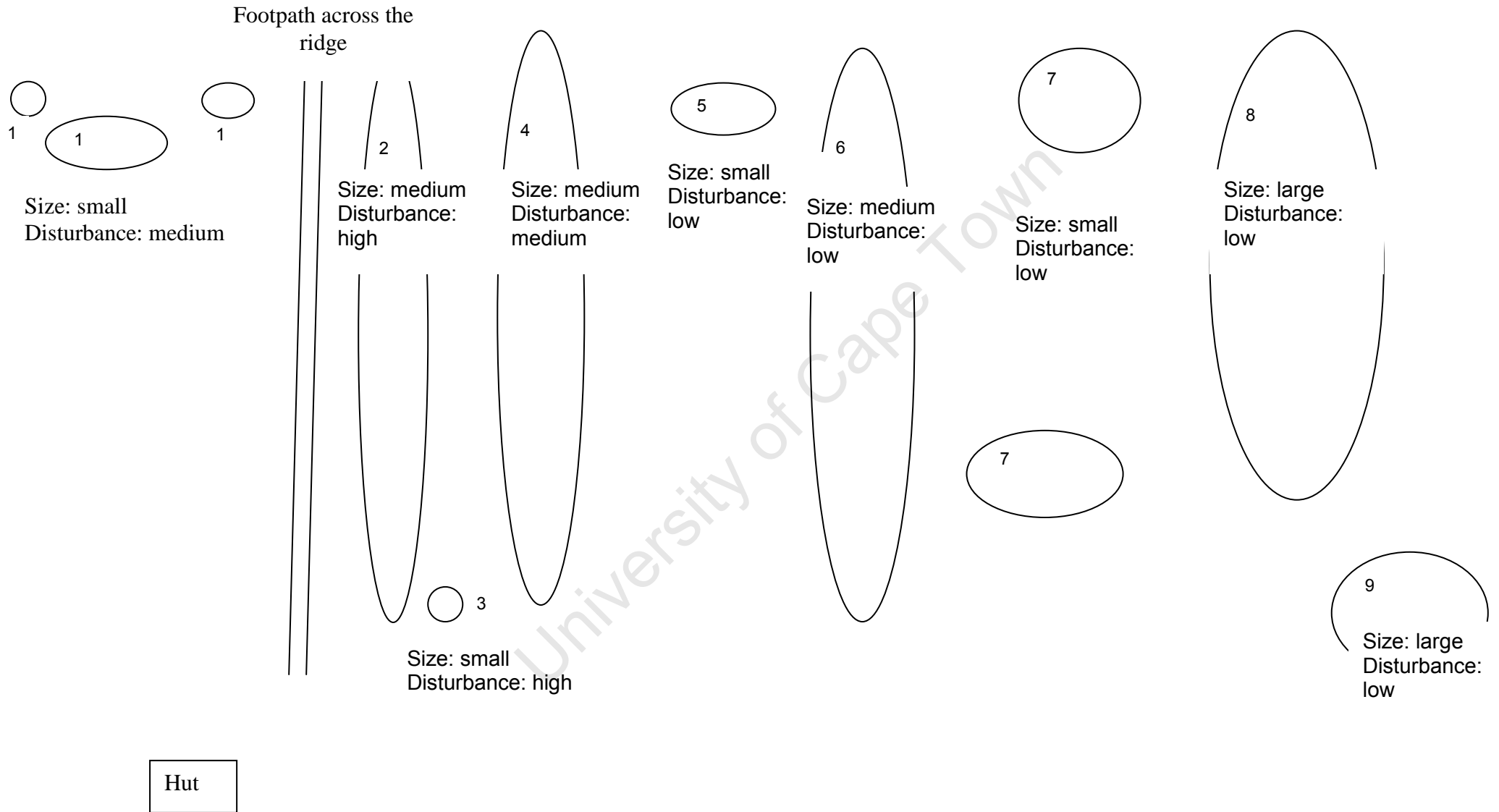
Figure 1 Layout of sections of the Grey-headed Albatross colony on Grey-headed Albatross Ridge, Marion Island. Sections were divided into three different size categories (small, medium and l arge) a nd three levels of c hronic di sturbance: hi gh (close t o the footpath and hut an d ent ered monthly), medium (close t o the footpath) and low (further along the ridge and not entered). Also indicating the position of the field hut and the pathway over the ridge. Illustration not drawn to scale.
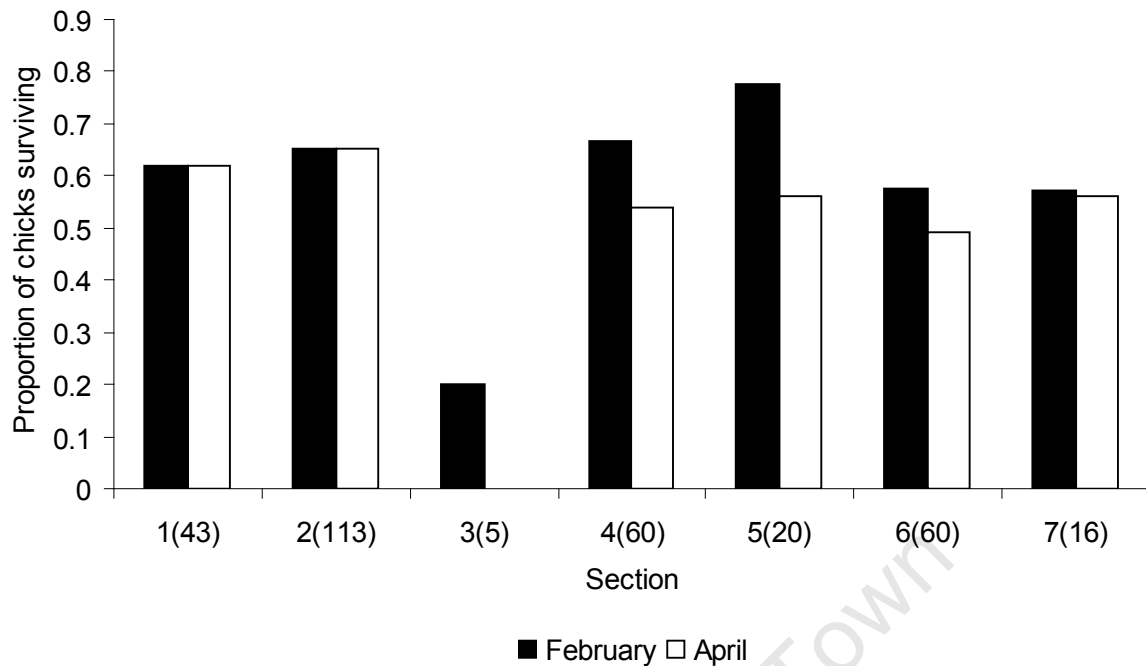
Figure 2 Proportion of Grey-headed Albatross chicks surviving in February and April during the 2004/5 breeding season for seven sections on Grey-headed Albatross Ridge, Marion Island. Section 2 was the long-term study sections where nests were monitored at least once a month. Section 3 was entered monthly to collect cephalopod beaks. The other sections were entered once in October, November, February and April and individual marked nests were monitored in February and April. Numbers indicate the number of the section and sample sizes in brackets indicate the number of nests marked out in October.
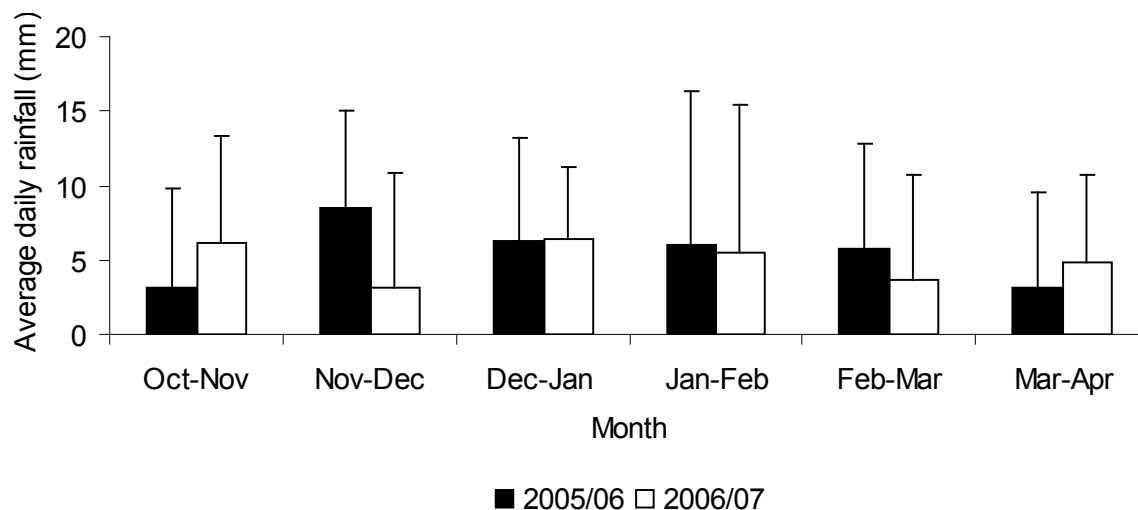
Figure 3 The average daily rainfall in 2005/06 and 2006/07 between the intervals at which photographs were taken of Grey-headed Albatrosses on Grey-headed Albatross Ridge.
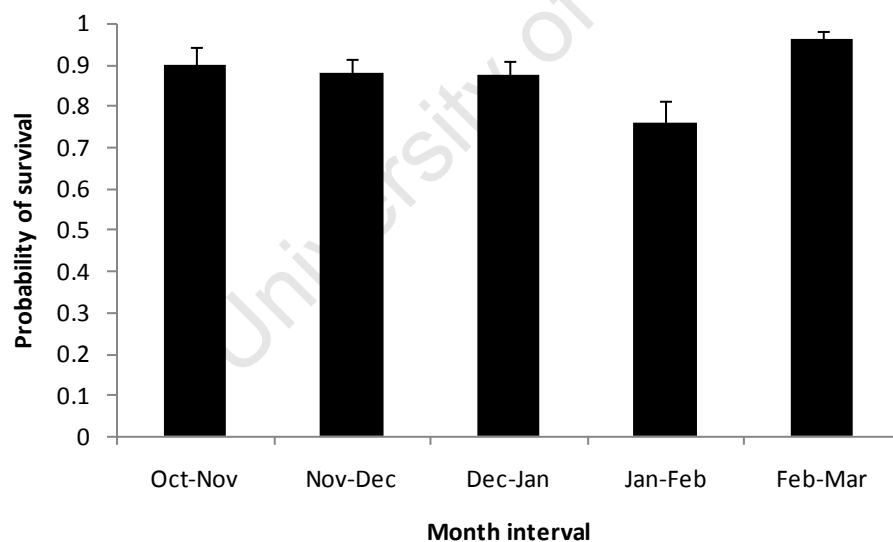
Figure 4 Probability of chick survival of Grey-headed Albatrosses on Grey-headed Albatross Ridge, Marion Island during five monthly intervals of the 2005/6 breeding season, as determined by the best capture-mark-recapture model.
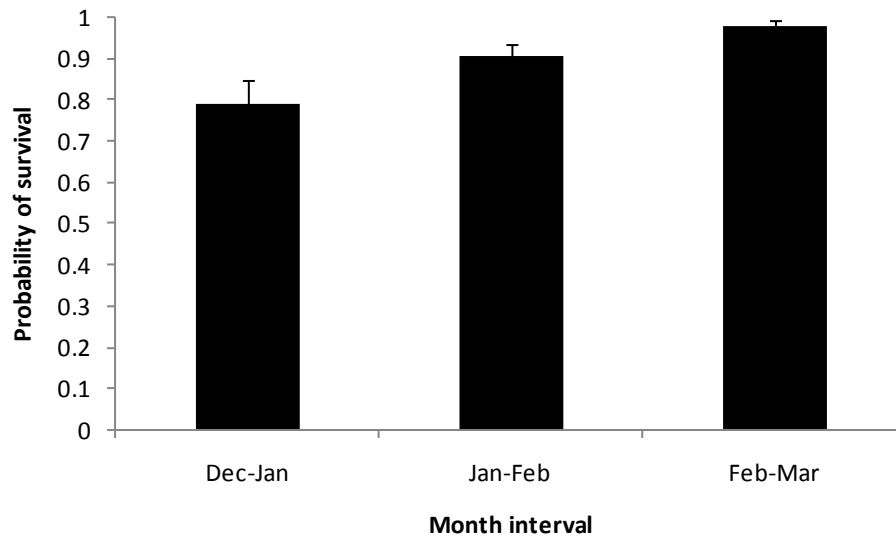
Figure 5 Probability of chick survival of Grey-headed Albatrosses on Grey-headed Albatross Ridge, Marion Island during three monthly intervals of the 2006/7 breeding season, as determined by the best Capture-mark-recapture model.

Table 1 Research activities in seven sections of Grey-headed Albatrosses on Grey-headed Albatross Ridge, Marion Island during the 2004/5 breeding season. Section 2 was the long-term study section.

Time of year	Colony sections		
	1, 4-7	2	3
October	Active nests marked	Active nests marked Partners bands monitor	Active nests marked Cephalopod beaks collected
November			
	Contents of some nests checked	Contents of some nests checked Partners bands monitored Nests checked	Contents of some nests checked Cephalopod beaks collected
	Nest count from distance	Nest count from distance	Nest count from distance
December		Nests checked	Cephalopod beaks collected
January		Nests checked	Cephalopod beaks collected
February	Nests checked	Nests checked	Nests checked Cephalopod beaks collected
March		Nests checked	Cephalopod beaks collected
April	Nests checked Census	Nests checked Census Chicks ringed	Nests checked Census Cephalopod beaks collected

Table 2 Results of the Generalised Linear Modelling of four behavioural responses (standing, inactive, responsive and comfort behaviour) of grey-headed albatross chicks on Grey-headed Albatross Ridge, Marion Island during and after research disturbance in 2004. The results for Section 4 are given relative to Section 2 and results during (researchers on ridge, researchers in subsection) and after disturbance are given relative to before disturbance. Significant results are indicated in bold.

Explanatory variables	Standing		Inactive		Responsive		Comfort behaviours	
	Estimate	(se) t_{162}, P	Estimate	(se) t_{162}, P	Estimate	(se) t_{162}, P	Estimate	(se) t_{162}, P
Section 4	0.101	(0.086) 1.16, P=0.244	**0.609**	**(0.090) 6.77, P<0.001**	−0.433	**(0.080) −5.41, P<0.001**	−0.0368	(0.0825) −0.45, P=0.655
Researchers on ridge	**0.317**	**(0.092) 3.47, P<0.001**	0.009	(0.103) 0.09, P=0.931	**0.678**	**(0.084) 8.08, P<0.001**	**−0.694**	**(0.098) −7.08, P<0.001**
Researchers in subsection	**1.55**	**(0.15) 10.28, P<0.001**	**−2.26**	**(0.41) −5.54, P<0.001**	**2.37**	**(0.21) 11.45, P<0.001**	**−1.74**	**(0.26) −6.71, P<0.001**
After disturbance	0.00	(0.21) 0, P=1	**0.625**	**(0.196) 3.19, P=0.001**	−0.008	(0.184) −0.05, P=0.964	−0.299	(0.206) −1.46, P=0.145

Table 3 Results of the Generalised Linear Modelling of four behavioural responses (standing, inactive, responsive and comfort behaviour) of grey-headed albatross adults on Grey-headed Albatross Ridge, Marion Island during and after research disturbance in 2005. The results for Section 4 are given relative to Section 2, and results during (researchers on ridge) and post-disturbance are given relative to before disturbance. Significant results are indicated in bold.

Explanatory variables	Standing		Inactive		Responsive		Comfort behaviours	
	Estimate	(se) t104, P	Estimate	(se) t104, P	Estimate	(se) t104, P	Estimate	(se) t104, P
Section 4	–0.0929	(0.0728) –1.28, P=0.202	**0.251**	**(0.067) 3.74, P<0.001**	–0.183	(0.096) –1.91, P=0.056	0.011	(0.110) 0.1, P=0.922
Researchers on ridge	**0.241**	**(0.094) 2.56, P=0.01**	**–0.290**	**(0.086) –3.38, P<0.001**	**0.375**	**(0.114) 3.28, P=0.001**	0.209	(0.143) 1.46, P=0.144
Post–disturbance	**0.190**	**(0.083) 2.3, P=0.021**	0.038	(0.078) 0.48, P=0.629	0.028	(0.1090) 0.26, P=0.799	0.102	(0.129) 0.79, P=0.429

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Table 4 Results of the model selection of capture-mark-recapture models for survival of grey-headed albatross nestlings at Marion Island. Survival varied among sections (section) and time of the season (time), and in relation to the size of the section (size) and disturbance level (disturbance). The re-sighting rate was constant and estimated to be equal to one in all models. Model selection was based on Akaike's Information Criterion (QAICc). Delta QAICc is the difference between the current model and the best one, and QAICc weights give the relative support for each model in relation to the others. K is the number of parameters. Model a 2005/06 breeding season. Model b 2006/07 breeding season.

Model		QAICc	Delta QAICc	QAICc Weights	K	QDeviance
a: 2005/06						
1	time	716.676	0.000	0.514	5	706.646
2	size + time	718.662	1.987	0.190	6	706.621
3	disturbance + time	718.687	2.012	0.188	6	706.646
4	size + disturbance + time	720.672	3.996	0.070	7	706.617
5	size X disturbance + time	722.352	5.677	0.030	8	706.281
6	section + time	725.135	8.459	0.007	13	698.956
7	constant	742.907	26.232	0.000	1	740.905
8	rainfall	744.843	28.168	0.000	2	740.837
b: 2006/07						
1	rainfall	219.088	0.000	0.545	2	215.080
2	time	221.066	1.978	0.203	3	215.050
3	size + time	222.330	3.242	0.108	4	214.303
4	disturbance + time	222.834	3.746	0.084	4	214.806
5	size + disturbance + time	224.261	5.173	0.041	5	214.220
6	size X disturbance + time	225.803	6.715	0.019	6	213.746
7	section + time	231.032	11.944	0.001	10	210.882
8	constant	239.552	20.464	0.000	1	237.550

Responses to standardised pedestrian approaches by breeding and non-breeding beach groups of king penguins (*Aptenodytes patagonicus*) at sub-Antarctic Marion Island

Abstract

The responses of breeding (guarding phase) and non-breeding groups of king penguins (*Aptenodytes patagonicus*) to pedestrian disturbance were investigated through 23 standardised single-person approaches on five beaches at Marion Island, Southern Ocean. Penguin groups were approached from different distances by a single person who stopped and stood 5 m from the perimeter of the group for a minute. The person then either retreated (short-duration visit), or moved around for a further five minutes before retreating (long-duration visit). The greater the starting distance of the approach, the greater the distance at which the first penguin began to walk. Breeding groups were less likely to walk away from the approacher than non-breeding groups. Penguins were more likely to be vigilant and to perform comfort behaviours after long visits than after short visits. Groups on frequently-visited beaches were less vigilant and less likely to perform comfort behaviours than groups on beaches that were visited less frequently. The zoning of the island and the recommendation in the revised Prince Edward Islands Management Plan of a minimum approach distance of 15 m to breeding king penguins, seem to be effective in protecting this species from current levels of pedestrian disturbance.

Introduction

Pedestrian visits can have negative effects on the behaviour and physiology of seabirds (Weimerskirch et al. 2002, de Villiers et al. 2006, Holmes et al. 2007). Birds that breed colonially are especially vulnerable (Boersma et al. 2001) because human disturbance, such as helicopter over-flights, can result in mass-stampede events that can lead to the trampling of eggs and chicks (Rounsevell and Binns 1991, Cooper et al. 1994, Hughes et al. 2008). Although penguins may appear to be relatively unaffected by human disturbance (Carney and Sydeman 1999),

studies have indicated that visits can lead to increased vigilance (Holmes et al. 2005), increased heart rate (Culik et al. 1990, Nimon et al. 1996, MS de Villiers, unpublished data), and increased body temperature (Boyd and Sladen 1971, Regel and Putz 1997).

Visitors at landing beaches can delay penguins from coming ashore (Wright 1998, Otley 2005), potentially affecting the quantity and quality of food delivered to chicks. Human disturbance at penguin breeding colonies can negatively affect chick growth (McClung et al. 2004, Ellenberg et al. 2007). Because fledgling mass influences juvenile survival (Garnett 1981, Reid et al. 2000), lower fledgling masses can result in population declines over time (McClung et al. 2004). Furthermore, the presence of visitors can influence nest site distribution, causing birds to choose nest sites in sub-optimal habitat away from centres of disturbance (Robertson 1997). Nevertheless, penguin colonies are popular tourist attractions and penguins are increasingly being exposed to visitors due to increasing demands from ecotourists (Boersma et al. 2001, Trathan et al. 2008).

The intensity of response to disturbance is species-specific. For example, adult Magellanic penguins (*Spheniscus magellanicus*) show rapid habituation to visits (Walker et al. 2006), but Humboldt penguin (*S. humboldti*) adults are extremely sensitive to disturbance (Ellenberg et al. 2006). Other factors that can influence the response behaviour of animals are phase of breeding as well as the history, intensity and duration of disturbance. Non-breeding birds are more likely to flee from disturbance, while breeding birds are more reluctant to abandon eggs or chicks (Harris 2005). Responses may depend on the nature of the disturbance - Magellanic penguins exposed to moderate levels of researcher disturbance respond more to human presence than those that are regularly visited by tourists (Fowler 1999). Approach distance can influence the response, with closer approaches provoking stronger responses (Beale and Monaghan 2004, Holmes et al. 2005, Ellenberg et al. 2006). The time required for behavioural patterns to return to

undisturbed l evels m ay be i nfluenced by a nu mber o f factors, i ncluding the du ration o f the disturbance (Rees et al. 2005).

At Marion Island (290 km²; 46°54'S, 37°45'E), most king penguins *Aptenodytes patagonicus* breed on beac hes on t he north and eas t coasts and some beaches are only used for roosting (Crawford et al. 2003). During the 1800s, king penguins were hunted on the island (Cooper and Avery 1986), but Marion I sland and P rince E dward I sland (44 km²; 46°38'S, 37°57'E) (together the Prince Edward Island group) were declared a Special Nature Reserve in 1995 in terms of the Environmental Conservation Act (Act No. 73 of 1989). Consequently, no tourism is allowed at the islands under the National Environmental Management: Protected Areas Act (Act No. 57 of 2003). However, there has been a permanent human presence on the island since 1948 when a research s tation was es tablished on t he nor theast c oast. Most logistic a ctivities and i ncidental disturbances occur at the research station and nearby adjacent areas (Hänel and C hown 1998, Wheeler et al. 2009). Between t en and fifteen personnel are stationed on the island throughout the year; the number of people at the station increases to approximately 100 people during the annual resupply period (April to May). Construction of a new station, adjacent to the station currently in use, commenced in 2003 and was still ongoing when this study was completed in 2006. This resulted in additional voyages and more personnel to the island.

King penguins can be disturbed by biological research (Crawford et al. 2003), logistic activities and incidentally by island personnel. At Marion Island, groups close to the station are passed by almost every day, especially during the annual resupply periods and construction phases. The aims of this study w ere to compare the effects of hu man approaches on br eeding and non - breeding groups of king penguins at Marion Island, and to investigate whether or not duration of visit influenced the response behaviour of birds. The influence of starting distance of approach was also considered.

Methods

In A pril and M ay 2006, s tandardised s ingle-person approaches were m ade t o breeding (guarding phase) and non-breeding groups of king penguins on five beaches: King Penguin Bay, Pinnacle Beach, Blue Petrel Bay, Sealer's Beach and Archway Bay (Figure 1). Approaches were made by one of three researchers. Before field work was conducted, approachers practiced to estimate distances in the field by placing a pole at 5 m to visualise the correct distance. Prior to approaches, a s ubsection o f pen guins present on t he bea ch w as filmed f or five minutes. A pedestrian wearing standardised clothing then approached the group at an av erage speed of one step per second to a distance of 5 m from the nearest penguins. The starting time, number of steps taken (equivalent t o distance bet ween appr oacher and group) and time spent at the group was recorded on di ctaphone, and the behaviour of t he pen guins was filmed during t he approaches. Due to differences in terrain, starting distances ranged from 30.2 m to 62.8 m. At the end o f all appr oaches, t he pedes trian s pent one minute a t 5 m from t he pen guins, first standing and then crouching to i mitate typical tourist behaviour. For short-duration visits, the pedestrian then retreated al ong t he approach route t o t he s tarting pos ition. For long-duration visits, the pedestrian remained at the penguins for a further five minutes, moving around on t he beach at approximately 5 m from the penguins, and then retreated. After approaches, the behaviour of t he peng uins was filmed f or a further five minutes. Weather c onditions and t he slope of the beach area were noted. Although approaches were repeated on the same beaches during the study period, no groups were approached more than once a day.

Distances to groups where behaviours occurred were worked out through the steps counted on the dictaphone and using the average length of a pace of the approachers (0.65 m, 0.70 m or 0.70 m r espectively). The r esponses o f penguin groups during app roaches w ere anal ysed b y determining the di stance from t he penguins at which t he first penguin s tarted to walk and the

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distance from the penguins at which more than 50% of penguins were walking. The distance at which more than 50% of penguins became alert (startle reaction) was also estimated.

The behaviour of penguins during the pre-approach period, the five minutes that researcher spent at the penguins and the post-approach period were analysed through Instantaneous Scan Sampling (Altmann 1974). Approximately 20–30 penguins were scanned on the video tapes and behaviour was recorded at 30 second intervals. Behaviour categories used were rest (all inactive behaviours such as resting (standing or lying) and sleeping); vigilance (head turns); comfort (preening, raising f lippers, tail-wagging and full bod y s tretches); pa rent-chick i nteractions (begging f rom parent, feeding o f chick, al lopreening); aggressive behaviours (threats and aggression towards o ther adul ts o r c hicks (Jouventin 1982, Marchant a nd H iggins 1990); and walking.

Generalised Linear Models with the binomial distribution and the logistic link function (Genstat 9 2005) were used to determine the effects of pedestrian disturbance on the penguins. Events that occurred at low frequencies were not modelled. Behavioural categories for which the effects of disturbance were modelled were rest, vigilance and comfort. Explanatory variables included in the model were whether groups were breeding or not; duration of approach; starting distance of approach; stage of approach; slope of the beach; history of disturbance; weather; and identity of approacher. Duration o f appr oach w as s cored as 1: long-duration visit, 2: short-duration visit. Approaches were categorised according to the distance from the penguins at which approaches were s tarted 1: short-distance approaches (30.2 m–37.4 m); 2: medium-distance approaches (39.8 m–49.3 m); and 3 : long-distance approaches (50.6 m–62.8 m). These c ategories w ere determined by dividing approaches according to starting distances into three categories, so that each category had a similar number of approaches. For stage of approach, behaviours recorded before appr oaches w ere all g iven a s ingle t ime-stamp ("before"). B ehaviours recorded dur ing

and after approaches were time-stamped according to the time elapsed since the start of the approach (e.g. "Start + 30 seconds") or end of the approach (e.g. "End + 30 seconds"). Groups were considered to have recovered from the disturbance when the probability of performing a behaviour after the disturbance was similar to the average probability prior to disturbance. The slope of each beach area was scored as 1: flat, 2: medium or 3: steep. Blue-Petrel Bay and Pinnacle Beach (less-frequently visited beaches) were visited every 7–10 days by researchers to record tagged southern elephant seals (*Mirounga leonina*) (Pistorius et al. 1999, Anon 2004), while King Penguin Bay, Sealer's Beach and Archway Bay (more frequently-visited beaches) were visited by these researchers as well as by other researchers *en route* to their study sites. Weather conditions were scored as 1: calm conditions (no precipitation and no to light wind), 2: precipitation (rain, snow or ice pellets) or 3: moderate to strong wind blowing (with no precipitation). Because three researchers with different heights (1.54 m, 1.67 m and 1.71 m) performed the single-person approaches over the study period, the identity of the approacher was also considered as an explanatory variable. When explanatory variables were not significant in a model, they were excluded and the model was re-run for the specific behaviour. Generalised Linear Model results were back-transformed to probabilities to facilitate interpretation.

Results

A total of 23 approaches was analysed, of which 11 were short-duration visits and 12 were long-duration visits. During approaches to breeding groups, a penguin was walking at the start of one of the approaches. During three approaches, no penguins walked. For breeding groups where at least one penguin walked during the approach (n=10), the mean distance between approacher and group at which the first penguin in a breeding group started walking was 26.8 m (range 9.2–48.8 m). At least one penguin walked in all non-breeding groups (n=9) and the mean distance at which the first penguin in a non-breeding group starting walking was 28.0 m (range

11–58.25 m, n=9). A Mann-Whitney test indicated that the distance at which the first penguin started to walk in breeding and non-breeding groups did not differ significantly. The greater the starting distance of the approach, the greater the distance at which the first penguin began to walk. This was true for both breeding groups (Figure 2a, r=0.74, P=0.007, one-sided test) and non-breeding groups (Figure 2b, r=0.62, P=0.038, one-sided test). Approaches that did not correspond to this pattern were the approaches to breeding groups that started at 39.8 m and 35.6 m and the approach to a non-breeding group that started at 54.5 m.

More than half of the group walked during approaches to four non-breeding groups. The mean distance at which these penguins responded was at c. 10 m away from the approacher (sd= 4.0, range 5–14.2 m, n=4). In groups of breeding birds, it was never the case that more than half of the penguins walked. It was rare for more than half the birds in a group to become alert – this occurred in one breeding group at a distance of 32.6 m, and two non-breeding groups at 17.9 m and 14.2 m.

The results of the Generalised Linear Models (GLM) are given in Table 1 and Figures 3–6. Penguins were less likely to be resting during the five minutes the approacher spent at the group than during the pre-approach period (Figure 3). During the five minutes spent at the penguins, the probability of resting was the lowest after 240 seconds spent at the group, although it increased to pre-approach levels during the 30-second period thereafter (Figure 3). The probability of resting decreased during the first 90 seconds of the post-approach period. It then increased once again but did not return to pre-approach levels during the five minutes of observation. The probability of resting at 270 seconds after approach was 8.4% and 11.8% smaller than pre-approach levels for penguins in breeding and non-breeding groups respectively (Figure 3). The GLM (Table 1) indicated that penguins in breeding groups were more likely to be resting than those in non-breeding groups, and this applied before, during and after approaches

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(Figure 3). The model also showed that penguins on frequently-visited beaches were more likely to be resting than those on beaches that were less-frequently visited. Penguins were more likely to be resting when beaches had medium slopes than when beaches had flat slopes. Penguins were more likely to be resting during precipitation than in its absence, but less likely to be resting in windy conditions than during calm conditions. The duration of the visit, starting distance from the group and approacher identity did not influence the probability of resting (Table 1).

The probability of vigilance was greater while the researcher was at the group than during the pre-approach period (Figure 4). It was greatest at 240 seconds, when the probability of being vigilant was 43.1% larger than pre-approach levels. Penguins were less likely to be vigilant after short-duration visits than after long-duration visits (Table 1). The probability of vigilance returned to pre-approach levels after 90 seconds for short visits and after 270 seconds for long visits (Figure 5). The probability of vigilance was lowest at the end of the post-approach period (Figure 5). According to the GLM, penguins on more-frequently visited beaches were less likely to be vigilant than those on less-frequently visited beaches. The probability of vigilance was greater during medium-distance and long-distance approaches than during short-distance approaches, and penguins on beaches with medium and steep slopes were more likely to be vigilant than those on beaches with flatter slopes. The breeding status of penguins, weather conditions and the identity of the approacher did not influence the probability of vigilance (Table 1).

Penguins were less likely to perform comfort behaviours during the five minutes the researcher spent at groups than during the pre-approach period (Figure 6). During the five minutes the researcher spent at the group, the probability of penguins performing comfort behaviours was the lowest at 270 seconds (62.2% and 57.5% lower than before approaches for birds in breeding and non-breeding groups, respectively). The probability of comfort behaviours by birds in breeding and non-breeding groups increased after approaches and was higher at 270 seconds

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than during the pre-approach period. (Figure 6). The GLM (Table 1) indicated that comfort behaviours were less likely for penguins in breeding than non-breeding groups. This was true before, during and after approaches (Figure 6). Penguins were also less likely to perform comfort behaviours after short-duration visits than after long-duration visits (Table 1). At 270 seconds of the post-approach, the probability of non-breeding birds performing comfort behaviours after the long-duration visit was 16.6% larger than during the pre-approach period (Figure 7). A similar trend was found for breeding groups. Other results of the GLM were that penguins were less likely to perform comfort behaviours during medium-distance than short-distance approaches and on beaches with medium than flat slopes. Penguins were less likely to perform comfort behaviours during precipitation than in its absence. The identity of the approacher did not influence the probability of performing comfort behaviours (Table 1).

Discussion

Behavioural responses to disturbance

Penguins may perceive human visitors as potential predators (Frid and Dill 2002). When approached, birds can either defend themselves or flee (Anderson and Keith 1980, Burger 1982). Optimality models predict that prey will remain in a threatening situation until the costs of staying exceed the costs of fleeing from the potential predator (Ydenberg and Dill 1986). Escaping is more costly for breeding than for non-breeding individuals, because breeding animals risk losing offspring. Breeding groups should therefore be less likely to flee when approached by predators than non-breeding groups, but as a result may experience higher stress levels than non-breeding groups (Harris 2005). This prediction was born out by the results of this study, king penguins in breeding groups were more likely to be resting (less likely to move away) than those in non-breeding groups, but as likely as non-breeding penguins to be vigilant when disturbed. The distance at which the first penguin in a group started to walk when approached by a pedestrian did not differ significantly between breeding or non-breeding

groups, but group movements (where more than 50% of penguins in a group started to walk away) occurred only in non-breeding groups.

The duration of disturbance can influence the time wildlife needs after disturbance events to recover to pre-disturbance levels. Rees et al. (2005) found that whooper swans *Cygnus c. cygnus* were alert for longer periods when disturbed by pedestrians than by faster-moving vehicles such as bicycles, motor vehicles and aircraft. For king penguins, the duration of the visit did not influence the probability of resting, but penguins were more likely to be vigilant and to perform comfort behaviours after long-duration visits than after short-duration visits. Comfort behaviours are often performed as displacement behaviour in response to disturbance (Kortmulder 1998, Jouventin 1982, Holmes et al. 2005); thus this result suggests that king penguins perceived longer visits as more threatening than shorter visits.

The distance at which animals become aware of a potential predator (the "alert distance"; Stankowich and Coss 2006) and the distance at which animals take flight correlate positively with the distance from the animal at which an approach starts (Blumstein 2003). It has therefore been recommended that starting distances should be included as a covariate in studies investigating human disturbance (Blumstein 2003). Animals that flee after detecting a predator from afar reduce both the cost of escaping and the cost of allocating attention to the predator (Dukas and Kamil 2000). However, beyond a certain distance, there will be a delay in detection and response to a predator (Stankowich and Coss 2006). Although this distance is likely to be species-specific (Blumstein 2003), there may also be individual variation within species, with more reactive (possibly less-habituated) individuals responding at greater distances than less-reactive individuals (Stankowich and Coss 2006). In our study, the first penguin in a group to walk started earlier when approaches began at greater distances away, supporting the finding of Blumstein (2003) that starting distance influences the distance at which animals respond to

disturbance. Penguins were al so m ore v igilant w hen appr oaches w ere s tarted at di stances greater than 38 m; perhaps because they had more time to observe the approacher.

An approacher on a steep slope may appear larger to birds at the bottom than an approacher on a flat slope. Approaches on s teeper slopes seem to be m ore direct and can therefore be more disturbing than a m ore i ndirect appr oach (Frid and D ill 2002). At Marion I sland, peng uins o n beaches with steep slopes were more likely to walk away from the approacher than groups on beaches with flatter slopes. The probabilities of being vigilant and performing comfort behaviours were also larger for groups on beaches with steep slopes than groups on beaches with flatter slopes.

History of disturbance can influence the responses of wildlife and animals may become habituated to disturbance (e.g. van Heezik and S eddon 1990, Yorio and Boersma 1992, Burger and G ochfeld 1999). H owever, habituation depends on the frequency, nature (Fowler 1999, Ratz and T hompson 1999) and predictability of the disturbance (van Polanen Petel et al. 2008) and the potential to habituate may be s pecies-specific (Ellenberg et al 2006). In this study, king penguins on beaches that were frequently visited were more likely to be resting, less likely to be vigilant and less likely to perform comfort behaviours when disturbed than were groups on less-frequently visited beaches. This suggests that king penguins at Marion Island have habituated to the current level of pedestrian visits to these beaches.

The response behaviour of animals can be influenced by weather conditions. Wind conditions seemed to influence the behaviour of Emperor Penguin (*Aptenodytes forsteri*) chicks (Giese and Riddle 1999), but t he resting and s leeping t ime budg ets o f b rooding king penguins were no t influenced by wind conditions (Dewasmes et al. 2001). In windy conditions, king penguins emit more display calls for partner recognition than during calmer conditions (Lengagne et al. 1999).

At Marion Island, some aspects of king penguin behaviour were influenced by weather, with penguins apparently being more active in the presence of moderate to strong winds or in the absence of precipitation (less likely to be resting and more likely to be performing comfort behaviours) than during calmer conditions and when precipitation was falling. This is probably due to thermoregulation. Wind conditions seemed to influence the behaviour of Emperor Penguin, *Aptenodytes forsteri*, chicks, with chicks being more vigilant and tending to stand together in the presence of wind than during calm conditions (Giese and Riddle 1999).

Management considerations

Because research at the king penguin colonies at Marion Island mainly involves remote censusing, four in 2005/06 (Crawford et al. 2003, Anon 2005), most disturbance of beach groups is by logistic activities and through incidental pedestrian disturbance by island personnel. To minimise the level of incidental disturbance to animals on the island, Marion Island has been demarcated into management zones (Figure 1, Prince Edward Islands Management Plan Working Group 1996, Chown et al. 2006). Most logistic activities occur in the Service Zone (Zone 1) that includes the permanent research station and its immediate surroundings (Hänel and Chown 1998, Wheeler et al. 2009). The Natural Zone (Zone 2) forms a buffer zone around Zone 1 and personnel are generally issued with permits to enter these two zones. The remainder of the island, with the exception of areas around the field huts (Zone 2) and certain Limited Access Zones (Zone 4), forms the Wilderness Zone (Zone 3). Only approved research activities are conducted in the Wilderness Zone, and Special Permits are required to access Zone 4 areas.

Two king penguin colonies, namely Trypot Beach and Ship's Cove, fall within Zone 2 and are therefore frequently visited by pedestrian groups, which are especially large during the annual resupply period in April/May each year. This period coincides with the guarding phase for king

penguins at Marion Island. Although these two beaches are not considered to support breeding colonies, a few chicks have been observed at Trypot Beach. Penguins on Trypot and Ship's Cove beaches seem to have habituated to human disturbance and often approach stationary pedestrians (personal observation). Such apparent curiosity has also been observed at Macquarie Island (Holmes et al. 2007a). Because groups of king penguins on frequently-visited beaches reacted less to pedestrian approaches than those on less-frequently visited beaches, and because king penguins at Trypot Beach and Ship's Cove are mainly non-breeding, the zoning system is effective in protecting this species from incidental disturbance. The continuation of frequent visit to these two king penguin sites and not to other beaches is recommended. According to the new, but not yet implemented Prince Edward Islands Environmental Management Plan (Chown et al. 2006), the team leader may decide on the number of pedestrians that may visit the beaches and the time of day. It is also stipulated that a guide accompanies the group. The recommendation of a guide is strongly supported as visitors unfamiliar to the island will not know where to walk at the beaches and may approach penguins closer than the recommended distance due to the terrain when penguins stand at the bottom of slopes.

Due to the asynchronous initiation of the breeding cycle in this species, at any time there may be non-breeding individuals between breeding adults in a beach group (Stonehouse 1960). Because most non-breeding individuals are likely to move when humans are at 10 m or less (this study), close approaches may result in increased territorial aggression (Hughes et al. 2008, Holmes 2007), loss of eggs and chicks (Hughes et al. 2008) and temporary abandonment of chicks by the breeding birds (Holmes 2007). At the Falkland Islands, king penguins seemed less defensive when tourists were maintaining the minimum approach distance of six metres (Otley 2005). In this Marion Island study, king penguin groups were approached by a single pedestrian and groups were not approached more than once a day. Penguins are likely to

respond more when the number of visitors and the frequency of visits are increased; thus the responses reported he re are likely to be minimum responses to visits. The new, but not yet implemented Prince E dward I slands Environmental Management P lan (Chown et al. 2006), recommends a minimum approach distance of 15 m to breeding king penguins. Considering that there m ight be br eeding pen guins bet ween no n-breeding peng uins an d t hat br eeding s tatus might onl y be visible f rom c loser di stances, a pr ecautionary appr oach of 15 m t o al l peng uin colonies is recommended. Furthermore, visitors should be on t he look-out for signs of agitation by peng uins, and should retreat if t hese are obs erved. Holmes (2007) suggested the us e o f vigilant and agonistic behaviours as telltale signs of disturbance in king penguins.

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penguin *Spheniscus magellanicus* behaviour and breeding success. Bird Conserv Int 2: 161–173
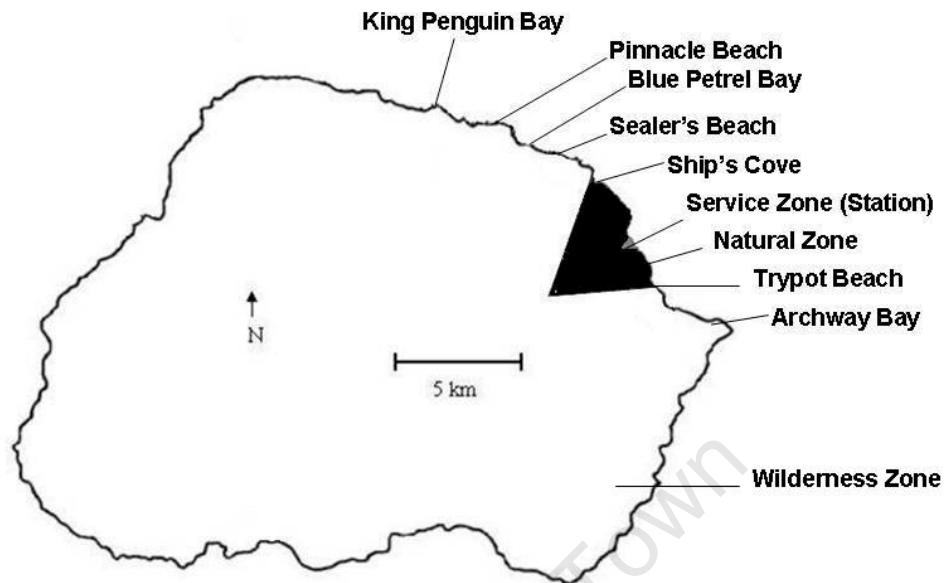
Figure 1 Outline of Marion Island indicating the location of the five beaches (King Penguin Bay, Pinnacle Beach, Blue Petrel Bay, Sealer's Beach and Archway Bay) where single-person approaches were made to king penguins in 2006. The Service, Natural and Wilderness Zones are indicated.
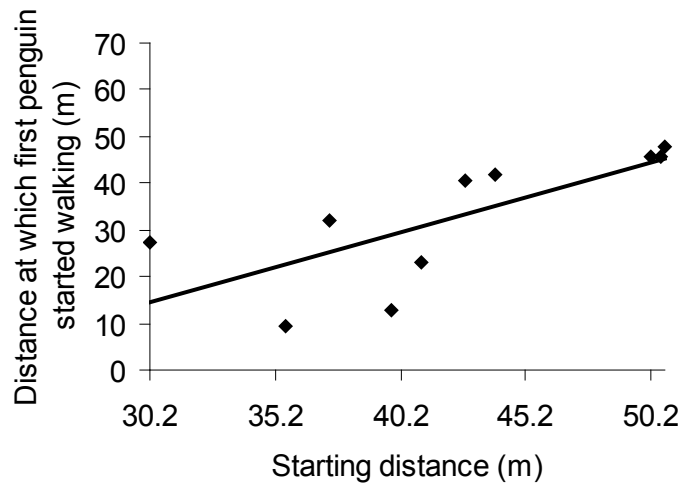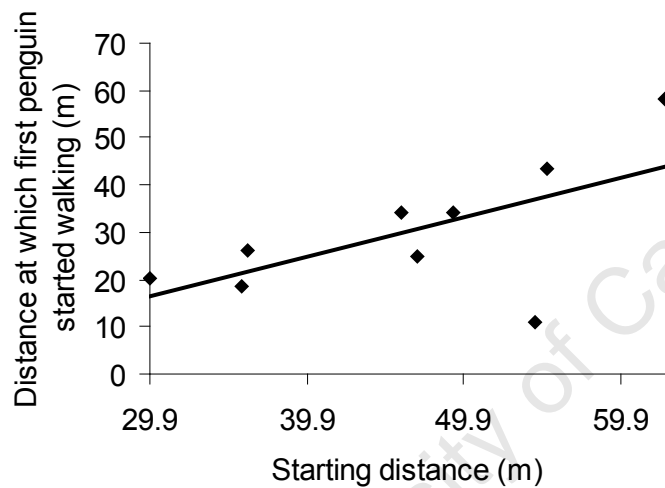
Figure 2 The distance at which the first king penguin in a beach group at Marion Island started to walk relative to the starting distance of approach. a) Breeding groups (10 approaches), b) Non-breeding groups (9 approaches). Regression lines indicating the trends were significant (see text).

◇ Non-breeding ■ Breeding

Figure 3 The modelled probability of king penguins (breeding and non-breeding groups, 14 and 9 approaches respectively) resting in response to standardised single-person approaches at Marion Island in 2006. Probabilities are shown for 30-second intervals during the five-minute period that the approacher stood at the beach groups, and during the five-minute period after the approacher had retreated. The modelled probability value for resting prior to the approach is indicated by the dashed line for breeding groups and the dashed-dot line for non-breeding groups.

while approacher at the penguins   after approacher retreated
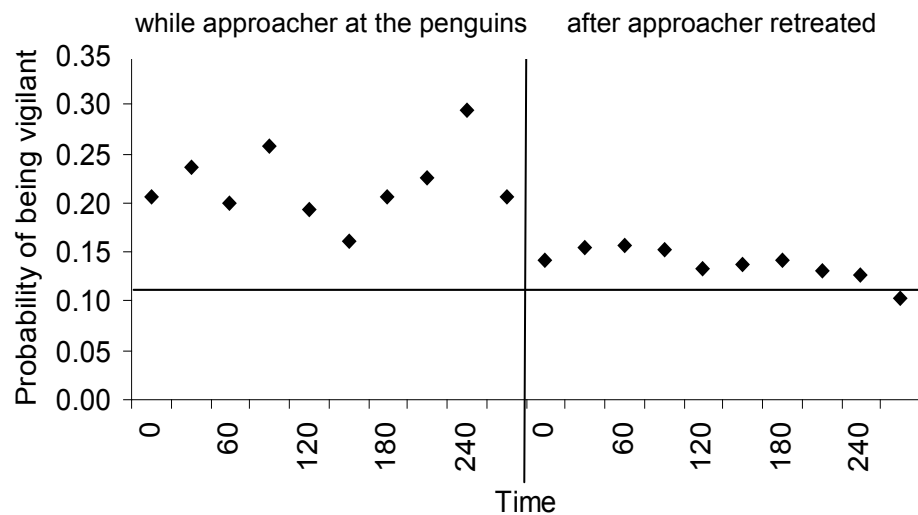
Figure 4 The modelled probability of king penguins (breeding and non-breeding groups combined) being vigilant in response to standardised single-person approaches (n = 23) at Marion Island in 2006. Probabilities are shown for 30-second intervals during the five-minute period that the approacher stood at the beach groups, and during the five-minute period after the approacher had retreated. The modelled probability value for vigilance prior to the approach is indicated by the solid line.
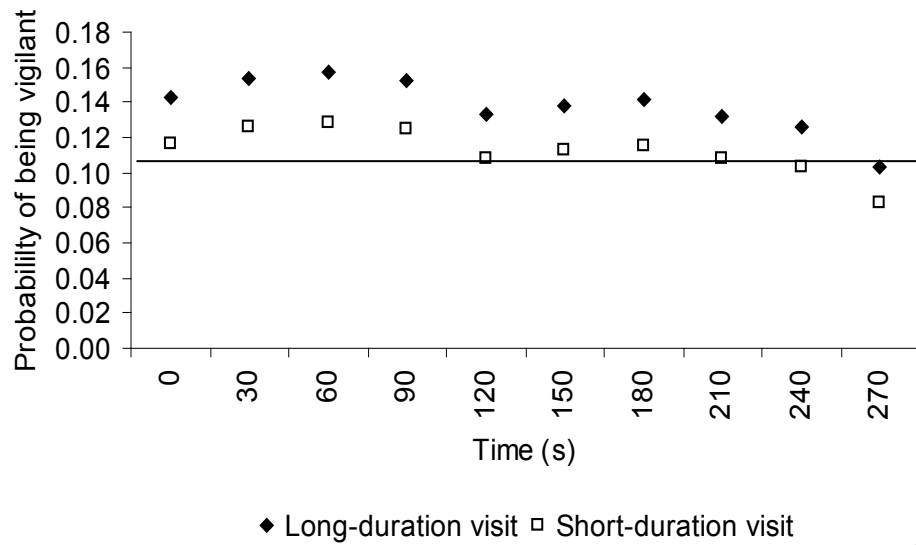
Figure 5 The modelled probability of groups of king penguins (breeding and non-breeding groups combined, n=23 approaches) at Marion Island being vigilant after short-duration and long-duration visits by a single pedestrian. The modelled probability value for vigilance prior to the approach is indicated by the solid line.
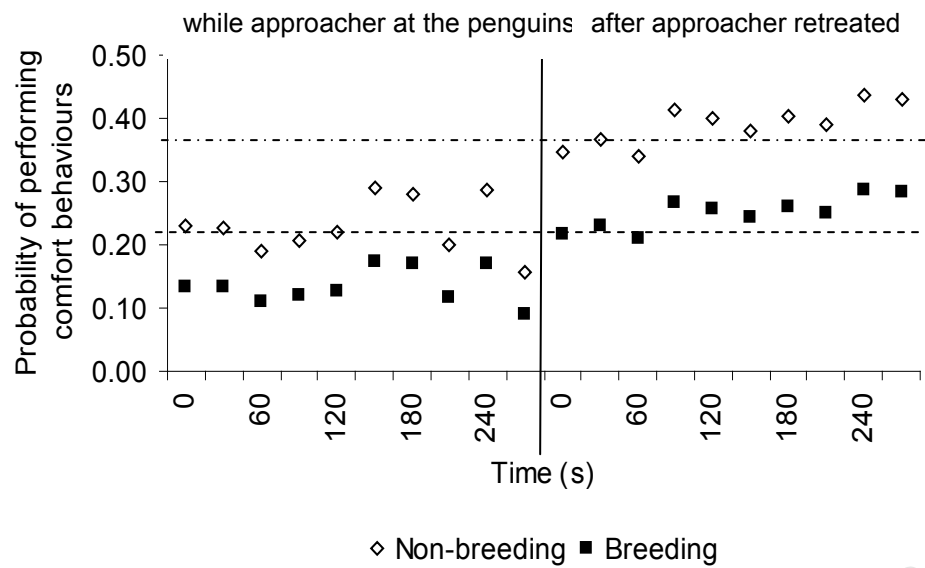
Figure 6 The modelled probability of king penguins (breeding and non-breeding groups, 9 and 14 approaches respectively) performing comfort behaviours in response to standardised single-person approaches at Marion Island in 2006. Probabilities are shown for 30-second intervals during the five-minute period that the approacher was at the penguins, and during the five-minute period after the approacher had retreated. The modelled probability value for performing comfort behaviours prior to the approach is indicated by the dashed line for breeding groups and the dashed-dot line for non-breeding groups.

◆ Breeding, long-duration visit   ■ Breeding, short-duration visit

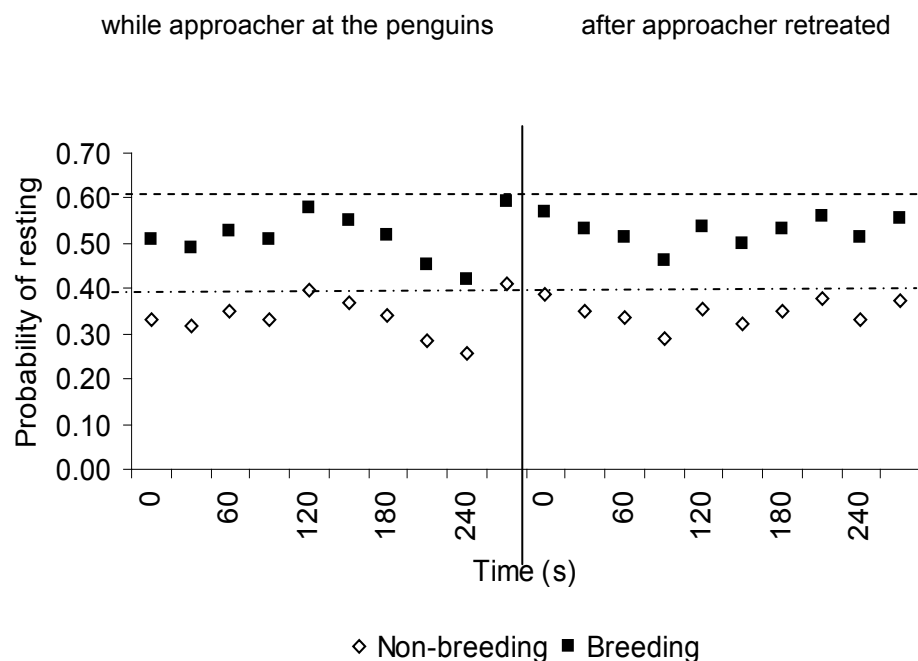△ Non-breeding, long-duration visit   × Non-breeding, short-duration visit

Figure 7 The modelled probability of king penguins (breeding and non-breeding groups, 9 and 14 approaches respectively) at Marion Island performing comfort behaviours after short-duration and long-duration visits by a single pedestrian. The modelled probability value for performing comfort behaviours prior to the approach is indicated by the dashed line for breeding groups and the dashed-dot line for non-breeding groups.

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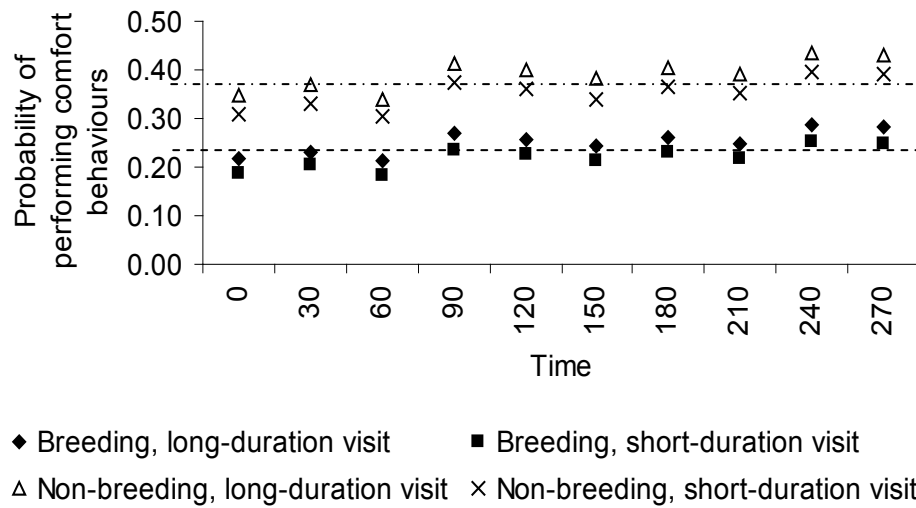Table 1 Results of the Generalised Linear Modelling of three behavioural responses (resting, vigilance and comfort behaviour) of king penguins to 23 standardised single-pedestrian approaches at Marion Island in 2006 . The responses of: birds in breeding groups are given relative to those in non-breeding groups; birds on frequently-visited beaches to those on less-frequently visited beaches; birds subjected to short-duration visits to those subjected to long-duration visits, birds subjected to medium-distance and long-distance approaches to those subjected to short-distance approaches, birds on medium and steeply sloped beaches to those on flat beaches, birds approached during precipitation relative to those approached in the absence of precipitation, and birds approached when a moderate to strong wind was blowing to those approached under calm conditions. Explanatory variables that were not significant were excluded from models. Bold font indicates significant explanatory variables.

Explanatory variables	Resting		Vigilant		Comfort	
	Estimate	(se) t_{517}, P	Estimate	(se) t_{517}, P	Estimate	(se) t_{514}, P
Breeders	**0.739**	**(0.053) 13.97, P<0.001**	Excluded		**−0.656**	**(0.072) −9.14, P<0.001**
Frequently visited beaches	**0.204**	**(0.052) 3.95, P<0.001**	**−0.754**	**(0.088) −8.59, P<0.001**	**−0.243**	**(0.106) −2.29, P=0.022**
Short-duration visits	–	–	**−0.234**	**(0.070) −3.33, P<0.001**	**−0.170**	**(0.058) −2.95, P=0.003**
Starting distance > 38 m	–	–	**0.211**	**(0.088) 2.4, P=0.017**	**−0.309**	**(0.095) −3.26, P=0.001**
Starting distance > 50 m	–	–	**0.340**	**(0.110) 3.1, P=0.002**	−0.043	(0.1100) −0.39, P=0.70
Medium slope	**0.254**	**(0.059) 4.27, P<0.001**	**0.397**	**(0.083) 4.8, P<0.001**	**−0.364**	**(0.080) −4.53, P<0.001**
Steep slope	−0.0595	(0.0477) −1.25, P=0.21	**0.508**	**(0.073) 6.92, P<0.001**	0.0767	(0.0629) 1.22, P=0.22
Precipitation falling	**0.156**	**(0.048) 3.25, P=0.001**	–	–	**−0.256**	**(0.070) −3.67, P<0.001**
Moderate to strong wind blowing	**−0.306**	**(0.096) −3.17, P=0.002**	–	–	0.197	(0.136) 1.46, P=0.15
Identity of approacher	Excluded		Excluded		Excluded	
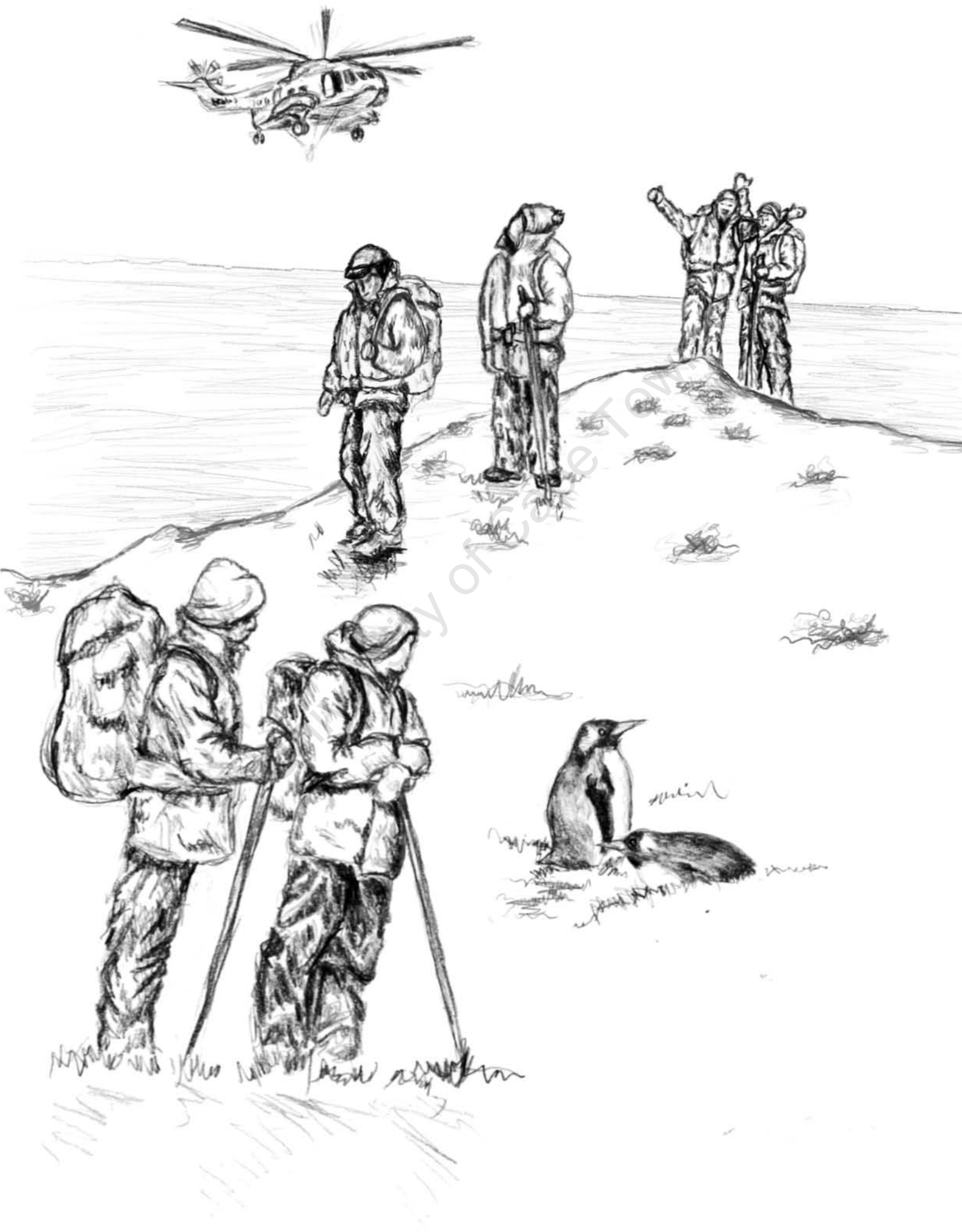
The effect of helicopter flights on seabirds at sub-Antarctic Marion Island

Abstract

At sub-Antarctic Marion Island, personnel and equipment are transferred from ship to island by helicopters. Flight operations can negatively impact seabirds, especially during sensitive breeding phases. Either quantitative behavioural observations or counts were made of gentoo penguins (*Pygoscelis papua*) (during the brooding and guarding phases), grey-headed albatrosses (*Thalassarche chrysostoma*) (chicks close to fledging), Crozet shags (*Phalacrocorax [atriceps] melanogenis*) (during the early incubation phase) and king penguins (*Aptenodytes patagonicus*) (non-breeding), before (control) and during logistic flight operations. No nest desertions or predation events were observed, but all three species responded to increasing levels of helicopter disturbance by being more likely to be alert or responsive. When a helicopter was close to a colony, gentoo penguins were more likely to attend to their nests than before. Penguins exhibited some signs of habituation to repeated flights. Grey-headed albatrosses and Crozet shags were less likely to perform comfort behaviours at high levels of disturbance. Behavioural responses were generally mild and usually transitory. Non-breeding king penguins moved away from a beach close to the source of helicopter disturbance at the island. Adherence to the current system of temporal zoning, which ensures that flight operations take place outside of the main breeding seasons of most seabird species, is recommended.

Introduction

In the Antarctic and sub-Antarctic, the only viable means of transport is often by aircraft, due to the harsh environment (Hughes et al. 2008). However, aircraft operations can cause disturbance to wildlife, because animals may perceive overflying craft as a threat (Cooper et al. 1994), even though the stimulus might be more auditory than visual (Giese and Riddle 1999). Because animals have evolved antipredatory responses to generalised threatening stimuli, disturbances

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are lik ely t o l ead t o t rade-offs bet ween av oidance behav iours and o ther fitness-enhancing activities (Frid and Dill 2002).

Aircraft disturbance can result in responses which vary from minor changes in behaviour such as increased l evels of al ertness and c hanges in t he us ual pa tterns o f c alling, di splays o r movements, to highly stressed states with large proportions of birds walking, running or "tobogganing" (Wilson et al . 1991, Harris 2005). For ex ample, em peror peng uin (*Aptenodytes forsteri*) chicks exposed to helicopter flights became more vigilant when the helicopter approached and 69% of them either walked or ran when the helicopter passed overhead (Giese and Riddle 1999). At Macquarie Island, 7 000 king penguins (*A. patagonicus*) stampeded and died due t o t rampling in 199 0, m ost l ikely due t o an ai rdrop and flypast by a fixed-wing aeroplane (Rounsevell and B inns 1991, C ooper et al . 1994). A ircraft di sturbance can b e especially har mful du ring s ensitive br eeding ph ases (Giese and R iddle 1999) . Non-breeding birds are more likely to flee from the disturbance, but breeding birds are reluctant to abandon eggs or chicks (Fjeld et al. 1988, Delaney et al. 1999). Breeding birds can therefore experience higher stress l evels bef ore deserting their nests (Harris 2005). If levels of disturbance are high, they might abandon their nests, potentially resulting in loss of eggs or chicks to breakages, trampling, c hilling or pr edation by s cavenging birds (Thompson 1977). Aircraft disturbance can also cause delays in partner change-overs at nests (Wilson et al. 1991).

Seabird r esponses to f lights are s pecies- and s ituation-specific (Southwell 2005) . A t M arion Island, brooding and guarding wandering albatrosses (*Diomedea exulans*) and their chicks exhibited no di scernable reactions during flights, but king penguin adults and c hicks showed signs o f di stress (Cooper et al . 1994) . A lthough k ing pen guins at S outh G eorgia s howed a tendency to habituate to r epeated flights (Hughes et al . 2008), emperor penguins in Antarctica

were unlikely to habituate to flights due to the sporadic nature of this activity (Giese and Riddle 1999).

The responses of animals can intensify with increasing levels of aircraft disturbance. Ringed seals (*Phoca hispida*) escaped into the water in larger proportions and at greater distances when disturbed by a helicopter than when approached by a fixed-wing aircraft which was less noisy (Born et al. 1999). Increasing numbers of Brünnich's guillemots (*Uria lomvia*) fled with increasing helicopter noise (Fjeld et al. 1988) and Mexican spotted owls (*Strix occidentalis lucida*) (Delaney et al. 1999) were only likely to take flight when a helicopter was nearby. If birds perceive aircraft as potential predators, then the greatest response should be elicited when aircraft are nearby, because the risk of predation increases as a predator approaches a nest (Beale and Monaghan 2004).

Due to these detrimental impacts on wildlife, there have been calls for the development of practical guidelines for aircraft operations (Harris 2005) and many countries have stipulated regulations regarding flight paths and distances from sensitive areas in their management plans (e.g. Heap 1994, Prince Edward Islands Management Plan Working Group 1996, DoC 1998, Modig et al. 1999, Australian Antarctic Division 2002). However, few regulations and guidelines have been based on scientific information on the circumstances, nature and extent of disturbance caused by aircraft (United Kingdom 2001). Quantitative studies are therefore needed to inform the development and improvement of policy (Giese and Riddle 1999, Southwell 2005). Aircraft disturbance studies have mainly been conducted on Adélie (*Pygoscelis adeliae*) (e.g. Ainley et al. 1983, Wilson et al. 1991, Giese 1996), emperor (e.g. Regel and Pütz 1997, Giese and Riddle 1999) and king (e.g. Cooper et al. 1994, Hughes et al. 2008) penguins, although interest in the responses of other bird species has recently been expressed (Hughes et al. 2008).

At Marion Island (290 km²; 46°54'S, 37°45'E), helicopters are mainly used to transfer personnel and equipment from the supply vessel to the research station on the northeast coast of the island. This mainly occurs during the annual resupply period in April and May. During this time, flights to other areas of the island are also undertaken for scientific and logistic purposes, such as the restocking of field huts. The construction of a new station, adjacent to the one currently in one, commenced in 2003 and was still ongoing when this study was completed in 2007. Additional flights were necessary during construction periods that took place in other months of the year. At Marion Island, qualitative observations of the response behaviour of king penguins, gentoo penguins (*P. papua*), wandering albatrosses, sub-Antarctic skuas (*Catharacta skua lonnbergi*) and giant petrels (*Macronectes* spp.) have been made during helicopter flights (Cooper et al. 1994). The aims of the present study were to quantify the behavioural responses of gentoo penguins, grey-headed albatrosses (*Thalassarche chrysostoma*), Crozet shags (*Phalacrocorax [atriceps] melanogenis*) and king penguins to repeated helicopter flights.

Methods

<u>Types of transport</u>

During the study period, a Bell 212 and a Sikorsky S61L were used for flight operations. The Bell 212 was powered by a twinned turboshaft PT6T Twin-Pac engine (Bell 212 Rotorcraft Flight Manual 1998) and the Sikorsky S61L was powered by two General Electric CT58-140-1 mfg shaft-turbine engines (L. Sonya, Sikorsky Customer Service Engineer, personal communication). The frequency of noise of the Sikorsky S61L is higher than the frequency of the Bell 212, but the Bell 212 is audible from further away (D.Hilland, personal communication). In October 2007 a Kamov KA32 helicopter was used for the placement of new field huts around the island. This aircraft is powered by two Klimov TV3-117MA turboshaft engines (http://www.aerospace-technology.com/projects/kamov32/). Passengers were transported from the ship to land in

November 2004 in a Gemini fast rescue craft (5 m with two 40 HP Mariner Outboard engines, Hall, personal communication).

Gentoo penguins

Quantitative obs ervations o f t he behav iour of adult g entoo pengui ns w ere m ade ov er t wo breeding seasons du ring the guarding (2004) a nd br ooding (2005) pha ses. The B ell 212 an d Sikorsky S 61L hel icopters w ere us ed dur ing these per iods and the helicopters m ainly flew between the ship (c. 50–100 m from shore) and the research station. Helicopters flew at heights from 500 ft (152.4 m) to gr ound l evel at t he s tation w hen i t landed (D. K ohl, pe rsonal communication). Observations were made at a gentoo penguin colony close to Trypot Beach (c. 0.88 km south of the station) and at Duiker's Point (c. 1.25 km north of the station) (Figure 1). Some flights passed close to and at times directly over the colonies. The ship was more often south of the station than north of the station and more flights occurred over the Trypot area than over Duiker's Point.

During t he guarding ph ase (2004), i nstantaneous s cans (Altmann 197 4) w ere m ade o f t he behaviour of all visible birds at Trypot Beach (mean of 27 birds) and at a colony at Duiker's Point (mean of 22 birds). The position of the helicopters relative to the colony was noted during each scan. S cans w ere m ade at t hree-minute i ntervals. At Trypot B each, pr ior t o t he a rrival of the cargo ship and hel icopters at the island, control observations (n=112 scans) were made on two days (8 and 9 August) for a total of five hours. Six scans were made over 18 minutes on the first day of f lying (12 August), before flights commenced. During flight operations, observations (n=120 scans) were made at the Trypot Beach colony for a total of 6.3 hours over two days (12 and 13 August). There were no flights (and no observations) on 14 August, due to bad weather. Observations started at Duiker's Point on the third day of flights (15 August), whereafter there was anot her non -flight d ay (and no obs ervations) be fore t he fourth day of flights (17 A ugust).

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Ten hours of observations (n=211 scans) were made at the Duiker's Point colony on these two flight days. Because observations were not made on the same days at Trypot Beach and Duiker's Point, a between-colony comparison could not be made for the guarding penguins, but comparisons of the number of penguins standing, alert and performing comfort behaviours were made between the two consecutive flights days at each colony.

During the brooding phase (2005), observations were made at the Trypot Beach colony. Instantaneous scans (Altmann 1974) were made of birds on 35 nests at three-minute intervals. When partner change-overs occurred at nests, the behaviour of both partners was noted. Prior to the arrival of the ship and helicopters at the island, control observations (n=144 scans) were made over three days (19, 21 and 22 August) for a total of 6.75 hours. A total of six hours of observations (n=129 scans) were made over two days (23 and 25 August) during flight operations. There were no flights on 24 August due to bad weather.

Grey-headed albatrosses

The effect of helicopter disturbance on the behaviour of grey-headed albatross chicks (close to fledging) was investigated during flights of the Bell 212. Instantaneous scans were made of the behaviour of chicks at two of the nine study sections (see Chapter 4) of the colony on Grey-headed Ridge (c. 14.5 km from the station) (Figure 1). Section 2 (mean of 50 visible chicks) was the main demographic study colony that was visited by researchers monthly during the breeding season, in order to check nest contents. Pre-fledging chicks and breeding adults were also ringed in this section (Ryan et al. 2006). Section 2 was opposite a field hut located approximately 80 m from the ridge. The hut was intermittently occupied by humans and was restocked during the flight operations. Section 4 of the colony (mean of 32 visible chicks) was approximately 40 m farther along the ridge. Observations of the behaviour of birds in both colony sections were made from the field hut at five-minute intervals.

These ob servations w ere m ade ov er a pe riod o f four day s i n 2004 (26–29 A pril). On D ay 1 , observations were made for 1.5 hours (n=23 scans) before researchers entered Section 2 to ring chicks. The r esponse behav iour of c hicks w as r ecorded du ring an d af ter the r esearch disturbance (Chapter 4) but these data were not used in the model to determine the effects of helicopter disturbance. A helicopter flew parallel to the ridge at very close range in the late afternoon, 50 minutes after the researchers had left the ridge. Observations started five minutes after the helicopter had left and scans (n=14 scans) were made for 1.25 hours after the flight. Approximately 2.5 hours of observations were made on Day 2 (n=34 scans) and 1.5 hours (n=19 scans) on Day 3. Poor weather conditions prevented flights on these days.

On Day 4, scans were made over approximately one hour (n=13) prior to helicopter flights and approximately 1.8 hours (n=34) during helicopter operations. The position of helicopters relative to the ridge was noted during the latter scans. There were seven flights in the area of the ridge. Five of these were to the field hut, with the helicopter usually approaching the hut from inland at a height of 304.8 m (1 000 ft) before landing or hovering near the hut (D Kohl, personal communication). No observations were possible after flight operations because the researcher had to leave the area on the last flight.

In O ctober 2007 , dur ing the i ncubation pha se, fixed-point pho tographs w ere t aken at four sections on the ridge (Sections 1–4) prior to and after a series of Kamov KA32 helicopter flights to r emove t he ol d f ield hut and pl ace t he new f ield hut . A n obs erver w as on t he r idge (approximately 10 m away from Section 2, in the open) during flight operations to note any nest desertions i n t his s ection. Photographs taken be fore and a fter t he flight per iod (approximately 1.5 hours) were compared to determine any nest desertions in the four sections.

Crozet shags

The effects of helicopter disturbance (Bell 212 and Sikorsky S61L) and rescue craft disturbance on the behaviour of incubating Crozet shags were investigated in 2004 through instantaneous scans at the Trypot Beach Crozet shag colony, comprising nine nests. Observations were made on the day before flight operations commenced (17 November), on the first day of flights (18 November) and on the morning of the second day of flights (19 November). Observations were made at two-minute intervals.

Scans (n=182) were conducted over approximately 5.25 hours on the first day of observations. The ship arrived at the island after three hours of observations (n=93 scans) and its engines were audible when it was close to the coast. Passengers were subsequently transported from the ship to land in a Gemini fast rescue craft. Flight operations commenced on the following day. Observations were made for approximately 4.2 hours (n=127 scans) on the first day of flights and for approximately 2.0 hours (n=60 scans) on the following day.

The presence of roosting birds standing or sitting on the cliff at the top of the colony was noted. The presence of potential avian predators (lesser sheathbills (*Chionis minor*), sub-Antarctic skuas and kelp gulls (*Larus dominicanus*)) flying over or sitting and standing close to or in the colony was recorded. The positions of the helicopters relative to the colony were noted at each scan. Helicopters flew between the ship and the station at heights from 500 ft (152.4 m) to ground level at the station when it landed (D. Kohl, personal communication) and at times flew less than 500 ft above the colony.

King penguins

In 2005, the number of king penguins present on Boulder's Beach was counted at 15h00 over four days prior to flight operations (11–14 March). These counts were continued on the two days of continuous flight operations with the Bell 212 and Sikorsky S61L and Bell helicopters (15 and 16 March) and for six days with intermittent flights thereafter (17–22 March). When helicopters flew from the ship to the station, they flew at heights from 500 ft (152.4 m) to ground level at the station (D. Kohl, personal communication). During the six days of intermittent flights, helicopters were mainly used to lift heavy cargo at the station and the continuous hovering resulted in higher noise levels (D. Kohl, personal communication). The number of king penguins present on the four days prior to flights was compared with the number present on two days of continuous flight operations.

Statistical analyses

The behaviours of the gentoo penguins (Table 1a), grey-headed albatrosses (Table 1b) and Crozet shags (Table 1c) were categorised into states and events (after Altmann 1974). Generalised Linear Models with the binomial distribution and the logistic link function (Genstat 8.2, 2005) were used to determine the effects of helicopter disturbance on the behaviour of the birds. Events that occurred at low frequencies were not modelled. Generalised Linear Model results were back-transformed to probabilities to facilitate interpretation.

Because brooding penguins were more likely to lie on their nests but partners stood before partner change-overs at nests, only birds that were lying on their nests were considered for the analysis of the probability of standing. Guarding birds tend to stand next to their nests, so the responses of both birds at the nest and partners were recorded as they would have been difficult to distinguish from each other. Events for both phases were analysed for both the partner and

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the bird on the nest. Behaviour for grey-headed albatrosses was analysed for all chicks in both colony sections. The behaviour of all Crozet Shags at nests was analysed.

Results

Gentoo penguins

No nest desertions or predation events were observed during the periods of observation. Birds at Trypot Beach were more likely to stand during guarding than birds at Duiker's Point (Table 2a). Guarding birds were less likely to be inactive than brooding birds but during guarding, birds at Trypot Beach were less likely to be inactive than birds at Duiker's Point. On non-flight days, more guarding penguins at Trypot Beach were alert (mean=15.6%) than during the brooding phase (mean=11.7%). According to the model, guarding birds were more alert than brooding birds and during guarding, birds at Trypot Beach were more likely to be alert than birds at Duiker's Point. The percentage of penguins attending to their nests over all observations was low during both phases of breeding (guarding mean=3.73% and brooding mean=3.64%). Guarding birds were as likely to attend to their nests as brooding birds were, but guarding birds at Trypot Beach were less likely to attend to their nests than birds at Duiker's Point (Table 2b).

Brooding penguins were as likely to stand on flight days than on non-flight days but the probability of guarding birds standing was greater on flight days than on non-flight days (29.7% larger at Trypot and 5.4% larger at Duiker's Point, back-transformed results from Table 2a). During brooding birds were 7.2% less likely to be inactive but 52.7% more likely to be alert on flight days than on non-flight days. On flight days, when the engine of a helicopter was switched on (but the helicopter was not yet in the air), brooding penguins were 10.5% less likely to be inactive and 82.8% more likely to be alert than when there was no helicopter disturbance. Similar patterns were found at both colonies during guarding (Table 2b).

During flights by the Bell 212, brooding penguins were 54.1% less likely to be standing than in the absence of disturbance (Table 2a), but guarding penguins were more likely to be standing (31.2% larger at Trypot and 22.2% larger at Duiker's Point). Other behaviours did not differ significantly when the Bell 212 flew compared to when there was no disturbance. When the Sikorsky S61L was in the air, birds of both phases were as likely to stand as in the absence of disturbance (Table 2a), but brooding birds were 10.6% less likely to be inactive and 14.9% more likely to attend to their nests. They also tended to be more alert when the Sikorsky S61L flew than in the absence of disturbance (Table 2b). When a helicopter was close to the colony brooding penguins were 27.3% less likely to be inactive, 177.1% more likely to be alert and 40.5% more likely to be attending to their nests than in the absence of disturbance. Brooding birds were more likely to stand when a helicopter was close to the colony than in the absence of a helicopter, but not significantly so. Similar patterns were found at both colonies during guarding, except that guarding penguins were as likely to be standing when a helicopter was close to the colony as they were in the absence of disturbance (Table 2b).

At Trypot Beach, fewer penguins stood (Fisher's exact test, v=1, n=3402, P=0.018) or attended to their nests (Fisher's exact test, v=1, n=3217, P=0.01) during observations on the second day of flights than on the first day. The proportion of alert penguins was similar on both days (Figure 2). At Duiker's Point, fewer penguins were alert on the second day of observations (fourth day of flying) than on the first day (Fisher's exact test, v=1, n=4400, P<0.001). The proportion of birds standing or attending to their nests did not differ between the two days (Figure 2).

Grey-headed albatrosses

No nest desertions were observed in the two sections during the period of observations. Birds in Section 4 were 27.8%, 51.3% and 24.9% more likely to be standing than birds in Section 2 before research disturbance occurred on Day 1 (t_{44}=3.32, P<0.001), after the flight on Day 1

(t_{25}=2.1, P=0.036) and during the flight period on Day 4 (t_{59}=3.12, P=0.002), respectively. No other behaviours differed significantly between the sections when time periods (before, during or after disturbance) were modelled separately. When all observations were modelled, chicks in Section 4 were more likely to stand and tended to be more likely to be responsive (vigilant, threatening or aggression behaviours) than birds in Section 2, but were less likely to perform comfort behaviours and tended to be less likely to be inactive than birds in Section 2 (Table 3).

After the flight on Day 1, birds in Section 2 were 64.6% less likely to stand, 27.9% less likely to be responsive and tended to be more likely to perform comfort behaviours than before the disturbance. During flight operations on Day 4, birds in Section 2 were 20.3% more likely to stand, 57.8% more likely to perform comfort behaviours, 16.9% less likely to be inactive and 46.0% less likely to be responsive than during non-flight periods. When the helicopter was in the area of the ridge, birds in Section 2 were 63.0% more likely to stand, as likely to be inactive, 32.7% more likely to be responsive and 28.6% less likely to be performing comfort behaviour than in the absence of a helicopter. When the helicopter was close to the hut, birds in this section were 45.6% more likely to stand, 48.3% less likely to be inactive, 70.2% more likely to be responsive and 41.6% less likely to perform comfort behaviours. A similar pattern was found for Section 4 (Table 3).

In October 2007, no nest desertions were observed or were evident from fixed-point photographs of 99 nests in four sections of the colony.

Crozet shags

No nests were deserted during the observations and no predation events were observed. In the presence of potential avian predators, shags were more likely to be standing, to be alert and to be performing comfort behaviours and less likely to be inactive than in the absence of the

predators, but these results were not significant (Table 4a). Roosting birds were significantly more likely to be present in the presence of potential predators than in their absence (Table 4b).

When the rescue craft was in the water and no potential predators were around, birds were 11.8% less likely to be inactive and 49.3% less likely to be alert, but 31.9% more likely to perform comfort behaviours, than in the absence of the rescue craft or a helicopter. On flight days, birds in the absence of predators were 36.2% more likely to be alert and 16.6% less likely to perform comfort behaviours than on non-flight days. When the Bell 212 was in the air, birds in the absence of predators were 19.0% more likely to be inactive and tended to be less likely to perform comfort behaviours than in the absence of the helicopter. When the Sikorsky 61L flew, birds in the absence of predators were 25.8% more likely to be inactive and 52.2% less likely to perform comfort behaviours. When a helicopter was close to the colony, birds were 172.0% more likely to be alert and 66.5% less likely to perform comfort behaviours than when it was further away. A similar pattern was found for birds in the presence of potential predators (Table 4a).

Roosting birds were as likely to be present on a flight day as on a non-flight day. During disturbance by the rescue craft and the helicopters, roosting birds in the absence of predators were less likely to be present than in the absence of the rescue craft or helicopters. In the absence of predators, the probability of roosting birds being present was lowest (74.0% less than when there was no helicopter disturbance) when a helicopter was close to the colony. A similar pattern was found when potential predators were present (Table 4b).

King penguins

Over the four days prior to flight operations there were between 99 and 148 king penguins on Boulder's Beach (mean $\pm$ sd, 123 $\pm$ 22) (Figure 3). King penguins responded to the helicopter

disturbance by walking farther inland. On the days of continuous flight operations the numbers of king pen guins on B oulder's beac h dec reased (t t est, t =4.4, v=4, P =0.014) t o 59 and 3 1 respectively. T he num ber o f peng uins pr esent on t he beac h r emained at t his l ow level f or a further six days (Figure 3).

Discussion

All s pecies of bi rds r esponded t o hel icopter di sturbance by bei ng m ore l ikely t o be al ert, responsive or walking away. Helicopters were thus perceived as a threat, but the intensity of the threat was not large enough to cause nest desertion.

Gentoo penguins

Some s pecies of seabirds ar e e specially s ensitive t o ai rcraft di sturbance (Wilson e t al . 1991 , Giese and Riddle 1999) and qualitative observations of gentoo penguins at Marion Island indicated that non-breeding gentoo penguins were sensitive in this respect (Cooper et al. 1994). However, al though gentoo peng uins responded t o hel icopter di sturbance dur ing t he current study, these responses were relatively mild and transitory (Harris 2005): no nest desertions were observed and par tner change-overs at nests still occurred during flight operations. Factors that influenced the responses of gentoo penguins in the current study were phase of breeding, the closeness of the helicopter to the colony and frequency of helicopter visits.

Cooper et al. (1994) o bserved that non -breeding gentoo penguins fled upon the s econd overflight of a SAAFC-130 Hercules aircraft, whereas guarding penguins remained at their nest sites and an incubating penguin remained at its nest during a single overflight. Brooding Adélie penguins i n A ntarctica al so di d not des ert t heir nes ts w hen appr oached by a S uper P uma helicopter, al though t heir hear t r ates and h ead m ovements i ncreased (Wilson et al . 1991) . Similarly, i n t his s tudy, no nes t d esertions were observed. B ecause l arger c hicks hav e hi gher

reproductive value t han s maller c hicks, par ents ar e ex pected t o r espond m ore dur ing l ater phases of the breeding season than during earlier phases (Trivers 1972). This expectation was supported in the present study, with brooding birds less likely to be alert than guarding birds.

Animals can respond to both the auditory and visual stimuli of helicopters (van Polanen Petel et al. 2006), both of which increase in intensity with decreasing distance. When the engines of a helicopter were switched on (but no hel icopter was in the air), penguins were more likely to be alert and l ess l ikely t o be i nactive than when t here w as no di sturbance. T his indicated that penguins were startled by the noise of the engines. Penguins seemed more likely to protect their nests during flights. Brooding birds responded to the Bell 212 in the air by being less likely to stand (more likely to "sit tight" on their nests), thereby protecting their chicks. Guarding penguins were more likely to stand during flights of the Bell 212. The chicks were too large to brood, and standing in this instance probably also indicates an attempt to protect chicks during flights. Birds were more likely to attend to their nests during flights by the Sikorsky S61L. When a helicopter was in close vicinity of the colony, birds were more likely to be alert and attentive and less likely to be inactive. T his seems to i ndicate a startle reaction i n response to the c loseness of the helicopter. Birds at Trypot were more likely to be alert and less likely to be inactive and to be attending to their nests than birds at Duiker's Point. Considering that flights occurred more often over t he Tr ypot ar ea t han ov er D uiker's P oint, this r esult also suggests that bi rds w ere m ore startled when a helicopter was close to a colony than when it was further away.

Responses to aircraft can vary according to the level of habituation to such disturbance (Hughes et al. 2008). Fewer penguins stood or attended to their nests at Trypot Beach on the second day of flights than on the first day. At Duiker's Point, fewer penguins were alert on the second day of observations (fourth day o f flights) than on t he first day of obs ervations at the c olony. T his suggests that penguins quickly began to habituate to helicopter disturbance. King penguins also

seemed to habituate to some degree and responded more during early flights (Hughes et al. 2008). However, complete habituation requires regular, predictable disturbance (van Polanen Petel et al. 2008). The frequency of flights at Marion Island is generally low and flight periods are unpredictable, because they are weather-dependent. It is therefore unlikely that gentoo penguins will habituate to helicopter disturbance in the long term. Helicopter disturbance will therefore remain potentially disturbing to these birds.

Grey-headed albatrosses

Grey-headed albatross chicks responded to an approaching helicopter. Chicks in Section 4 were more likely to stand than chicks in Section 2, even before any disturbance occurred. Chicks in Section 2 were monthly visited for nest checks and were ringed on Day 1 of this study. The hut from where observations were made and where hut restocking activities occurred on Day 4 is close to Section 2, while Section 4 is further along the ridge. The observation that chicks in Section 4 were more likely to stand than chicks in Section 2 is surprising and remains unexplained.

Chicks were more likely to stand up upon detection of the helicopter in the area than in the absence of a helicopter. Chicks were startled upon first detection of the helicopter, but then settled down again. On Day 1, the Bell 212 flew parallel to the ridge c. 20 m from sections on the ridge. Behavioural scans were not made during this flight but from the helicopter it was observed that almost all chicks in the sections stood up from their nests and rapidly flapped their wings (personal observation). During observations of flights on Day 4, chicks were more likely to be standing when the helicopter was close than in the absence of flights, but this probability was lower than when the helicopter was first noted in the area. The large proportion of chicks that stood during the flight on Day 1 also seems to indicate a startled reaction in response to the unexpected disturbance. During the flight period on Day 4, birds were less likely to be inactive

and more likely to be responsive and to be performing comfort behaviours than in the absence of a helicopter. The responsive category included alert, threatening and aggressive behaviours. The approaching helicopter seemed to cause a higher stress response, resulting in an increase threatening and aggressive behaviours towards conspecifics. A similar response was found for king penguins, with the presence of aircraft resulting in an increase in active behaviour that might have been due to more aggressive encounters (Hughes et al 2008). Comfort behaviour can be considered to be a form of displacement behaviour (Jouventin 1982, Holmes et al. 2005) and was one response of chicks to the helicopter disturbance. After the flight on Day 1, chicks were more likely to be standing and were more responsive, indicating that they were still recovering from the disturbance during post-flight observations.

Crozet shags

The rescue craft was used to transport personnel from the ship to the station on the first day that the ship arrived at the island. While the engine noise of the ship was audible, the rescue craft were noisier than the engines of the ship. The noise of the ship and the craft combined was louder than the background noise from the station. This increase in noise level resulted in birds being less likely to be inactive and more likely to perform comfort behaviours. However, the rescue craft did not approach the colony closely. Closer approaches might have resulted in birds becoming more responsive. New Zealand fur seals (*Arctocephalus forsteri*) and Australian fur seals (*A. pusillus doriferus*) responded more during closer approaches by tour boats than when boats were at larger distances (Shaughnessy 2008).

Incubating Crozet shags seemed to be more likely to stand, were more likely to be alert and less likely to perform comfort behaviours with increasing levels of helicopter disturbance. This indicates that birds perceived the helicopter disturbance as a threat. However, no nests were deserted and partners were seen displaying while helicopters were flying. Disturbance had a

relatively minor influence (Harris 2005) on the breeding behaviour of these birds. There were

fewer roosting Crozet shags at the top section of the colony in the presence of disturbance than

in its absence. These birds were not nesting and were therefore more likely to leave the area

than birds defending eggs or nest sites.

Animals are likely to be more vigilant in the presence of predators (Frid and Dill 2002). The

presence of potential avian predators at the shag colony resulted in higher probabilities of birds

standing, being alert and performing comfort behaviours. There were more roosting birds on the

top cliff in the presence of potential predators. Some of these birds might have been partners of

the incubating birds and might therefore have been more protective of their nests than in the

absence of predators. However, the increases in these probabilities were small when compared

to changes in the probabilities due to the disturbance caused by the rescue craft or the

helicopters. This may have been due to the relative unfamiliarity of the rescue craft and the

helicopters and may indicate that Crozet shags respond more to the auditory stimulus of the

vehicles (Giese and Riddle 1999). Royal penguins (*Eudyptes schlegeli*) were more vigilant

during a disturbance that they were relatively unfamiliar with than during more familiar overflights

by sub-Antarctic skuas (Holmes 2005). However, birds in urban areas are more habituated to

frequent aircraft disturbance and birds at Paardevlei, South Africa, therefore responded more to

an overflight by a predator than during repeated helicopter flights (Williams 2007).

King penguins

At Marion Island, adults and chicks in two breeding colonies moved away from a passing

helicopter (Cooper et al. 1994). At South Georgia, non-incubating adults and juveniles showed a

similar response (Hughes et al. 2008). In this study, non-breeding king penguins responded to

flights by walking farther inland, away from the disturbance. Such movements of penguins on a

non-breeding beach are unlikely to have long-term effects. However, movements of non-

breeding penguins in breeding colonies can lead to increased territorial aggression as well as losses of eggs and chicks (Hughes et al. 2008) and possibly death (Rounseville and Binns 1991, Cooper et al. 1994). It has been recommended that helicopters at Marion Island should minimise disturbance to breeding colonies by avoiding flights at low altitudes in the vicinity of colonies and by not approaching or landing within 500 m of colonies (Cooper et al. 1994). We support this recommendation. Different helicopters are used at different periods according to logistic requirements. It is important that distances to breeding colonies be considered and that behavioural observations are made at breeding colonies when more noisy helicopters are used. Mass movements of guarding king penguins at Archway Bay was observed to be moving in response to helicopter noise when a Kamov KA 32 helicopter was flying at a distance of 1.5 km away (B. M. Dyer, personal communication).

This study indicated that seabirds at Marion Island responded behaviourally to helicopter disturbance. Although helicopter flights resulted in increased vigilance and other behavioural changes, these responses can be considered to be minor or transitory (Harris 2005). No nest failures were observed during the study. However, the study would not have detected longer-term effects on breeding success or survival. We did not investigate long-term breeding success and did not measure any physiological parameters such as increased heart rates or body temperatures, which can occur in the absence of overt behavioural reactions (Weimerskirch 2002). Increases in heart rates in response to over-flights have been recorded for Adélie Penguins (Wilson et al. 1991). It is therefore important to exercise caution and to avoid close flights to breeding colonies. Flights during the main breeding season can result in responses that can lead to reduced breeding success and survival and it is therefore recommended that the current system of temporal zoning, which ensures that flight operations take place outside of the main breeding seasons of most seabird species be maintained. If flights have to be during breeding seasons due to important logistical considerations, experts and the conservation officer

should be consulted prior to flight operations and breeding colonies should be monitored at the time.

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Duiker's Point gentoo penguin colony

Station and Boulder's Beach (roosting king penguins)

Trypot Beach Crozet Shag colony

Trypot Beach gentoo penguin colony

Grey-headed Albatross Ridge grey-headed albatross colony

N

5 km
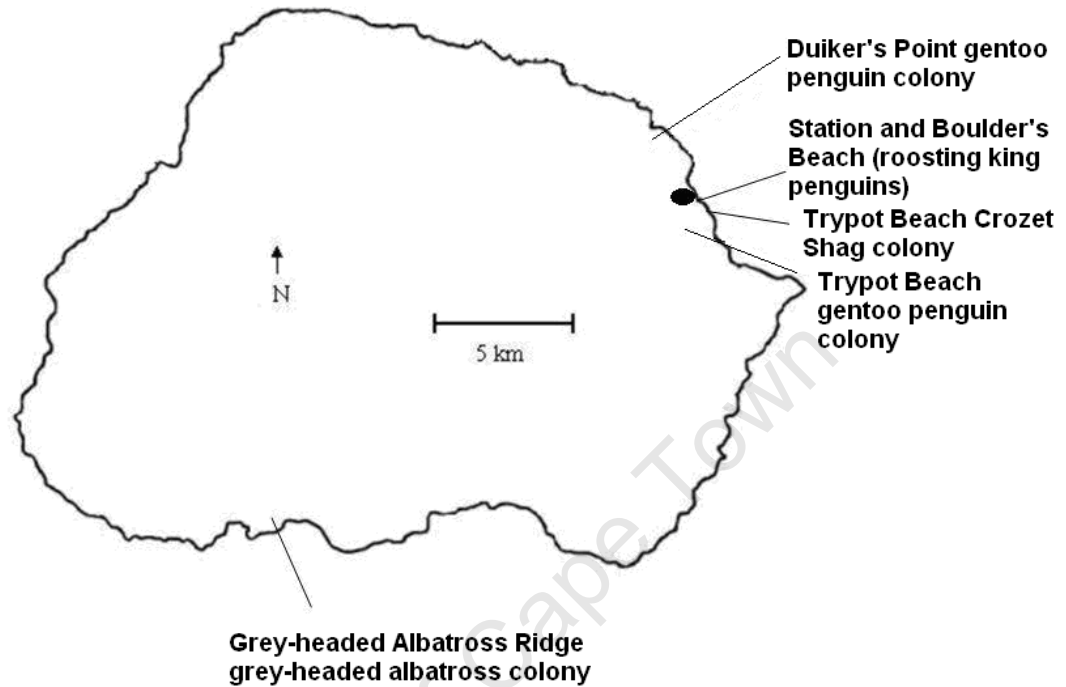
Figure 1 Outline of sub-Antarctic M arion Island indicating the position of the gentoo penguin colonies, g rey-headed a lbatross c olony, C rozet shag c olony and t he r oosting king pen guins studied on non-flight days and during logistic helicopter flight operations in 2004 and 2005.

Footpath across the ridge

1

1

1

Size: small
Disturbance: medium

2

Size: medium
Disturbance:
high

4

Size: medium
Disturbance:
medium

5

Size: small
Disturbance:
low

6

Size: medium
Disturbance:
low

7

Size: small
Disturbance:
low

8

Size: large
Disturbance:
low

3

Size: small
Disturbance: high

7

9

Size: large
Disturbance:
low

Hut
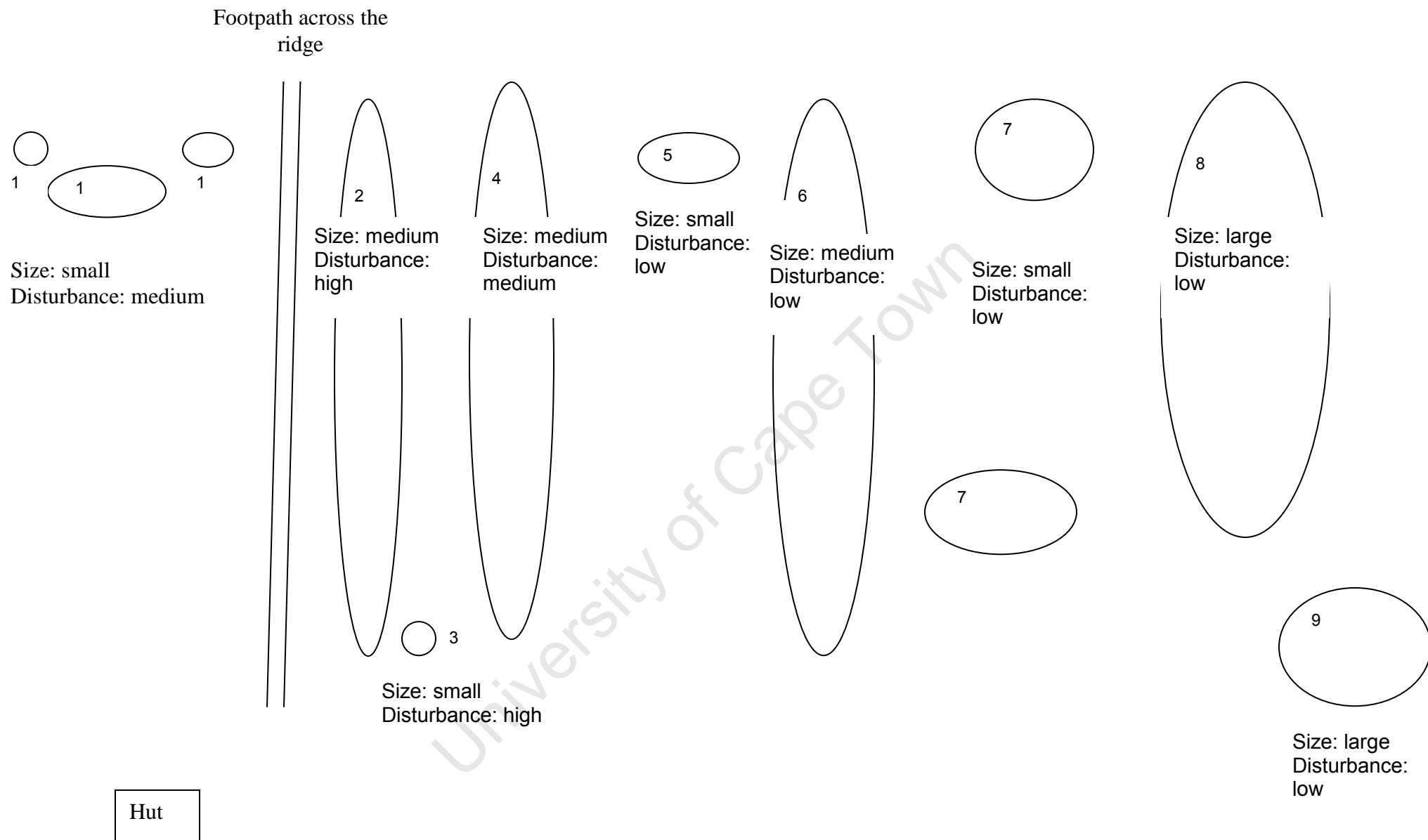
Figure 2 Layout of sections of the Grey-headed Albatross colony on Grey-headed Albatross Ridge, Marion Island. During this study, Instantaneous Scan Sampling of the behavioural responses of grey-headed albatross chicks in Section 2 and Section 4. Also indicating the position of the field hut from where observations were made. Illustration not drawn to scale.

a.
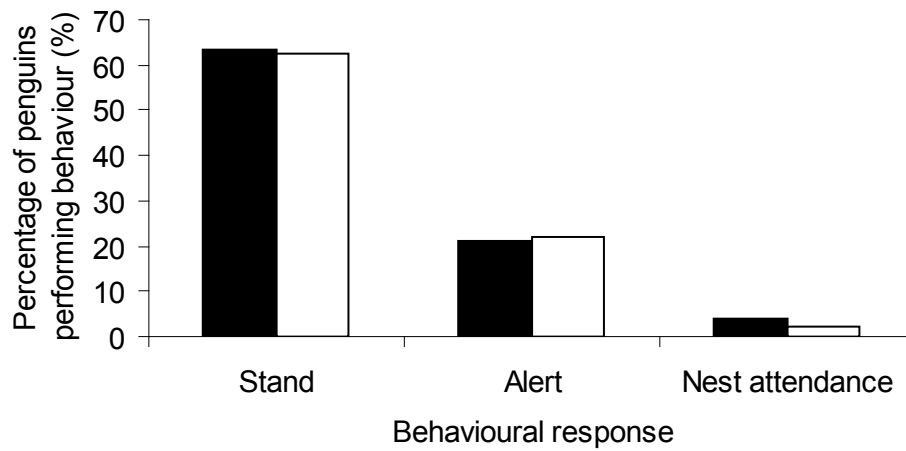
b.
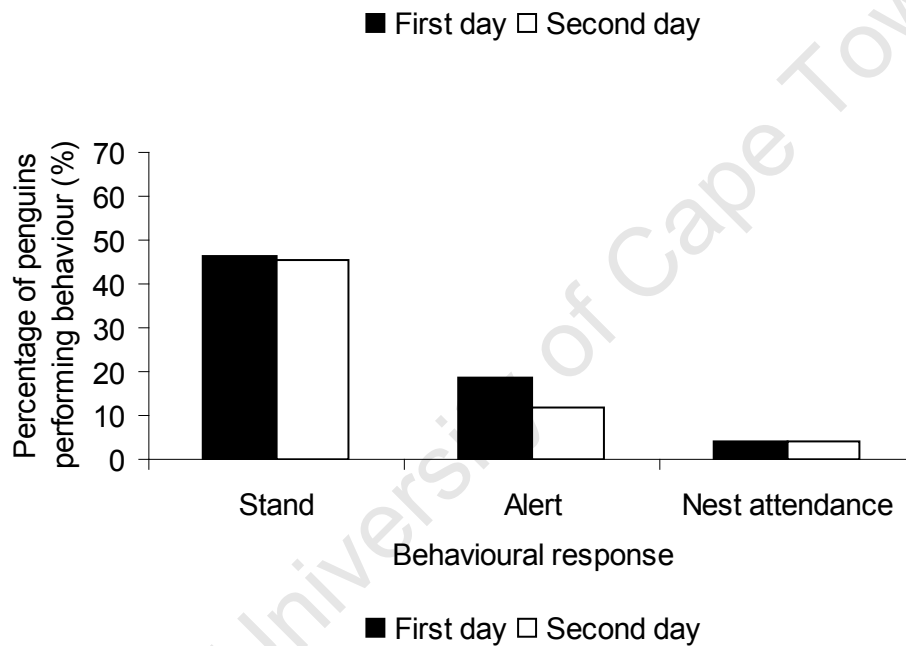
Figure 3 The proportion of gentoo penguins at two colonies at Marion Island that were standing, alert and attending to their nests during two consecutive helicopter flight days in 2004. a. Trypot colony. b. Duiker's Point colony.
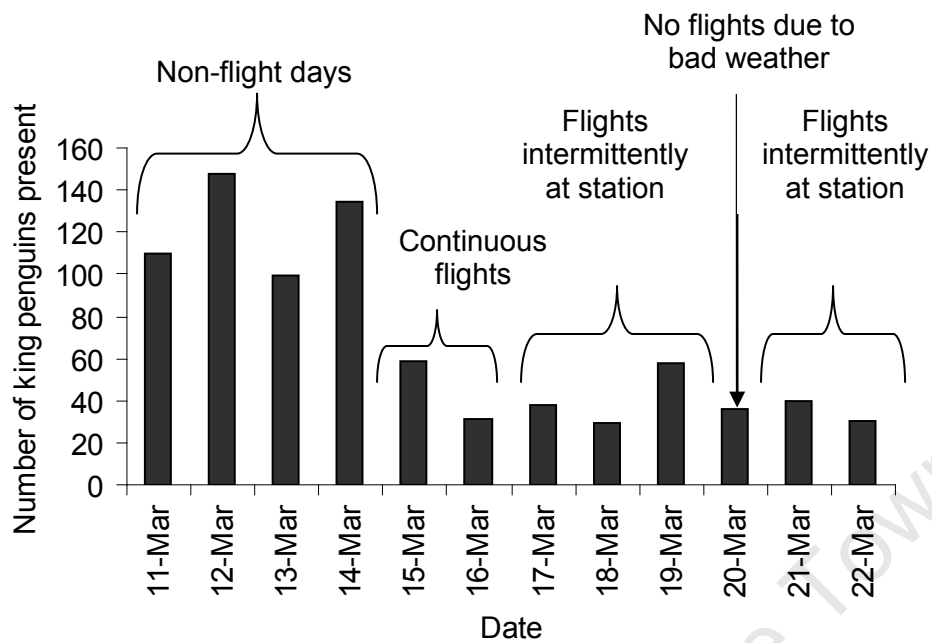
Figure 4 Number of king penguins present on Boulder's Beach (non-breeding beach), Marion Island, prior to and during two days of continuous helicopter operations, and during six days of intermittent helicopter operations thereafter in 2005.

Table 1a Behaviour categories recorded (behaviours modelled indicated in bold) as well as explanatory variables used in Generalised Linear Models

to determine the effects of helicopter disturbance on the behaviour of gentoo penguins at Marion Island in 2004 and 2005.

Behaviour categories recorded		Explanatory variables modelled	
States	lying	colony	Trypot Beach
	standing		Duiker's Point
	walking	breeding phase	brooding
	inactive (resting or sleeping)		guarding
		flight day	non-flight
Events	**Head-Turns (alert)**		flight
	aggressive interactions	level of helicopter disturbance on flight	helicopter grounded and engines off
	attending to nest	days	helicopter grounded, engines audible
	comfort behaviours (preening, shaking or stretching)		Bell 212 in air
	vocalisations		Sikorsky 61 in air
			helicopter close to colony

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Table 1b Behaviour categories recorded (behaviours modelled indicated in bold) as well as explanatory variables used in Generalised Linear Models

to determine the effects of helicopter disturbance on the behaviour of grey-headed albatrosses at Marion Island in 2004

	Behaviour categories recorded	Explanatory variables modelled	
States	lying	section of colony	two
	sitting		four
			non-flight (before disturbance on Day 1 and Day 4
	standing	flight periods	as well as Day 2 and Day 3)
	walking		after flight on Day 1
	inactive (resting or sleeping)		during flight period on Day 4
		level of helicopter	no helicopter in vicinity of ridge
		disturbance during flight	
Events	**responsive (vigilant, threatening or aggression)**	period	helicopter in vicinity of ridge
	comfort behaviours (preening, shaking or stretching)		helicopter close to hut
	nest repair (i.e. pecking at nesting material)		
	parent-chick interactions		
	wing movements (flapping or shaking wings)		

Table 1c Categories recorded (behaviours modelled indicated in bold) as well as explanatory variables used in Generalised Linear Models to determine the effects of disturbance caused by a rescue craft and helicopters on the behaviour of Crozet shags at Marion Island in 2004

	Behaviour categories recorded		Explanatory variables modelled
States	lying	flight day	non-flight
	standing		flight
	walking	natural disturbance:	potential predators present
	flying away		no helicopter or rescue craft
		level of vehicular	helicopter grounded, engines of helicopter or ship
	inactive (resting or sleeping)	disturbance	audible
			Bell 212 in air
Events	**Head-Turns (alert)**		Sikorsky S61L in air
	threatening		helicopter close to colony
	comfort behaviours (preening, stretching, head shakes)		
	gaping (Marchant and Higgins 1990)		
	garling (Marchant and Higgins 1990)		

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Behaviour categories recorded	Explanatory variables modelled
attending to nest	
mate interaction	
wing flapping	
vocalisations	
Roosting birds	
number of roosting birds present on top part of colony	

Table 2a Results of the Generalised Linear Modelling of the standing response of gentoo penguins to helicopter disturbance at Marion Island in 2004 and 2005. The results of Trypot is given relative to Duiker's Point, flight day relative to non-flight day, and level of helicopter disturbance on flight day (helicopter grounded, but engines audible; Bell 212 in air, not close; Sikorsky S61L in air, not close; and helicopter close to colony) relative to in the absence of helicopter disturbance. Bold font indicates significant explanatory variables.

Explanatory variables	Brooding Stand		Guarding Stand	
	Estimate	(se) t_{267}, P	Estimate	(se) t_{442}, P
Trypot	n.a. (data for Trypot colony only)		0.615	**(0.048) 12.82, P<0.001**
Flight day	−0.0350	(0.1850) −0.19, P=0.85	1.16	**(0.06) 19.44, P<0.001**
Helicopter grounded and engines audible	−1.21	(1.02) −1.18, P=0.24	0.0658	(0.0671) 0.98, P=0.33
Bell 212 in air, not close	−0.763	**(0.302) −2.53, P=0.011**	0.129	**(0.056) 2.31, P=0.021**
Sikorsky S61L in air, not close	−0.0180	(0.2110) −0.09, P=0.93	0.0131	(0.0808) 0.16, P=0.87
Helicopter close to colony	0.443	(0.488) 0.91, P=0.36	−0.0720	(0.1090) −0.66, P=0.51

Table 2b Results of the Generalised Linear Modelling of three responses (inactive, alert, nest attendance) of gentoo penguins to helicopter disturbance at Marion Island in 2004 and 2005. The results of Trypot is given relative to Duiker's Point, flight day relative to non-flight day, and level of helicopter disturbance on flight day (helicopter grounded, but engines audible; Bell 212 in air, not close; Sikorsky S61L in air, not close; and helicopter close to colony) relative to in the absence of helicopter disturbance. Bold font indicates significant explanatory variables.

Explanatory variables	Inactive		Alert		Nest attendance	
	Estimate	(se) t_{714}, P	Estimate	(se) t_{714}, P	Estimate	(se) t_{714}, P
Trypot	−0.469	**(0.0545) −8.61, P<0.001**	0.636	**(0.059) 10.79, P<0.001**	−0.402	**(0.119) −3.39, P<0.001**
Guarding	−0.219	**(0.0419) −5.24, P<0.001**	0.261	**(0.045) 5.81, P<0.001**	−0.0451	(0.0935) −0.48, P=0.63
Flight day	−0.401	**(0.0524) −7.64, P<0.001**	0.498	**(0.056) 8.83, P<0.001**	−0.165	(0.117) −1.42, P=0.16
Helicopter grounded and engines audible	−0.156	**(0.0778) −2.01, P=0.044**	0.225	**(0.083) 2.7, P=0.007**	−0.181	(0.173) −1.04, P=0.30
Bell 212 in air, not close	−0.0087	(0.0569) −0.15, P=0.88	0.0532	(0.0605) 0.88, P=0.38	−0.207	(0.133) −1.56, P=0.12
Sikorsky S61L in air, not close	−0.164	**(0.062) −2.67, P=0.008**	0.120	(0.066) 1.83, P=0.068	0.310	**(0.132) 2.34, P=0.019**
Helicopter close to colony	−0.821	**(0.104) −7.87, P<0.001**	0.798	**(0.111) 7.2, P<0.001**	0.521	**(0.204) 2.56, P=0.010**

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Table 3 Results of the Generalised Linear Modelling of four responses (standing, inactive, alert, comfort behaviours) of grey-headed albatross chicks to helicopter disturbance at Marion Island in 2004. The results of Section 4 is given relative to Section 2, after first flight and during flight period relative to non-flight periods (before any disturbance on Day 1 and data for Day 2 and Day 3), and level of helicopter disturbance (helicopter in area, helicopter close) relative to when no helicopter was in the vicinity of the ridge. Bold font indicates significant explanatory variables.

Explanatory variables	Stand		Inactive		Responsive		Comfort behaviours	
	Estimate	(se) t249, P	Estimate	(se) t245, P	Estimate	(se) t245, P	Estimate	(se) t245, P
Section 4	**0.106**	**(0.054) 1.97, P=0.049**	–0.118	(0.071) –1.67, P=0.096	0.107	(0.063) 1.69, P=0.091	**–0.137**	**(0.062) –2.2, P=0.028**
After first flight	**–1.28**	**(0.11) –11.27, P<0.001**	0.220	(0.147) 1.49, P=0.136	**–0.449**	**(0.155) –2.9, P=0.004**	0.240	(0.135) 1.77, P=0.077
Flight period	**0.273**	**(0.075) 3.65, P<0.001**	**–0.237**	**(0.098) –2.43, P=0.015**	**–0.811**	**(0.100) –8.12, P<0.001**	**0.815**	**(0.079) 10.28, P<0.001**
Helicopter in vicinity of ridge	**0.519**	**(0.155) 3.35, P<0.001**	0.0800	(0.2040) 0.39, P=0.69	**1.26**	**(0.18) 7.15, P<0.001**	**–1.29**	**(0.19) –6.84, P<0.001**
Helicopter close	**0.312**	**(0.138) 2.27, P=0.023**	**–0.567**	**(0.209) –2.71, P=0.007**	**1.74**	**(0.16) 11.16, P<0.001**	**–1.55**	**(0.17) –9.05, P<0.001**

Table 4a Results of the Generalised Linear Modelling of four responses (standing, inactive, alert, comfort behaviours) of Crozet shags to helicopter disturbance at Marion Island in 2004. The results of predators present is given relative to when predators were absence, rescrue craft relative to in the absence of disturbance by the rescue craft or a helicopter, flight day relative to non-flight day, level of helicopter disturbance (helicopter grounded, but engines audible; Bell 212 in air, not close; Sikorsky S61L in air, not close; and helicopter close to colony) relative to in the absence of any disturbance by the rescue craft or a helicopter. Bold font indicates significant explanatory variables.

Explanatory variables	Stand			Inactive			Alert			Comfort behaviour		
	Estimate	(se) t_{194}, P		Estimate	(se) t_{361}, P		Estimate	(se) t_{361}, P		Estimate	(se) t_{361}, P	
Predators present	0.0480	(0.1820) 0.27, P=0.79		−0.169	**(0.074) −2.28, P=0.022**		0.107	(0.116) 0.92, P=0.39		0.113	(0.078) 1.45, P=0.15	
Rescue craft	0.337	(0.231) 1.46, P=0.14		−0.240	**(0.110) −2.19, P=0.029**		−0.732	**(0.229) −3.19, P=0.001**		0.471	**(0.110) 4.29, P<0.001**	
Flight day	0.0000	(0.2460) 0,00, P=0.10		0.140	(0.102) 1.38, P=0.17		0.350	**(0.153) 2.28, P=0.022**		−0.269	**(0.109) −2.46, P=0.014**	
Helicopter grounded and engines audible	0.197	(0.270) 0.73, P=0.47		−0.0340	(0.1230) −0.27, P=0.78		−0.154	(0.187) −0.82, P=0.41		0.035	(0.133) 0.26, P=0.79	
Bell 212 in air, not close	0.263	(0.237) 1.11, P=0.27		0.252	**(0.115) 2.2, P=0.028**		−0.140	(0.169) −0.83, P=0.41		−0.226	(0.126) −1.79, P=0.073	
Sikorsky S61L in air, not close	0.0540	(0.3720) 0.15, P=0.88		0.398	**(0.171) 2.32, P=0.02**		0.124	(0.235) 0.53, P=0.60		−0.722	**(0.209) −3.45, P<0.001**	
Helicopter close to colony	0.165	(0.421) 0.39, P=0.67		0.146	(0.203) 0.72, P=0.47		0.862	**(0.241) 3.58, P<0.001**		−1.14	**(0.29) −3.9, P<0.001**	

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Table 4b Results of the Generalised Linear Modelling of the number of roosting Crozet shags present at the top part of the colony during different levels of rescue craft and helicopter disturbance at Marion Island in 2004. The results of predators present is given relative to when predators were absence, rescrue craft relative to in the absence of disturbance by the rescue craft or a helicopter, flight day relative to non-flight day, level of helicopter disturbance (helicopter grounded, but engines audible; Bell 212 in air, not close; Sikorsky S61L in air, not close; and helicopter close to colony) relative to in the absence of any disturbance by the rescue craft or a helicopter. Bold font indicates significant explanatory variables.

Explanatory variables	Number of birds on top cliff	
	Estimate	(se) t_{320}, P
Predators present	**0.395**	**(0.114) 3.46, P<0.001**
Rescue craft	**−0.471**	**(0.178) −2.65, P=0.008**
Flight day	0.0500	(0.1640) 0.3, P=0.762
Engines audible, not in air	**−0.848**	**(0.237) −3.57, P=<0.001**
Bell in air, not close	**−0.659**	**(0.196) −3.36, P=<0.001**
Sikorsky in air, not close	**−0.797**	**(0.321) −2.48, P=0.013**
Helicopter close to colony	**−1.48**	**(0.53) −2.8, P=0.005**

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The influence of helicopter, pedestrian and research disturbance on the response behaviour of Subantarctic fur seals *Arctocephalus tropicalis* at Marion Island

Abstract

The quantification o f w ildlife r esponses t o h uman di sturbance i s i mportant t o i nform management plans at sub-Antarctic islands, but few studies have collected such data for fur seals. At Marion Island, Subantarctic fur seals (*Arctocephalus tropicalis*) can be influenced by logistic, pedestrian and research disturbance. Counts of non-breeding fur seals and Instantaneous Scan Sampling of behaviour on helicopter non-flight and flight days indicated that fur seals escaped into the ocean or moved further inland during the first hours of flight operations. They w ere l ess l ikely t o be i nactive and m ore l ikely t o be upr ight, al ert and t o perform c omfort behav iours during f lights. Instantaneous scans pr ior to, dur ing and a fter pedestrian v isits by two, four, s ix or ei ght persons showed t hat l arge pedes trian g roups resulted in more intense behavioural responses than smaller groups. As a proxy measure of disturbance to Subantarctic fur seal mothers delivering milk to their pups, the maximum pre-weaning mass of pups that were weighed monthly did not differ from that of pups that were not previously weighed. It is recommended that flights over breeding sites should be avoided, while the size of pedestrian g roups and t he frequency of visits should be regulated. The current l evel of r esearch ac tivities does not s eem t o hav e a ne gative i nfluence o n fur s eal pup growth.

Introduction

Number of fur seals hauled out ashore peak during both the breeding and moulting seasons (Bester 1981, Kerley 1983). During these times, when they are energetically and thermoregulatory constrained (Bester and Rossouw 1994), they may also be exposed to a variety of human activities. Activities, such as vehicular traffic, pedestrian visits and research

activities can negatively influence the behaviour and physiology of seals (Engelhard et al. 2002a, Southwell 2005, van Polanen Petel et al. 2007, 2008).

The intensity of response to human disturbance is influenced by a variety of factors, ranging from the nature of the disturbance stimulus to the individual characteristics of an animal (van Polanen Petel et al. 2007). Seal responses to vehicles may be influenced by the type (Born et al. 1999), distance and speed of the vehicle (van Polanen Petel et al. 2007). Because approaching pedestrians might be perceived as potential predators (Frid and Dill 2002), a larger group of pedestrians might evoke a more intense response than a smaller group (Geist et al. 2005). When animals are repeatedly exposed to disturbance, they can habituate and respond less (Walker et al. 2006, Holmes et al. 2005a), or become sensitised to the stimulus and respond more over time (Müllner et al. 2004, Walker et al. 2005). Adult Weddell seals (*Leptonychotes weddellii*) habituated to predictable single-person approaches, but not to irregular, unpredictable approaches over long periods of time. Pups seemed to become sensitised to the disturbance over time (van Polanen Petel et al. 2007). Harp seal (*Pagophilus groenlandicus*) pups became sensitised to tourist disturbance over time (Kovacs and Innes 1990). Time of day and environmental conditions during disturbance, such as the relative wind direction and wind chill factor also influenced the escape behaviour of ringed seals (*Pusa hispida*) (Born et al. 1999).

Disturbance events have different effects on individuals depending on their gender, age and stage of the breeding cycle (Boren et al. 2002). During the pupping and mating season, dominant New Zealand fur seal (*Arctocephalus forsteri*) bulls were more likely to fight than females and pups (Boren et al. 2002). Harp seal pups exhibited a freeze response when approached closely or touched by tourists (Kovacs and Innes 1990).

South American fur seals (*Arctocephalus australis*) in Peru selected breeding sites where habitat features minimised human access, but these features can reduce pup survival

(Stevens and Boness 2003). As lactation bouts in southern elephant seals (*Mirounga leonina*) can be shorter in stressful environments (Arnbom et al. 1997), pups in disturbed areas can have lower masses at weaning than undisturbed pups. This can result in reduced survival rates for disturbed animals as an elephant seal pup's body mass at weaning is directly related to its chances of survival in its first year (McMahon et al. 2000). These examples illustrate that some responses of seals to disturbance can be associated with reduced survival and reproduction (Engelhard et al. 2002b). However other responses, such as increased alertness, can be temporary and have little or no impacts on fitness. It is therefore important to quantify the fitness consequences of the responses being measured (Gill 2007).

At sub-Antarctic Marion Island (290 km²; 46°54'S, 37° 45'E), Subantarctic fur seals (*Arctocephalus tropicalis*) and Antarctic fur seals (*A. gazella*) can be disturbed by logistic activities (such as helicopter flights), incidentally by island personnel and by research activities. Boulder's Beach, adjacent to the research station, is primarily used by non-breeding Subantarctic fur seals (Hofmeyr et al. 2006) that haul out there to rest and moult (Kerley 1983). Boulder's Beach falls within the island's Service Zone, which encompasses the research station and nearby areas (Hänel and Chown 1998, Wheeler et al. 2009). Helicopters are used to transport personnel and cargo from the ship to the island during the annual relief period (April to May) and, since the start of construction of a new station in 2003, also at other times of the year. Helicopters usually fly directly across Boulder's beach. Most incidental disturbance on the island occurs in the Service Zone and although pedestrians visit several beaches close to the station throughout the year, large pedestrian groups are mainly found on Boulder's Beach during relief and construction periods. At other times of the year, the Subantarctic fur seal pups are weighed monthly at Sealer's Beach, Cape Davis (Kirkman et al. 2002, Anon 2004) from around their median birth dates, 16 to 20 December (Hofmeyr et al. 2007), to attainment of maximum pre-weaning mass at around 200 days of age (in July - Kirkman et al. 2002, Anon 2004) and just before weaning (in

October - Kerley 1983, 1985). The pup-attendance patterns of female Subantarctic fur seals (Kirkman et al. 2002) and Antarctic fur seals (Kirkman et al. 2003) are also monitored at beaches close to the research station, on the northeastern side of the island and this is another potential source of research disturbance. In addition, most beaches on the island, including the study site on the northeastern coast, but excluding west coast sites, are visited on a 7-10 day cycle by 1–2 researchers to record tagged southern elephant seals (Pistorius et al. 1999, Anon 2004).

Few studies have focused on the effects of human disturbance on sub-Antarctic pinnipeds (e.g. Wilkinson and Bester 1988, Engelhard et al. 2001, Engelhard et al. 2002a, Engelhard et al. 2002b). Therefore, the aim of this study was to investigate the effects that helicopter disturbance, pedestrian disturbance and biological research has on fur seals at Marion Island.

Methods

This study concentrated on the Subantarctic fur seal population at Marion Island, and focussed on seals at Boulder's Beach where observations were made in March and April 2005. The construction period from March to May 2005 coincided with the duration of this behavioural study. Pups were weighed in July 2004 at Swartkop Beach and Mixed Pickle Cove (see below).

Study sites

Boulder's Beach

The Boulder's Beach (non-breeding colony) area (Figure 1) was divided into three sections, namely Boulders (the area closest to the water, consisting of boulders), the Grass Intersection (the area between Boulders and Gentoo Lake, covered in vegetation) and Up Slope (the area that was higher than the Grass Intersection, covered in vegetation) (Figure 2).

Sealer's Beach, Mixed Pickle Cove and Swartkop Beach

Sealer's Beach, Cape Davis, on the northern side of the island (Figure 1), is one of the main breeding beaches for Subantarctic fur seals. Pups were weighed there monthly as part of a long-term monitoring study (Kirkman et al. 2002, Anon 2004). Mixed Pickle Cove and Swartkop Beach (Figure 1) are Subantarctic fur seal breeding beaches on the western side of the island, which experience relatively low levels of human disturbance. Subantarctic fur seal pups at these beaches are not weighed as part of the long-term research programme and the beaches are seldom visited by pedestrians. At Mixed Pickle Cove, a field hut is situated at the top of the cliffs, close to, but partly out of sight of the beach while the field hut at Swartkop Point is situated further away from and completely out of sight of the beach (Wilkinson et al. 1987). Prior to this study, the beaches at Mixed Pickle Cove and Swartkop Point were last visited in May 2004. Behind the beaches of Sealer's Beach and Mixed Pickle Cove is vegetation where pups can be found during the later stages of the breeding cycle. At Swartkop Beach, the beach is surrounded by cliffs and pups are only found on the beach.

Disturbance

Helicopter disturbance

During the study period, a Bell 212 and a Sikorsky S61 were used for flight operations. Helicopers flew between the ship (approximately 100 m offshore) and the station where pedestrians and equipment were offloaded. Helicopters flew at heights from 500 ft (152.4 m) to ground level at the station. During most flights, the helicopter flew directly across or close to the beach. After the first two days of continuous flights (15 and 16 March 2005), helicopters were mainly used at the station to lift heavy cargo at the station and the continuous hovering resulted in higher noise levels (D. Kohl, personal communication). The number of fur seals (both species) on Boulder's Beach was counted once daily over four days prior to flight operations, on the two days of continuous flights and for six days thereafter. On the fourth day after the continuous flights (20 March 2005), there were no

flights due to weather conditions. Counts were done daily at 15h00, because the greatest number of Subantarctic fur seals were usually present from 10h00 to 11h00 and from 14h00 to 15h00 at a nonbreeding colony beach at temperate Gough Island (Bester and Rossouw 1994).

Behavioural responses

Counts of all fur seals in each section and Instantaneous Scans of behaviour (Altmann 1974), whereby the behaviour of each visible seal was recorded once during the scan, were made at five-minute intervals during two days prior to flights and during the two days of continuous flights. The behavioural repertoire of seals was categorised according to postures and behaviours, adapted from Bester and Rossouw (1994). Postures included being in repose, upright, and locomotion. Behaviours included alert, inactive (included resting and sleeping), comfort behaviours (including grooming, stretching, and flipper waving) and interactions with conspecifics.

Generalised Linear Models, GLM, with the binomial distribution and the logistic link function (Genstat 9 2005) were used to estimate the effects of helicopter disturbance on the behaviour of the seals. Events that occurred at low frequencies were not modelled. Postures modelled were in repose and upright and behaviours modelled were alert, inactive and comfort. Explanatory variables included in the models were the section of the beach (Boulders, Grass Intersection or Up Slope), whether or not flights took place on a day, and level of helicopter disturbance. Disturbance levels were recorded as: no disturbance; helicopter not in air but engines audible; helicopter/s in air; and direct overflight. Generalised Linear Model results were back-transformed to probabilities to facilitate interpretation.

Distribution across sections

To assess the effect of helicopter disturbance on the distribution of seals across sections of beach, the number of seals per section on non-flight days and during the first hours of flights

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were determined. This was done at five-minute intervals from 08h30–11h35 on non-flight days and the numbers of the two days were averaged. The number of fur seals present in each section was determined at five-minute intervals on flight days under three conditions (before the day's flying commenced and helicopter engines running; during the first flights of the day; and during 100–155 minutes after flights commenced) and the numbers were averaged for each condition.

Pedestrian disturbance

Prior to pedestrian disturbance, the behaviour of seals on the sections of Boulder's Beach was recorded at three-minute intervals for 30 minutes through Instantaneous Scan Sampling. Groups of two, four, six or eight persons were sent to the beach at 10h00 and 16h00. The behaviour of pedestrians and the duration of the disturbance varied within small limits, thus imitating normal pedestrian visits to the beach. Scans were continued throughout the visits and for a further 30 minutes thereafter, to determine the time required for the seals' behaviours to return to pre-visit levels.

Behaviours were categorised as for the helicopter disturbance observations. The effect of pedestrian group size on the response behaviour of seals was estimated through GLM (see above). Postures and behaviours modelled were the same as for the helicopter disturbance study above. Stages of approaches were defined as before, during and after approaches. For the purposes of the behavioural models, behaviours recorded before approaches were all given a single time-stamp ("before"). Behaviours recorded during and after approaches were time stamped according to the time after the approach started (e.g. "Start + 3 minutes") or ended (e.g. "End + 3 minutes"), respectively. Seals were considered to have recovered from the disturbance when the probability of performing a behaviour after the disturbance was similar to the average probability prior to disturbance. Other explanatory variables included in the models were the section of the beach (Boulders, Grass Intersection or Up Slope), time of day of the visit (morning or afternoon), the number of visit for the day (first or

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second visit, due to bad weather conditions only two afternoon visits occurred on t he same day as a m orning visit), the number of pedestrians in the group (two, four, six or eight), the presence or absence of precipitation, and the presence or absence of strong winds. Explanatory variables that were not significant in a model were excluded and the model was re-run for the specific behaviour. Generalised Linear Model results were back-transformed to probabilities to facilitate interpretation. As seals moved down onto the beach during visits, the probability of seals being on the Boulders section were also determined through a GLM (see above) with the same explanatory variables.

<u>Research disturbance</u>

Subantarctic fur seal pups were monthly weighed at Sealer's Beach, Cape Davis (disturbed site) as part of a long-term study (Anon 2004). To avoid possible bias due to the effects of spatial distribution of pups according to age, size, health or milk consumption, sampling was done comprehensively a nd eq ually f rom the rocky and (when p resent) vegetated a reas of beaches (Kirkman et al. 2002 and references therein). As a control, 200-day old pups (calculated from the median birth date - Hofmeyr et al. 2006) were also weighed in July 2004 (this s tudy) at M ixed P ickle C ove and S wartkop B each (relatively undi sturbed s ites). At Sealer's Beach and Mixed Pickle Cove, half of the pups were weighed on the beach and the rest on t he vegetation. At Swartkop Beach all t he pups w ere weighed on t he beac h. The weighing procedure is described in Kirkman et al. (2002).

Results

<u>Helicopter disturbance</u>

Over the four days prior to flight operations there were between 110 and 123 fur seals on the beach (mean=115, SD=5.74). On the two days of continuous flights the numbers of fur seals present on t he beach decreased (t test, t_4=16.48, P<0.001) to 28 and 16 seals respectively. The number of seals present on t he beach i ncreased after the day when hel icopter flew

due to weather conditions, but decreased again when there were more flights on the 22nd of March (Figure 3).

Seals were displaced from their locations on the beach during the first hours of flight operations. On non-flight days, over the same time period as during the first hours of operations, similar proportions of seals were found on each section (Figure 4a). Before flights commenced, but when engines were switched on and audible, seals started to move either farther inland than Up Slope or down on the beach towards the sea and 61.3% of seals present on the beach were found on Grass Intersection (Figure 4b). This trend held during the first flights, with 62.9% of seals present on Grass Intersection (Figure 4c). During the period 100–155 minutes after flights commenced, the seals had moved further down the beach with 67.5% present on Boulders (Figure 4d). From Boulders, seals moved into the ocean during disturbance. During the first four hours of flights the total number of fur seals present on the entire beach decreased by 43%.

The models showed, that on flight days seals were less likely to be inactive and to perform comfort behaviours, but more likely to be upright and to be alert than on non-flight days. Compared to the probability in the absence of disturbance, seals were less likely to be inactive (30%, 20% and 30% smaller), but more likely to be upright (90%, 140% and 290% larger), alert (140%, 90% and 160% larger) and to be performing comfort behaviours (70%, 50% and 60% larger) when engines were switched on, when the helicopter was in the air and during direct overflights respectively (Table 1).

Seals on the Grass Intersection were more likely to be inactive, but less likely to be upright, alert and to be performing comfort behaviours than seals on Boulders. On Up Slope, seals were more likely to be inactive and less likely to be performing comfort behaviours but as likely to be upright and alert than seals on Boulders (Table 1).

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The numbers of fur seals present on the beach at the beginning of each observation session varied, w ith an average of 19 (range 15–28) seals being present in the morning and 25 (range 13 –51) bei ng pr esent i n the a fternoon. During app roaches, s eals m oved from U p Slope and Grass Intersection to Boulders. Seals were more likely to be on Boulders during (t test, t_{188}=5.49, P <0.001) and af ter appr oaches (t te st, t_{188}=9.73, P <0.001) than be fore, indicating that during approaches seals moved down to Boulders (Figure 5). No seals were seen going into the ocean during or after approaches.

When undi sturbed, s eals s pent m ost o f t he t ime i nactive. T he mean prop ortion o f i nactive seals on t he bea ch w as 81. 6%, 50 % and 57 .9% be fore, dur ing and a fter app roaches respectively. During approaches, seals were l ess likely to be inactive (Figure 6a), but more likely to be upright (Figure 6b), al ert (Figure 6c) and to perform comfort behaviours (Figure 6d) than before t he v isits. With i ncreasing nu mber o f pede strians, the p robability of bei ng inactive decreased (Figure 6a), while the probability of being upright (Figure 6b) and of being alert (Figure 6c) increased. The probability of performing comfort behaviours was highest when two people were on the beach, but lowest when eight people were present (Figure 6b). Seals al so s eemed t o be responding m ore t o noisier groups. Larger pedestrian g roups tended to be noisier than smaller groups.

The probability of being inactive (Figure 6a) and of being alert (Figure 6d) returned to pre-disturbance levels by the 24th minute after approaches, while the probability of being upright (Figure 6c) returned to pre-disturbance levels by the 27th minute. During 27 minutes of post-disturbance observations, t he p robability of per forming c omfort behav iours (Figure 4b) di d not return to pre-disturbance levels.

Seals on G rass Intersection tended to be more likely to be i nactive, were as likely to b e performing comfort behaviours and were less likely to be upr ight and to be alert than seals

on Boulders. On Up Slope, seals were less likely to be inactive, but more likely to be performing comfort behaviours, to be upright and to be alert than seals on Boulders.

During second approaches, seals were more likely to be performing comfort behaviours, but less likely to be upright and to be alert than during first approaches. In the afternoon, seals were more likely to be inactive, but less likely to be performing comfort behaviours, to be upright and to be alert. During precipitation, seals were less likely to be performing comfort behaviours than in its absence. In windy conditions, seals were less likely to be inactive, but more likely to be performing comfort behaviours, to be upright and to be alert than during calm conditions.

Research disturbance

At Sealer's Beach, Cape Davis and at Swartkop Beach, 50 males and 50 females were weighed at a median age of 200 days. At Mixed Pickle Cove, 51 males and 51 females were weighed at this time. The mean maximum pre-weaning mass of pups at Cape Davis was 15.2 $\pm$ 3.04 kg and 14.3 $\pm$ 1.77 kg for males and females respectively. At Mixed Pickle Cove, the mean maximum pre-weaning mass of pups was 15.3 $\pm$ 2.82 kg and 13.9 $\pm$ 2.29 kg for males and females respectively. At Swartkop Beach, the mean maximum pre-weaning mass of pups was 16.0 kg $\pm$ 2.90 kg and 14.2 $\pm$ 2.41 kg for males and females respectively. The maximum pre-weaning mass of males (ANOVA, $F_{2,148} = 1.04$, P=0.36) and females (ANOVA, $F_{2,148} = 0.54$, P=0.58) did not differ between beaches.

Discussion

Helicopter disturbance

The extent to which human disturbances influence the behaviour of animals depends on the amount of risk that the animal perceives (Frid and Dill 2002, Harris 2005). Responses vary from changes in vigilance and other behavioural patterns, to fleeing and ultimately to reduced reproduction or survival. The responses of animals depend on the stage of the breeding

cycle, as escaping will be more costly for breeders that need to protect their offspring, than for non-breeders. Breeders will therefore be less likely to move away during stress than non-breeders (Harris 2005) . Lactating Weddell s eals di d not flee i n r esponse t o ov er-snow vehicles (van P olanen Petel 2007) . In th is s tudy, non-breeding seals per ceived hel icopter disturbance as a large enough threat to abandon the beach and to move further inland or into the ocean. There seemed to be a slight recovery in terms of number of seals present on the beach a fter a day w hen t here w ere no f lights. This m ovement w as al so ev ident f rom the proportion of seals in each of the three sections of the beach, with seals first moving to Grass Intersection and t hen to Boulders. This escape behaviour might result in reduced survival if marine predators, such as killer whales (*Orcinus orca*), are present at the time of disturbance (Southwell 2005) . K iller w hales a re regularly p resent o ff the s tudy be ach dur ing s ummer (Keith et al . 200 1). In c ontrast, t he l ess mobile (than fur s eals on shore) c rabeater seal (*Lobodon carcinophagus*), leopard seal (*Hydrurga leptonyx*) and Ross seal (*Ommatophoca rossii*) also responded to flights of Sikorsky S75 helicopters in Antarctica by moving, but movements by t hese no n-breeding s eals on the s ea i ce were m inor (90% of s eals m oved 5 m or less during close approaches) and seals were observed to escape into the water on a few occasions (Southwell 2005). Non-breeding ringed s eals in Greenland also escaped into the water during flights by a Bell 206/III Long Ranger helicopter and a Partenavia PN68 Observer fixed-wing aircraft (Born et al. 1999).

Wildlife may respond to the auditory and visual stimuli of helicopters (Giese and Riddle 1999, van Polanen Petel et al. 2006), both of which would increase with decreasing distance from the hel icopter. Smith and H ammill (1981) hav e s hown t hat t he noi se f rom hel icopters i s disturbing to seals. Ringed seals in Alaska that did not respond to industrial noise reacted to the noise of Bell 212 helicopters (Blackwell et al. 2004). Differences in noise levels of various aircraft i nfluence the r esponse behav iour of s eals. R inged s eals es caped i nto the water i n larger proportions and at gr eater di stances w hen di sturbed by a helicopter t han w hen approached by a relatively quiet fixed-wing aircraft (Born et al. 1999). It has been theorised

that northern fur seals (*Callorhinus ursinus*) can hear the noise of a Bell 212 helicopter from a distance of 2 km (Richardson et al. 1995). Van Polanen Petel et al. (2006) experimentally found that the noise levels of an Aerospatiale AS350B single engine helicopter were clearly audible to Weddell seals in Antarctica up to distances of 250 m. At Marion Island, seals started to respond when the engines of a helicopter were audible, but the helicopter was not yet in the air. As the ship with the helicopter onboard was approximately 100 m offshore, this indicated that seals responded to the auditory stimulus of the helicopter noise within this distance.

Seals on Boulder's beach were more likely to be upright and alert when a helicopter was in the air and these probabilities were even higher when a helicopter was flying directly over the beach. These responses might have been due to both the increased noise levels and closer visual stimulus. Born et al. (1999) and Southwell (2005) found that seals responded more with decreasing distance between seals and aircraft. Weddell seals were more likely to look at over-snow vehicles and to look for longer periods of time when the vehicle was closer to the seals (Van Polanen Petel et al. 2007). Similarly, New Zealand fur seals (*A. forsteri)* and Australian fur seals (*A. pusillus doriferus*) were less likely to be resting and more likely to move when the distance between tourist boats and the seals decreased (Shaughnessy et al. 2008). Flight distances that may be considered to be far enough that seals would not be disturbed by the noise, may still not be far enough that seals would not be disturbed by the visual stimulus (van Polanen Petel et al. 2006).

Pedestrian disturbance

Animals may perceive an approaching pedestrian as a predator (Frid and Dill 2002). In this study, seals changed their behaviour in response to pedestrian approaches from mostly being inactive to being upright, alert, and performing more comfort behaviours. This disturbance posed a severe enough threat to elicit an escape response – at Boulder's beach, pedestrian approaches resulted in a movement of seals down the beach to the Boulders

section, in preparation for escape into the sea. Similarly, tourists posed a severe enough threat for harp seals in Canada to result in reduced female attendance to pups. These seals were also less likely to be idle and more likely to be alert during the disturbance (Kovacs and Innes 1990). Southern elephant seals at Macquarie Island exhibited a threefold increase in alertness in the presence of humans (Engelhard et al. 2002b).

Larger pedestrian groups could be more threatening to animals than smaller groups (Beale and Monaghan 2004), because larger numbers of predators might result in reduced chances of survival (Abrams 1993). Larger numbers of pedestrians resulted in greater responses in crimson rosellas, *Platycerus elegans* (Geist et al. 2005) and gentoo penguins, *Pygoscelis papua* (Holmes et al. 2007) and the response behaviour of killer whales varied with the number of boats in the area (Williams and Ashe 2007). At Boulder's beach, the probability of being inactive decreased with increasing numbers of pedestrians, while the probability of being alert and upright increased. The probability of performing comfort behaviours was also the lowest when 8 people were on the beach. Larger groups of pedestrians were therefore perceived to be a more severe risk to seals than smaller groups.

Seals might also have been influenced by the behaviour of the pedestrians as the pedestrians reactions varied within limits and were therefore unpredictable to the seals. Weddell seals seemed to habituate to predictable, single-person approaches but not to irregular, unpredictable visits by one or more persons (Van Polanen Petel et al. 2007). Harp seals reacted more when tourists were noisy, when there was a lot of activity and when tourists clumped around individual animals (Kovacs and Innes 1990).

Activity patterns of seals varied temporally. In the afternoon, seals were more likely to be inactive and less likely to be upright, alert or to be performing comfort behaviours than in the morning. This contrasts with the finding that Subantarctic fur seals in a nonbreeding colony at temperate Gough Island were most active in the early morning and late afternoon (Bester

and Rossouw 1994), a probable result of their haulout/departure behaviour under the warmer temperatures experienced there. There was also spatial variation in fur seal behaviour. Seals on the Boulders section of the beach were more active than those on higher sections of the beach, corresponding with the finding that seals on Gough Island were more active in the surf zone and that most of the interactions between Subantaractic fur seals occurred there (Bester and Rossouw 1994). At Marion Island, seals also moved down onto the Boulders when disturbed, resulting in more activity in this section.

After approaches, the probability of being inactive, alert and being upright returned to pre-disturbance levels within the 27 minutes of post-approach observations. The alertness levels of southern elephant seals also returned to pre-disturbance levels shortly after people had left the area (Engelhard et al. 2002b). However, the probability of fur seals performing comfort behaviours did not return to pre-disturbance levels within the period of observation, indicating that they might not have fully recovered from the disturbance despite the reduction in the levels of other behaviours. Animals often respond to disturbance through displacement behaviours (Kortmulder 1998). These behaviours are often comfort or maintenance movements (Holmes et al. 2005b).

Behaviour patterns of Subantarctic fur seals are influenced by the prevailing weather conditions. High levels of inactivity amongst seals serve to reduce heat-loading and to preserve energy (Bester and Rossouw 1994). The incidence of grooming behaviour increased during warmer conditions. At Marion Island, seals were more likely to be active during windy conditions than in calm conditions, but they were more likely to perform comfort behaviours in the absence of precipitation. This might have been due to warmer conditions in the absence of wind-chill and the cooling effect of rain.

Seals were more likely to be upright and alert, and less likely to perform comfort behaviours, during first than second approaches. Due to weather conditions, only two afternoon

approaches c ould be c onducted on t he s ame day as m orning appr oaches. The i nterval between morning and afternoon approaches was approximately 5.5 hours; differences between t hese first and s econd appr oaches w ere m ore l ikely due t o the diurnal activity trends (e.g. Bester and Rossouw 1994) than to the effects of repeated approaches.

Research disturbance

In this study, maximum pre-weaning masses of Subantarctic fur seals in an area where pups were weighed monthly did not differ significantly from pups in areas with low disturbance and from which pups were not weighed previously in the year. This research activity therefore did not seem to have long-term effects on, or fitness consequences for the pups. Similarly, the growth rate of harp seals was not affected by weighing (Kovacs and Lavigne 1985) and research activities did not directly influence the lactation efficiency of southern elephant seals at sub-Antarctic Macquarie Island (Engelhard et al. 2001). Weekly counts and the marking of recently weaned pups was not found to influence the spatial distribution or pre-weaning mortality of southern elephant seal pups at Marion Island (Wilkinson and Bester 1988).

Management considerations

The P rince E dward I slands ar chipelago (consisting o f Marion I sland a nd P rince E dward Island (44 km²; 46°38'S, 37°57'E)) was declared a Special Nature Reserve in 1995 in terms of the Environmental Conservation Act (Act No. 73 of 1989) and no tourism is allowed under the N ational E nvironmental M anagement: P rotected A reas A ct (Act No. 57 o f 2003) . Although one of the most populous species of fur seals (Hofmeyr et al. 2006), it has been speculated t hat the lower population growth r ate of Subantarctic fur s eals on Marion Island compared t o the s maller, neighbouring P rince E dward I sland (Bester e t al. 2003) c ould b e due to the almost complete absence of humans from the latter (Hofmeyr et al. 2006). There is no per manent r esearch s tation on P rince E dward I sland and according t o management regulations, one visit per year by a maximum of six persons and for a maximum of four days is allowed (Prince Edward Islands Management Plan Working Group 1996), and this seldom

happens. The new management plan, accepted but not yet implemented, will allow for one visit every second year by a maximum of 10 people and for a maximum of eight days (Chown et al. 2006).

Flight operations resulted in fur seals escaping into the ocean or moving further inland from the non-breeding colony beach. Such movements are likely to have greater consequences at breeding beaches, potentially resulting in the trampling of pups by adults (Le Boeuf and Briggs 1977, Boren et al. 2002) the disruption of mother-pup bonds (Kovacs and Innes 1990) and potential reduced survival if killer whales are present. These impacts would be more severe at dense aggregations of seals (Wilkinson and Bester 1988). It is therefore important that helicopter pilots adhere to stipulated flight paths (Chown et al. 2006), avoiding overflights of seal beaches where possible, and that flight paths be adjusted according to season to ensure that breeding colony beaches are avoided.

Management considerations for pedestrian visits to Boulders Beach should consider both the number of people interested in visiting the beach and the frequency of visits. Pedestrian groups should be kept small as fur seals showed more intense responses to larger pedestrian groups. Recovery from disturbance was slow, as levels of alertness returned to pre-disturbance levels by 24 minutes and levels of comfort behaviour were still higher than pre-disturbance levels at the end of the 27 minutes of observations. Repeated approaches at short intervals, even by smaller pedestrian groups, might result in greater responses than fewer visits. Although Weddell seals habituated to predictable single-person approaches over short time periods (van Polanen Petel et al. 2007), the behaviour of pedestrians on Boulder's Beach is unlikely to be predictable and seals might not habituate to repeated approaches. Pedestrians should be informed about suitable behaviour such as not gathering at individual seals. They should also be instructed to watch for telltale signs of disturbance. Holmes (2007) found that increased alert, agonistic and threat behaviours were useful indicators of

disturbance for penguins. For seals, level of alertness would be a useful telltale, since it is relatively easy for novices to gauge and is clearly influenced by pedestrian group size.

Monthly weighing of pups at Sealer's Beach, did not seem to influence pup growth, because seals at the disturbed area did not weigh less than seals at low-disturbance areas. Because research activities are essential to determine demographic parameters (Hofmeyr et al. 2007) and since these activities did not seem to negatively influence the population, the level of research disturbance on the island appeared to be acceptable.

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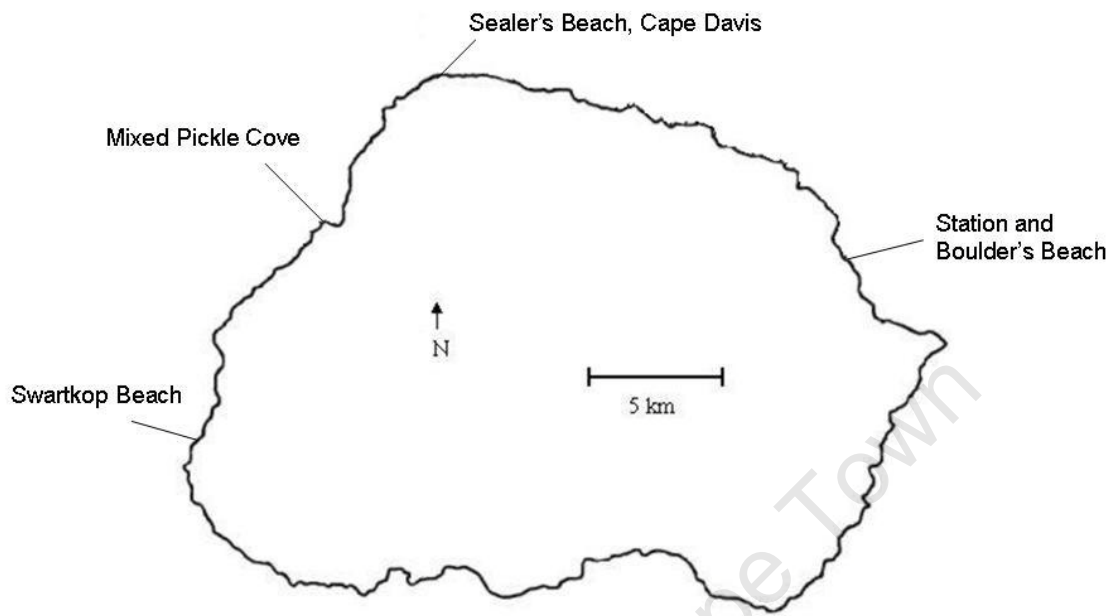
Figure 1 Outline of Marion Island, indicating the locations of the station, Boulder's Beach (where the effects of helicopter disturbance and pedestrian disturbance were investigated) and the 3 beaches where seals were weighed (Sealer's Beach, Mixed Pickle Cove and Swartkop Beach). Seal pups were weighed monthly at Sealer's Beach, Cape Davis, while there were low levels of disturbance at Mixed Pickle Cove and Swartkop Beach.
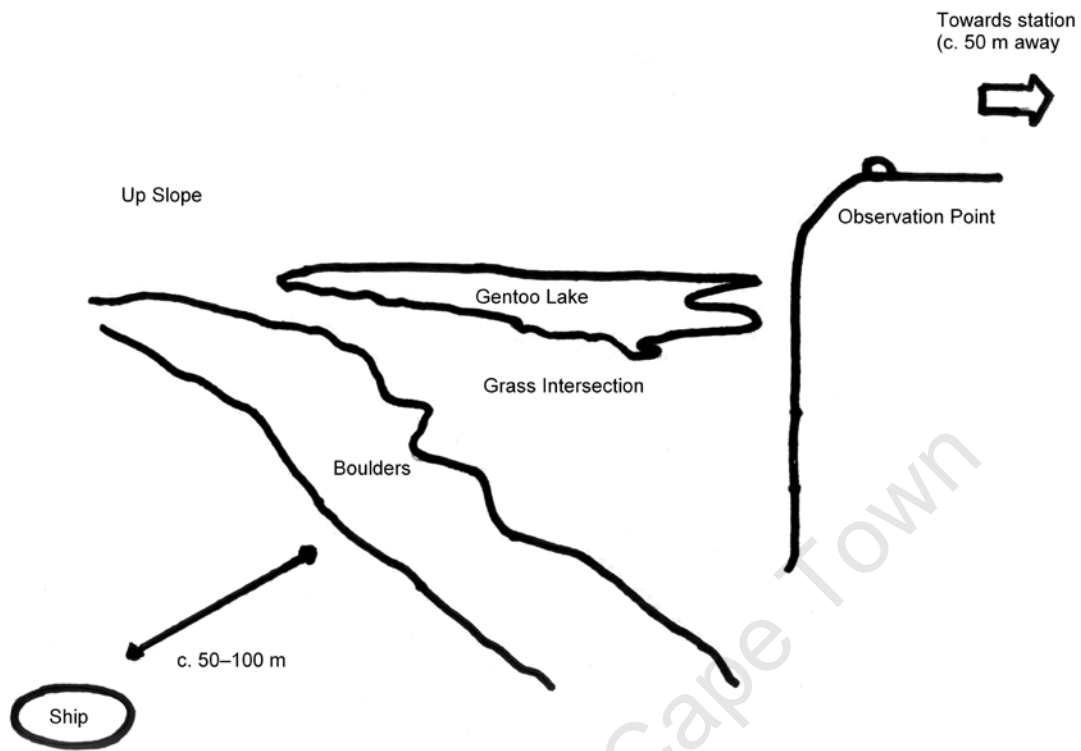
Figure 2 Illustration of Boulder's Beach. For the purpose of this study, the beach was divided into 3 sections (Boulders, Grass Intersection – the section between Boulders and Gentoo Lake, and Up Slope). The approximate position of the ship during helicopter flights is indicated and the arrow indicates the direction of the station.
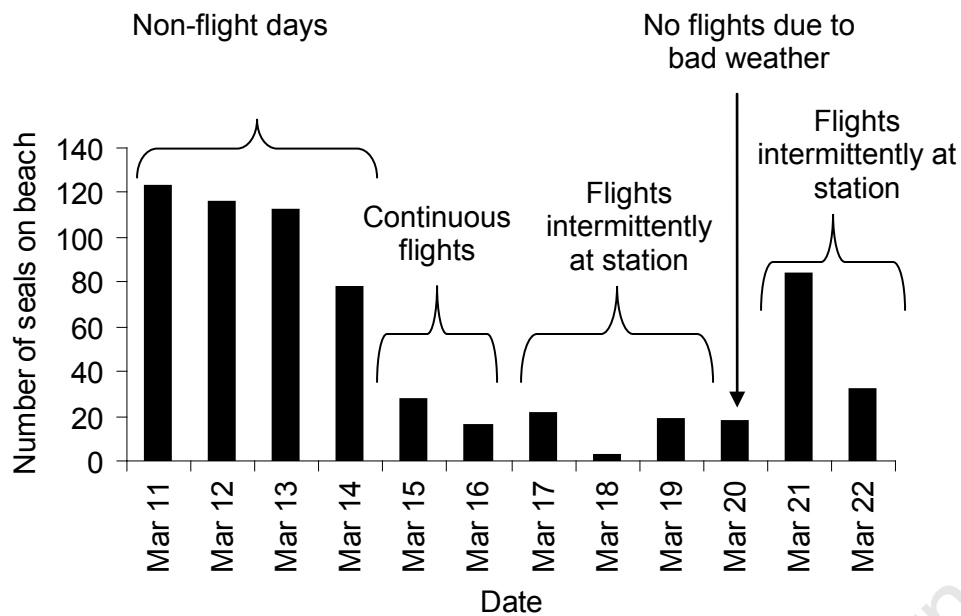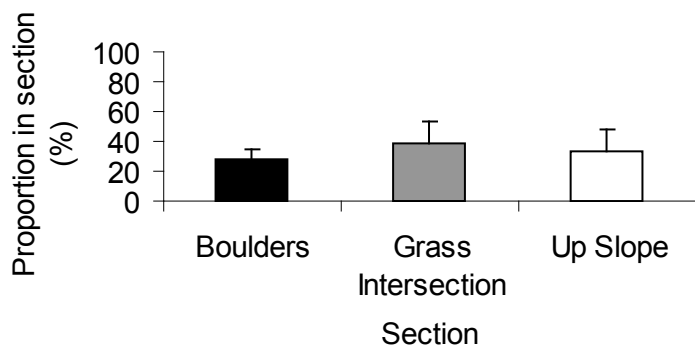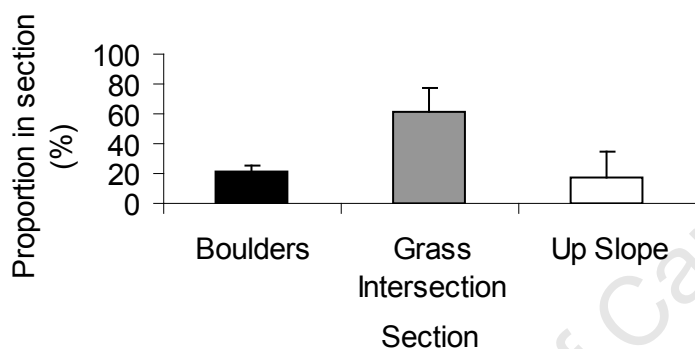
Figure 3 Number of fur seals present on Boulder's Beach, Marion Island, prior to and during two days of continuous helicopter operations, and during six days of intermittent helicopter operations thereafter in 2005.
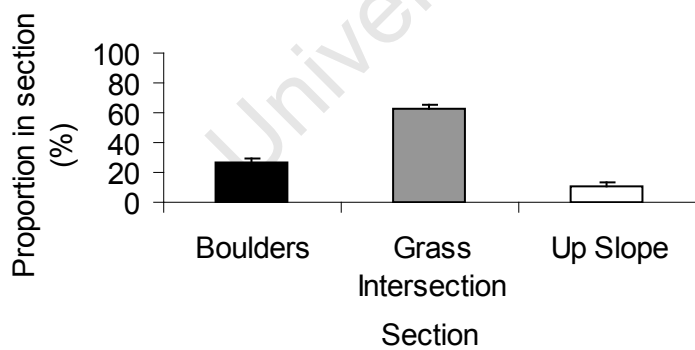
211

a Non-flight days

b Engines of helicopter audible

c First flights

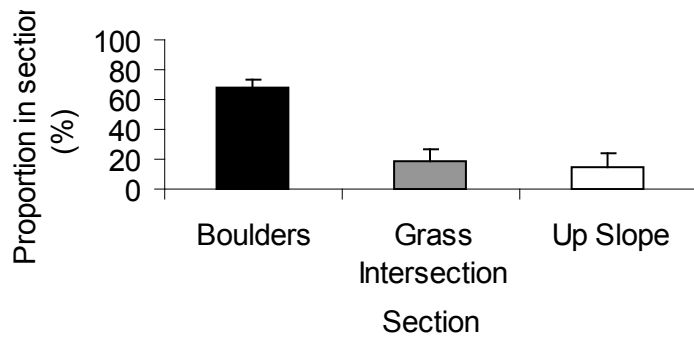d During the period 100–155 minutes after flights commenced

Figure 4: Proportion of non-breeding fur seals present in each section (Boulders, Grass Intersection or Up Slope, see text for description) of Boulder's Beach, Marion Island on non-flight days and over the first few hours of flight on the first day of flight operations.
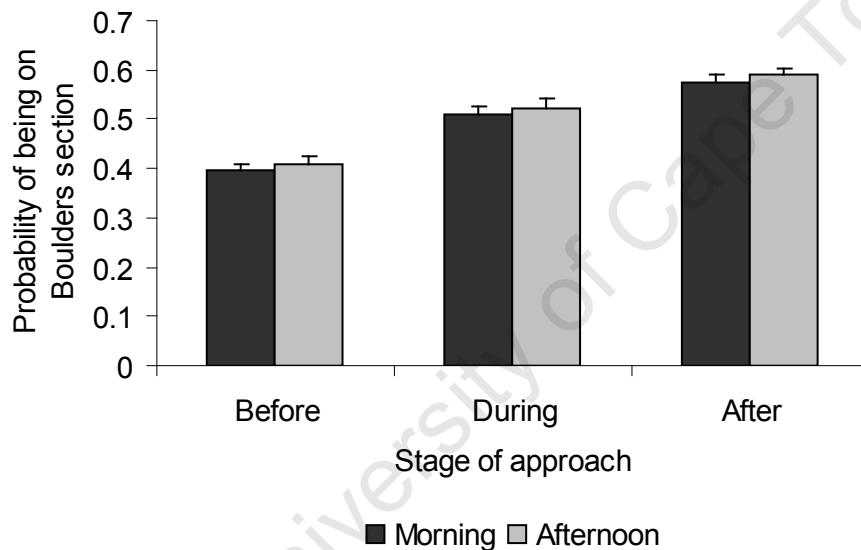
Figure 5: The probability of non-breeding fur seals being on the Boulders section of Boulder's Beach, Marion Island before, during and after pedestrian approaches in the morning and in the afternoon.

a

Before   During   After

Probability of being inactive

◆ 2 people ■ 4 people ▲ 6 people ○ 8 people

b

Before   During   After

Probability of performing comfort behaviours

◆ 2 people ■ 4 people △ 6 people ○ 8 people

c

d
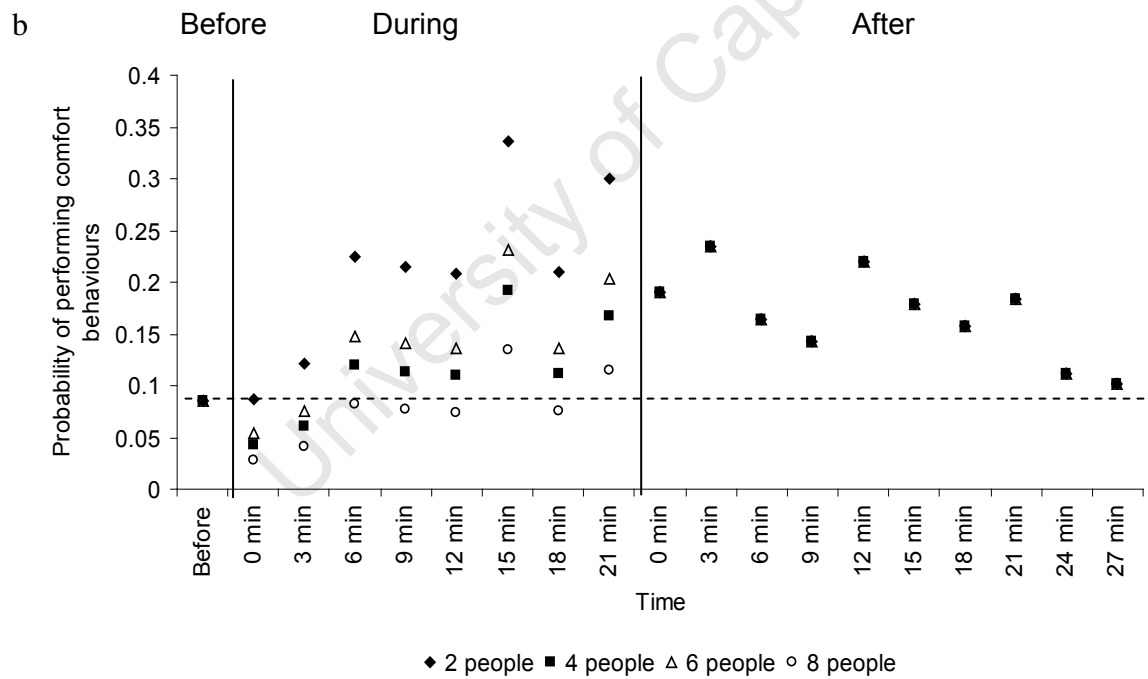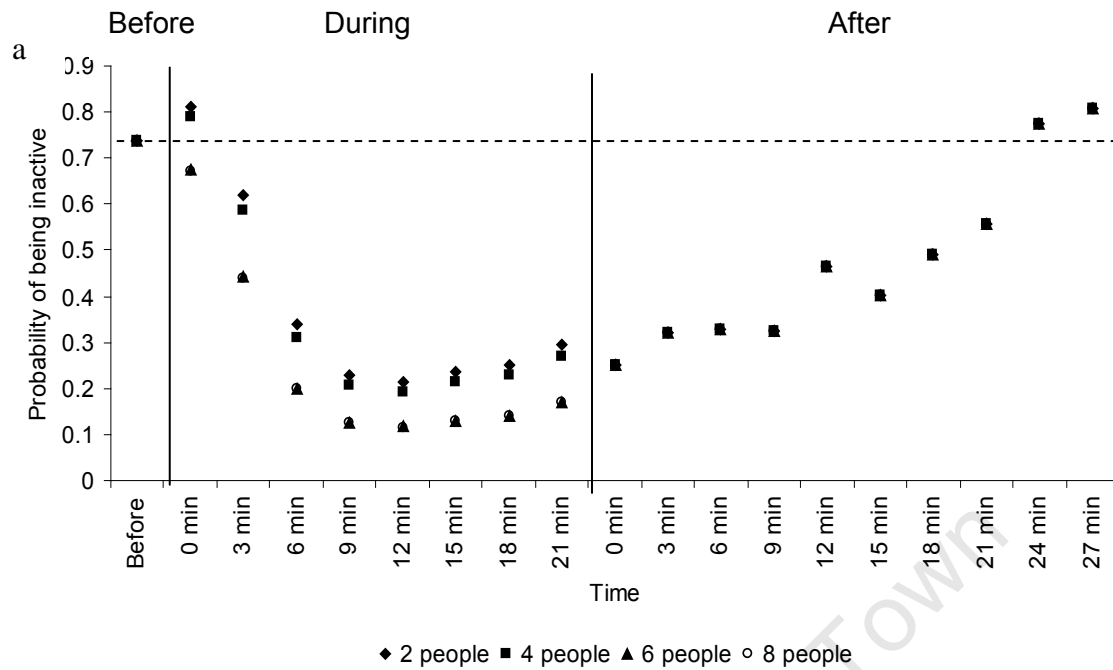
Figure 6: Response behaviour of non-breeding fur seals at Boulder's Beach, Marion Island when visited by pedestrian groups of 2, 4, 6 or 8 people. Probability of being being a) inactive, b) performing comfort behaviours, c) upright and d) alert. The dashed lines indicate the predisturbance level.

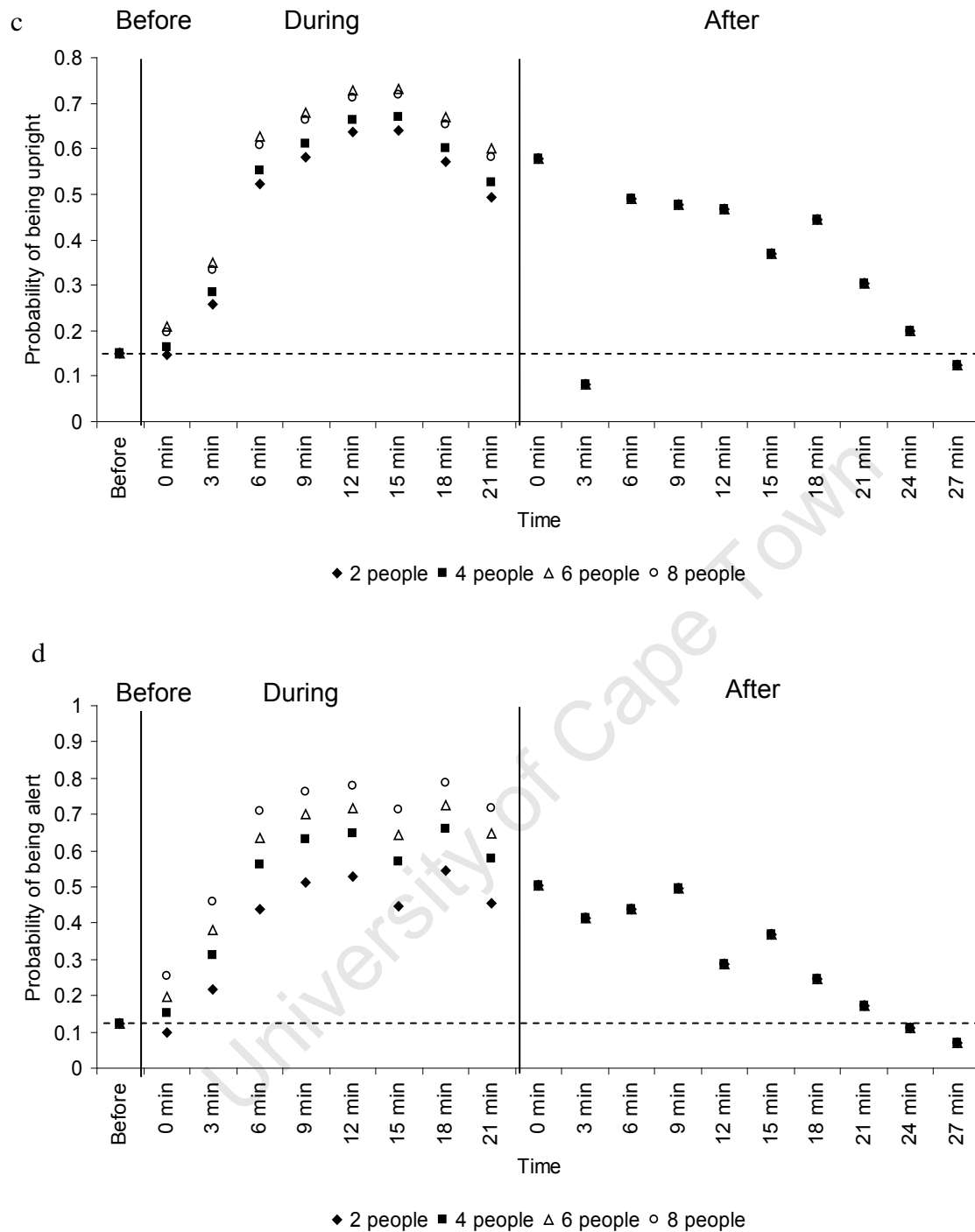Table 1 Results of the Generalised Linear Modelling of four behavioural responses (upright, inactive, alert and comfort behaviours) of non-breeding fur seals (mainly Subantarctic fur seal) at Boulder's Beach, Marion Island when exposed to helicopter disturbance in 2005. The result of responses on flight days are given relative to on non-flight days, levels of helicopter disturbance (engines audible, not in air, helicopter/s in air, direct overflight) to in the absence of disturbance, and Grass Intersection and Up Slope relative to Boulders. Significant results are indicated in bold.

Explanatory variables	Upright		Inactive		Alert		Comfort behaviours	
	Estimate	(se) t_{627}, P	Estimate	(se) t_{627}, P	Estimate	(se) t_{627}, P	Estimate	(se) t_{627}, P
On flight day	**0.499**	**(0.124) 4.03, P<0.001**	-0.163	(0.084) -1.94, P=0.053	**0.563**	**(0.109) 5.15, P<0.001**	-0.249	(0.135) -1.85, P=0.065
Engines audible, not in air	**0.748**	**(0.207) 3.61, P<0.001**	**-1.27**	**(0.15) -8.67, P<0.001**	**1.08**	**(0.18) 6.16, P<0.001**	**0.599**	**(0.250) 2.4, P=0.017**
Helicopter/s in air	**1.00**	**(0.14) 7.04, P<0.001**	**-0.897**	**(0.117) -7.68, P<0.001**	**0.754**	**(0.145) 5.2, P<0.001**	**0.464**	**(0.195) 2.38, P=0.017**
Direct overflight	**1.70**	**(0.19) 8.99, P<0.001**	**-1.28**	**(0.11) -11.34, P<0.001**	**1.17**	**(0.14) 8.61, P<0.001**	**0.518**	**(0.191) 2.71, P=0.007**
Grass Intersection	**-0.624**	**(0.084) -7.42, P<0.001**	**0.314**	**(0.054) 5.79, P<0.001**	**-0.352**	**(0.075) -4.69, P<0.001**	**-0.180**	**(0.079) -2.28, P=0.023**
Up Slope	0.0176	(0.0899) 0.2, P=0.85	**0.286**	**(0.064) 4.49, P<0.001**	-0.0980	(0.0866) -1.13, P=0.26	**-0.511**	**(0.101) -5.07, P<0.001**

Table 2. Results of the Generalised Linear Modelling of four responses (upright, inactive, alert and comfort behaviours) of non-breeding fur seals (mainly Subantarctic fur seal) at Boulder's Beach, Marion Island when exposed to pedestrian disturbance. Results are given for the number of people present on the beach. The results for Grass Intersection and Up Slope are given relative to Boulders, second approaches relative to first approaches, and afternoon relative to morning. Explanatory variables that were not significant were excluded from the model. Significant results are indicated in bold.

Explanatory variables	Upright		Inactive		Alert		Comfort behaviours	
	Estimate	(se) t_{503}, P	Estimate	(se) t_{505}, P	Estimate	(se) t_{504}, P	Estimate	(se) t_{503}, P
2 persons	**1.71**	**(0.37) 4.6, P<0.001**	**−1.90**	**(0.31) −6.14, P<0.001**	**1.77**	**(0.36) 4.94, P<0.001**	**1.52**	**(0.43) 3.52, P<0.001**
4 persons	**1.83**	**(0.40) 4.56, P<0.001**	**−2.03**	**(0.34) −6.02, P<0.001**	**2.26**	**(0.39) 5.79, P<0.001**	0.762	(0.519) 1.47, P=0.14
6 persons	**2.13**	**(0.42) 5.11, P<0.001**	**−2.62**	**(0.37) −7.06, P<0.001**	**2.57**	**(0.41) 6.32, P<0.001**	1.00	(0.57) 1.78, P=0.076
8 persons	**2.06**	**(0.44) 4.73, P<0.001**	**−2.62**	**(0.39) −6.79, P<0.001**	**2.89**	**(0.42) 6.83, P<0.001**	0.333	(0.658) 0.51, P=0.61
Grass Intersection	**−0.410**	**(0.114) −3.6, P<0.001**	0.185	(0.099) 1.87, P=0.061	**−0.354**	**(0.116) −3.06, P=0.002**	−0.160	(0.152) −1.05, P=0.29
Up Slope	**−0.844**	**(0.114) −7.42, P<0.001**	**0.906**	**(0.100) 9.05, P<0.001**	**−0.777**	**(0.115) −6.76, P<0.001**	**−1.20**	**(0.19) −6.45, P<0.001**
2nd Approaches	**−0.417**	**(0.198) −2.1, P=0.036**	–		**−0.667**	**(0.202) −3.3, P<0.001**	**0.931**	**(0.330) 2.82, P=0.005**
Afternoon	**−1.03**	**(0.16) −6.67, P<0.001**	**1.43**	**(0.09) 16.12, P<0.001**	**−0.812**	**(0.155) −5.24, P<0.001**	**−0.824**	**(0.231) −3.57, P<0.001**
Precipitation falling	–		–		–		**−0.809**	**(0.252) −3.2, P=0.001**
Windy conditions	**0.897**	**(0.119) 7.55, P<0.001**	**−0.793**	**(0.094) −8.44, P<0.001**	**0.981**	**(0.122) 8.04, P<0.001**	**0.400**	**(0.180) 2.22, P=0.026**

Quantitative evidence of responses to human disturbance and consequent recommendations for the management of disturbance at Marion Island

Main findings of this thesis

Guidelines and r egulations t o reduce po tential neg ative ef fects o f hu man di sturbance on wildlife are more l ikely t o be effective i f ba sed on q uantitative ev idence o f r esponses o f animals (Booth and Bio 2001, Harris 2005, Holmes et al. 2007) than on *ad hoc* observations. The aim of this thesis was to investigate the responses of a suite of seabirds and seals at Marion I sland (290 k m²; 46°54'S, 37° 45'E) to human ac tivities with t he potential to c ause disturbance, and to determine the effects of various extrinsic and intrinsic factors on these responses.

Wandering al batrosses (*Diomedea exulans*) responded behaviourally to s tandardised pedestrian approaches. Chicks close to the station responded least, indicating that they had habituated to frequent i ncidental disturbance. Adults far from the station responded least, indicating t hat adults close to the s tation and in the study colony had become s ensitised to disturbance over t ime. A dults were m ost r esponsive to di sturbance during prospecting f or nest sites and early incubation (Chapter 1). Sensitisation by adults of this species to chronic disturbance w as c onfirmed by t he r esults pr esented i n C hapter 2. B irds at t he s tation responded most. Adults at a second site far from the station that is seldom visited by humans were less likely to stand up on their nests than birds at the station and in one of t he study colonies. The frequency of r epeated approaches over three consecutive d ays did not affect the behavioural responses of t hese far-station bi rds, but bi rds t hat w ere appr oached m ost often (six times over three consecutive da ys) had l ower chick survival two weeks later than birds that were approached fewer times. The intensity of non-vocal response of birds did not differ between the three distance intervals tested (5–10 m, 10–15 m, 15–20 m away from nest) (Chapter 2) . N o s ignificant di fferences i n corticosterone l evels w ere found between

birds w ith di fferent l evels of c hronic di sturbance. However, f ar-station f emales had significantly higher prolactin levels than disturbed birds near the station and in the study colony. P rolactin i nfluences t he behaviour, phy siology and m orphology of ani mals dur ing parental stages (Sharp et al. 1988, Buntin 1996) and disturbance might negatively affect the parental behaviours of chronically disturbed birds (Chapter 3).

Grey-headed albatrosses (*Thalassarche chrysostoma*) responded to research disturbance by being more likely to stand up and t o be r esponsive (alert, aggressive, or threatening) during disturbance than before disturbance. Rates of recovery to pre-disturbance levels of behaviour were variable. Breeding success of the demographic study section of the colony (where nest contents were checked monthly during the breeding season) did not differ from sections where nest contents were checked less frequently (2004/05) or from sections that were monitored remotely through fixed-point photography (2005/06 and 2006/07). The size of t he colony sections d id not i nfluence br eeding s uccess, but av erage r ainfall i nfluenced success in the 2006/07 breeding season (Chapter 4).

Single-person visits to king penguin (*Aptenodytes patagonicus*) groups resulted in decreased probabilities of resting and increased probabilities o f vigilance and comfort behaviours. Breeding groups were as vigilant as non-breeding groups, but more likely to be r esting (less likely to move away) and less likely to perform comfort behaviours than non-breeders. T he greater the starting distance of the approach, the sooner the first bird in a group started to walk. More time was r equired for recovery after long-duration visits t han after short-duration visits. Penguins on more-frequently visited beaches seemed to have habituated to disturbance, as they w ere less v igilant and l ess l ikely t o per form comfort behav iours t han penguins on beaches that were visited less frequently (Chapter 5).

Animals perceived helicopter flights as threatening, but no nest desertions and no pr edation events were observed. Animals might have responded to both the auditory and visual stimuli

of hel icopter flights, bo th o f which would have increased in intensity as t he hel icopter got closer. Breeding gentoo penguins responded to helicopter disturbance by being more alert, especially during the initial frights they received when the helicopter was grounded but engines w ere audi ble and when the helicopter w as c lose t o t he c olony. During f lights penguins were more likely to be protecting their nests, especially when the Bell 212 flew - brooding penguins were more likely to "sit-tight" on their nests while guarding penguins were more l ikely t o s tand n ext t o their c hicks. These responses were similar t o an tipredatory responses. Grey-headed albatross chicks also seemed to be startled by the Bell 212 when it was noticed in t he area and during a flight c. 20 m f rom t he ridge, but s ome chicks had resettled on nes ts by t he t ime t he hel icopter reached the field hut. Chicks were more responsive and more likely to perform comfort behaviours during flight periods than non-flight periods. After the flight on Day 1, chicks were more likely to be standing and to be performing comfort behav iours, i ndicating that t hey r equired t ime t o r ecover from t he di sturbance. No nest des ertions by i ncubating grey-headed al batrosses w ere obs erved or r ecorded from photographs taken before and after flights by a Kamov KA32 helicopter. Incubating Crozet shags (*Phalacrocorax melanogenis*) r esponded t o a r escue c raft by bei ng l ess l ikely t o be inactive, less likely to be alert and more likely to be performing comfort behaviours. On flight days, birds were more likely to be alert and less likely to be performing comfort behaviour. When a hel icopter (Bell 212 or Sikorsky S61L) was close to the colony, birds were startled and were 172.0% more likely to be alert than when no helicopter was flying. The reactions of the incubating birds in response to the helicopter were more intense than reactions to potential avian predators close to the colony (Chapter 6).

Non-breeding birds were more likely to flee from disturbance than breeding birds, which were reluctant to abandon e ggs or c hicks. There were fewer r oosting Crozet shags at the colony during disturbance by rescue craft or helicopters. However, there were more roosting birds when potential avian predators were nearby. Some of these roosting birds may have been partners of the incubating birds and thus have stayed close to the colony to protect their eggs

from predators. Non-breeding king penguins responded to flights by the Bell 212 and the Sikorsky S61L by moving away from the area in large numbers (Chapter 6).

Many non-breeding Subantarctic fur seals (*Arctocephalus tropicalis*) also responded to helicopter flights by fleeing, either escaping into the ocean or moving farther inland during the first hours of flight operations. Individuals that remained on Boulder's Beach (where a Bell 212 and a Sikorsky S61L repeatedly flew over) were less likely to be inactive and more likely to be upright, alert and to perform comfort behaviours during flights than when there were no flights. Larger pedestrian groups resulted in more intense behavioural responses by seals on Boulders Beach than smaller groups. The maximum pre-weaning mass of pups that were weighed monthly at Sealer's Beach, Cape Davis, did not differ significantly from the mass of pups on beaches (Mixed Pickle Cove and Swartkop Beach) where pups were not weighed and where personnel seldom visited, indicating that the current level of research disturbance on this species did not influence pup condition (Chapter 7).

Management considerations

Incidental disturbance

Minimum approach distances are often set at the distance at which animals begin to flee (Blumstein et al. 2003). However, it has been suggested that they should rather be set at the distance at which an animal begins to exhibit alert behaviours (Rodgers and Smith 1997) or even at a distance far enough that no effects are visible (Holmes et al. 2005). At Marion Island, the results presented in this thesis support the current recommended minimum approach distance of 15 m to breeding seabirds, which seems effective and even conservative during most phases of the breeding cycle. However, wandering albatrosses were more sensitive to disturbance during prospecting and early incubation and it is recommended that the minimum approach distance to birds during these phases should be the same as the 50-m proposed distance for courting birds (Chown et al. 2006). A minimum

approach distance of 15 m is effective for visits to king penguins, because more than half of a group did not walk at distances greater than 15 m from the group and group-alert responses were rare (only two groups became alert at distances greater than 15 m and one group became alert at a smaller distance). However, these responses of king penguins should be considered to be minimum responses to visits. Responses are likely to be more intense when beaches are visited more frequently or by larger groups of people. It has been recommended that approach distances be increased as the number of visitors to breeding birds increases, that pedestrian group size be capped or that minimum approach distances be set at a distance appropriate to the largest expected visitor group size (Beale and Monaghan 2004). It is therefore recommended that the current recommended distance of 15 m be maintained for king penguins. When regulating visits to non-breeding seals on beaches, the number of visitors, their behaviour and the frequency of visits should be considered. Further research to determine the minimum approach distance to seals is recommended. To ensure that personnel can visualise a minimum approach distance of 15 m when in the field, a small pole can be placed 15 m away from each pathway close to the station.

The behaviour of visitors to the island can influence the responses of the animals. Currently copies of the introductory guide to Marion and Prince Edward Island (Hänel and Chown 1998) and the management plan (Prince Edward Island Management Plan Working Group 1996) are made available to personnel of the overwintering team, resupply personnel and construction personnel. During resupply voyages, the conservation officer also presents a talk onboard the ship to inform personnel about management regulations on the island. However, it is recommended that the main results of this study also be made available to personnel by means of a brochure and displayed posters. The minimum approach distances at the island are recommendations only. Personnel often approach closer than these distances because the responses of animals at the island appear minor. Awareness of the potential negative effects of human approaches might result in greater respect for the

animals and improved adherence to the recommended distances. This study also identified response behaviours that visitors can use as signals of stress in animals. Vigilance was a useful sign for wandering albatrosses, king penguins and seals. The intensity of vocalisations of wandering albatrosses is especially useful and can easily be identified by scientists and non-scientists. Agonistic behaviours of king penguins can also be used to assess disturbance levels. If personnel observe these responses then they should retreat, even if they have not yet reached the recommended minimum approach distance.

The annual resupply period at Marion Island takes place from April to May. This important logistical period is characterised by high levels of incidental disturbance to animals in the Natural Zone, as well as helicopter flights to other areas on the island to resupply the field huts (Chown et al. 2006). These months seem to be the optimal time frame for these operations, because they do not coincide with the incubation or pupping periods of any of the animals on the island.

Research disturbance

Long-term population demography studies on the island are important to obtain data on trends through time and factors that can influence breeding success and survival. However, research activities influenced the behaviour and physiology of wandering albatrosses and the behaviour of grey-headed albatrosses. The demographic study colonies have been established for monitoring purposes and have been afforded Zone 4 status (the highest level of management protection on the island) to restrict the level of incidental disturbance to these birds. However, birds in study colonies are directly approached and handled and are therefore more disturbed than birds in other areas. Disturbance levels are especially high at the Macaroni Bay study colony due to the high level of research disturbance and incidental disturbance caused by pedestrians walking on a footpath along the seaward colony boundary. Birds in this colony have been found to have low prolactin levels and high levels of stress proteins (de Villiers et al. submitted). After the field work for this study was completed,

a more intensive and more intrusive study on the wandering albatrosses at Goney Plain commenced with birds visited daily. Although wandering albatrosses in these colonies are affected by research, only 5% of the annual breeding population of the Prince Edward Islands nests in these areas (Crawford and Cooper 2003). The effect on the local population is thus likely to be minimal, nevertheless it is recommended that research programmes should consider the potential effects of their studies on the birds and use nonintrusive methods where possible.

Although grey-headed albatrosses responded during research disturbance, birds in the study section did not have reduced breeding success compared to birds in other sections. Visits to the study section, and the ringing of chicks and breeding adults, provide valuable information. It is recommended that fixed point-photography be used in other sections to assess breeding success in the absence of disturbance.

Monthly weighing of pups did not influence pup condition. Comparisons of pre-weaning weights between sites is a useful way of controlling for the effects of disturbance associated with research and one that could be built into future seal research programmes on the island.

Helicopter disturbance

Recommendations for aircraft operations at Marion Island have been made by Cooper et al. (1994) and the new management plan (Chown et al. 2006) provides more extensive guidelines. The effects of helicopter flights during this study were minor, because no nest desertions or predation events were observed. However, the closeness of the helicopter to the colony was an important variable influencing the responses of birds. The proposed recommendation to avoid flights closer than 250 m to breeding colonies (Chown et al. 2006) is therefore supported. Further research on the effects of helicopter disturbance should include measurements of height and distance from colonies.

The noise level of different helicopters can differ. In this study, gentoo penguins were more likely to be protecting their nests when the Bell 212 flew than when the Sikorsky S61L flew. Different helicopters are used during different periods at Marion Island according to logistic requirements. It is important that distances to breeding colonies be considered when helicopters with greater noise levels are used. The Kamov KA32 helicopter, for example, has the potential to create particularly high levels of disturbance.

Some species are especially sensitive during certain phases of the breeding cycle. It is also important to note that possible physiological responses and therefore long-term effects due to helicopter disturbance were not assessed in this study. The new management plan (Chown et al. 2006) suggests that flight paths might have to be adapted seasonally and that experts and the conservation officer be consulted prior to flight operations. This is strongly supported.

Further considerations

Although tourism is allowed at many sub-Antarctic islands, with numbers of tourists as great as 5 436 during 49 visits at South Georgia in the 2005/06 season (Government of South Georgia and the South Sandwich Islands 2006) and 750 per season at Macquarie Island (Tasmanian Parks and Wildlife Service 2003), tourism is not allowed at several other Southern Ocean islands, including the Prince Edward Island group (de Villiers et al. 2006). Despite the fact that tourism at the Prince Edward Islands is not allowed under the National Environmental Management: Protected Areas Act (Act No. 57 of 2003), the Department of Environmental Affairs and Tourism received three applications from tourist companies in the 1990s. An Environmental Impact Assessment of the negative and positive effects of future tourism at the island was conducted (Heydenrych and Jackson 2000). Land-based tourism at the island is still prohibited, however an offshore tourist cruise was made into the islands' territorial waters in 2002. If the frequency of such offshore cruises increase, studies should

be done on t he m inimum appr oach di stances for c ruise v essels as t hey m ight di sturb the feeding patterns of inshore feeders and the breeding colonies along the coast.

In future, if decisions are to be made on the potential impact of increased levels of incidental disturbance to the island it would be important to consider the responses of the species studied here as minimum responses. Most of the approaches done during this thesis were made by s ingle per sons and at l ow f requencies. Lar ger groups o f peopl e at higher frequencies w ould m ost likely r esult i n greater responses from animals. Further studies on the e ffects o f pede strian gr oup size c ould be done by u sing a rtificial dummies t o im itate larger group sizes as used by Schuster (2008) to determine the behaviour and hear t rate of Adélie peng uins (*Pygoscelis adeliae*) dur ing pe destrian app roaches. This pr otocol w ill al so allow different factors of pedestrian behaviour, for example noise levels to be controlled. If logistic activities are planned that are different in terms of timing, intensity or location on t he island than tested here, the effects of disturbance are likely to be di fferent from the findings here. It is recommended that dedicated monitoring should co-occur with such activities.

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