Measuring the Effect of Human Activity on Weddell Seals (*Leptonychotes weddellii*) in Antarctica

Submitted by

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Statement of Originality

This thesis contains no material which has been accepted for a degree or diploma by the University of any other institution, except by the way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief, this thesis contains no material previously published or written by another person except where due acknowledgement is made in the text.

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Abstract

Although guidelines exist for approaches to, and vehicle use (over-snow vehicles, aircraft and watercraft) in the vicinity of, Weddell seals (*Leptonychotes weddellii*), there has been no scientific assessment of the effectiveness of these guidelines in minimising disturbance to the seals. This study examined the response of Weddell seals to various forms of human activity that the seals are currently exposed to. A series of controlled experiments were conducted to measure, (i) the immediate behavioural and physiological responses of lactating Weddell seals (and their pups) to approaches on foot, and the factors affecting the seals’ response, (ii) the temporal nature of the seals’ response to repeated pedestrian activity and (iii) the immediate behavioural response of lactating cows to over-snow vehicle operations, and the factors that affect their response. In addition, sound/distance profiles were developed for commonly used Antarctic vehicles and the assumed detection threshold of Weddell seals was determined to investigate whether the noise generated by a range of vehicles had the potential to affect Weddell seals.

Most lactating Weddell seals and lone pups responded to visits on foot (from 20-5 m from the seals) by becoming alert. The separation distance at which the cows became alert was dependent upon the approach type (a single person or group of people), the distance a cow was from the water, the distance she was from a conspecific, and whether her pup was exposed (i.e. whether the pup was between the approachers and the cow). The relative importance of these factors indicated that the seals perceived pedestrians to be a threat, but that the level of threat was low.

Regular and frequent approaches by a single person to lactating Weddell seals over a short time period (< 2 hours) produced evidence of rapid habituation. However, irregular approaches over a longer time period (~3 weeks), did not result in seals showing any sign of having habituated. The results suggested that the cows may have already become sensitised to human activity prior to the experiment and that pups became sensitised to pedestrian activity.

Onshore heart rate of the seals in the absence of people revealed a daily periodicity in rate as well as three distinct heart rate patterns during resting behaviour and when the seal was looking in the water, i.e. the seal has its head immersed in water. Intra-seal variation in heart rate highlighted the importance of obtaining baseline data at a fine scale (e.g. hourly) before heart rate can be used as a proxy for stress in human-
wildlife interactions studies. Pedestrian approaches to a lactating seal did not elicit a heart rate response, suggesting that the approaches were not considered to be negative stimuli.

Most lactating Weddell seals responded to the operation of over-snow vehicles by becoming alert. Response was dependent upon the distance at which the vehicles were driven, the position of the pups in relation to the cow and the distance the cow was from the water. The relative importance of these factors indicated that the seals perceived the vehicles to be a threat, but that the level of threat was low.

Quantifying the effect of noise on the vocal behaviour of Weddell seals required the development of an assumed detection threshold of the species and sound/distance profiles of the commonly used vehicles in Antarctica. Much of the noise generated by these vehicles at the tested distances and speeds was barely audible to seals. However, there were some instances where the noise would have been clearly audible to seals both hauled out on ice and underwater. These higher noise levels were, however, still below the noise levels generated by the animals themselves and were therefore not expected to cause physical damage to the seals. Manipulative experiments did indicate that the underwater vocal behaviour of Weddell seals could be affected by continuous Hagglund noise, manifest as a decrease in the calling rate of seals.

This study has shown that the existing guidelines used in the Australian Antarctic Territory could be improved if the goal of management is to minimise disturbance to Weddell seals. Furthermore, the study has shown that the responses of the seals were influenced by a number of factors and that these could be incorporated into visitor and operational guidelines in order to increase their effectiveness and sensitivity.
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1 Introduction
In 1959 the Antarctic Treaty System was created to perpetuate peaceful activity in Antarctica and to develop a range of measures and agreements to control human impacts on the Antarctic environment as needed (Kimball 1999). In 1991 several tourist companies followed suit and founded the International Association of Antarctic Tour Operators (IAATO) to promote safe and environmentally responsible private-sector travel (IAATO 2004a). The concerns expressed in 1959 and 1991 are still relevant today, particularly as the number of people visiting Antarctica continues to increase (IAATO 2004a). Currently, guidelines for managing human activity are based on the 1991 Protocol on Environmental Protection to the Antarctic Treaty (also known as The Madrid Protocol) (Rothwell and Davis 1997). While these guidelines attempt to protect the wildlife by minimising disturbance, their scientific basis has never been objectively investigated to determine their validity as a means of minimising disturbance to wildlife.

The focus for this study is the guidelines for managing human activity in regard to Weddell seals (*Leptonychotes weddellii*). Specifically, the purpose of the study was to measure the effects of pedestrian, vehicle, aircraft and watercraft operations in the vicinity of the seals, with the view of verifying the existing guidelines and to make recommendations as appropriate.

### 1.1 Human-wildlife interactions

Interactions with wildlife occur through various ways, including research (e.g. Salter 1979; Hindell and Lea 1998), hunting (e.g. Tustin and Challies 1978; Peres 2001), tourism (e.g. Erwin 1989; Fowler 1999), and the operation of vehicles, aircraft and watercraft (e.g. Platt 1974; Henry and Hammill 2001). All of these interactions have the potential to negatively affect wildlife.

Effects vary in nature, some being transient, and others lasting for longer periods of time. For example, Lesage *et al.* (1999) found that exposure to small motorboat and ferry operations caused beluga whales (*Delphinapterus leucas*) to change their vocal behaviour (short term), while Creel *et al.* (2002) found that snowmobile usage caused elevated stress hormone levels amongst wolves (*Canis lupus*) and elk (*Cervus elaphus*) (short term with potential longer term consequences). Further, Safina and Burger (1983) found that scientific research activity significantly reduced the hatching and fledging success of black skimmers (*Rynchops niger*) (longer term). These examples also show that human activity can affect wildlife at the individual level and at the population level, so in the case of the black skimmers, individual
birds are directly affected by human activity, which in turn affects their offspring and therefore the future of the colony (Safina and Burger 1983).

The above examples demonstrate that human activities can affect the behaviour, physiology and breeding success of individuals. Researchers and wildlife managers worldwide have become increasingly interested in both the actual responses of wildlife to human activity as well as the follow-on affects of human activity. Thus, there have been investigations, for example, into the effect of wildlife tourism operations on the behaviour of polar bears (*Ursus maritimus*) (Dyck and Baydack 2004) and of tourist boat operations and swimmers on the behaviour of bottlenose dolphins (*Tursiops truncatus*) (Constantine 2001; Constantine et al. 2004) and the reproductive success and fitness of penguins (e.g. Giese 1996; Cobley and Shears 1999). The benefit of such studies is that it allows both researchers and wildlife managers to development management strategies to reduce any negative effects on the wildlife.

1.1.1 Factors affecting wildlife responses
Interpreting the results of human-wildlife interaction studies is complicated by the nature of human activity and the demographics of the species under consideration. Not only do the kinds of human activity take many different forms (e.g. approaches on foot, vehicles, aircraft and watercraft traffic), but each activity may also contain a range of visual, acoustic, and olfactory stimuli that impact on how the animals respond. As a consequence, the response of wildlife can be stimulus, species and situation specific. For example, New Zealand fur seals (*Arctocephalus forsteri*) were significantly more affected by approaches on land than by approaches by kayaks or boats (Boren et al. 2002), for a colony of harbour seals (*Phoca vitulina concolor*), paddleboats are more likely to cause a flushing event than motorboats (Lelli and Harris 2001), and for ringed seals (*Phoca hispida*), escape responses are greater when exposed to helicopters than when exposed to fixed-wing aircrafts (Born et al. 1999).

For vehicular activity, including aircraft, watercraft and over-snow vehicles, a range of factors related to the stimulus that can influence an animal’s response include the physical structure of the vehicles (*i.e.* size and shape), its speed of travel, the operation distance, the manner in which it is operated and the level and frequency of sound generated (e.g. Richardson et al. 1995; Richardson and Würsig 1997; National Research Council 2003). A large vehicle generally elicits stronger responses among wildlife than a small one and an increase in speed often results in
higher noise levels (McCauley and Cato 2003). The speed of an approaching stimulus may also make it appear more threatening (Dill 1974). The duration of exposure to vehicles can also affect wildlife behaviour. Harbour seals are less likely to haul-out again if disturbance from boat traffic persists for a long time (Allen et al. 1984).

For pedestrian activity, factors related to the stimulus that can influence wildlife response include group size, visitor behaviour and approach distance. For example, the frequency of threat behaviour, escape behaviour and aggressive behaviour of South American fur seals (Arctocephalus australis) in response to tourist approaches appears related to approach distance and visitor behaviour, as approaches to $< 10$ m elicit strong responses, while approaches $> 10$ m elicit weak responses (Cassini 2001). In the same study, the behaviour of visitors had a significant effect on fur seal reactions, with approaches by calm people resulting in almost no response, while tourists who shouted, ran and/or moved their arms elicited strong responses (Cassini 2001). Similarly, in a study on female harp seals (Phoca groenlandica) with pups, tourists who remained calm, moved slowly, crouched while viewing the seals and kept some distance, caused little or no response amongst the seals (Kovacs and Innes 1990).

Factors related to the animal, such as its gender, stage of breeding, age and previous exposure to a stimulus, can also influence wildlife responses to human activity (e.g. Kovacs and Innes 1990; Constantine 2001; Lusseau 2003). Adult female Atlantic walruses (Odobenus rosmarus) will respond sooner to aircraft overflights at terrestrial haul-outs than will their male counterparts (Salter 1979). Equally, the response of New Zealand fur seals approached by pedestrians and small boats will vary according to the sex and age of individual seals, with adult females entering the sea, adult males staying to fight and pups running and hiding from the approaching people (Boren et al. 2002). In the same study, previous exposure to the stimulus was considered to be one of the most important factors influencing how a fur seal responded to human activity (Boren et al. 2002). Specifically, the seals at an undisturbed site showed higher levels of avoidance/aggressive responses and more changes in behaviour than did seals at regularly exposed sites, indicating that experience is another important factor.

The response of wildlife to human activity is to some extent analogous to the response of wildlife to predators (Frid and Dill 2002). In both circumstances, time is
diverted from ‘fitness-enhancing activities’ such as feeding, parental care or mating displays, in favour of responding to the perceived threat associated with the stimulus. Response to predators and even conspecifics is influenced by the distance the animal is to a shelter, the distance the animal is to a conspecific and whether the animal has offspring, including the position of that offspring relative to the adult (Robinson 1981; Ydenberg and Dill 1986; Dill and Houtman 1989; Blumstein et al. 2003). The distance that the animal is to a refuge can influence the flight response, i.e. fleeing, of an animal exposed to a predator. For example, in a study on grey squirrels (Sciurus carolinensis), a model predator (a stuffed cat) was able to approach to a closer distance when the squirrels were closer to a refuge, in this case, a tree (Dill and Houtman 1989). Similarly, the distance an animal is to a conspecific can influence its behaviour, in particular vigilance behaviour. For example, wedged-capped capuchin monkeys (Cebus nigrivittatus) will show reduced vigilance with increasing proximity to the nearest neighbour (Robinson 1981), and rabbits (Oryctolagus cuniculus) will display reduced vigilant behaviour with increasing proximity to consorts, while vigilant behaviour increases with proximity to non-consorts (Roberts 1988).

Females with young tend to be more aggressive than adult females without young (Bones et al. 1982; Harcourt 1991; Miller 1991; Maestripieri 1992). Aggression and vigilance have been associated with territory maintenance and the protection of offspring. For female rhesus monkeys (Macaca mulatto), the position of the young influences vigilance behaviour, with females spending significantly more time looking up when infants were out of physical reach than others whose infants were within arm’s length (Leighton-Shaprio 1986).

The above examples demonstrate that various factors influence the response of wildlife to human activity and that these need to be taken into account in studying the response of wildlife to human activity.

1.1.2 Human-wildlife interactions in Antarctica
Antarctic wildlife has been exposed to human activity since the advent of scientific research expeditions to Antarctica in the early 1900s, the building of scientific research stations and the development of commercial tourism in the late 1950s (Spletstosser and Folks 1994; Kimball 1999; Bauer 2001). Although research specifically directed at measuring the effects of human activity on Antarctic wildlife is limited and biased towards avifauna, particularly penguins, work done to date has
shown that human activity can cause changes in the behaviour and physiology of animals, with further consequences for reproductive success and the stability of local populations (e.g. Ainley et al. 1983; Muller-Schwarze 1984; Wilson et al. 1990; Young 1990).

Comprehensive studies have been conducted on the effects of pedestrian visitation and human activity in general on Adélie penguins (Pygoscelis adeliae) by Wilson et al. (1989; 1990), Culik et al. (1990), Woehler et al. (1991), Nimon et al. (1995) and Giese (1996; 1998; 1999), and on the behaviour of emperor penguin chicks (Aptenodytes forsteri) in response to helicopter operations (Giese and Riddle 1999). In other studies, the effects of aircraft and scientific handling on emperor penguins have also been examined (Boyd and Sladen 1971; Regel and Pütz 1997). Gentoo penguin (Pygoscelis papua) breeding performance has also been examined (Cobley and Shears 1999).

The only studies to date that have examined the effects of human activity on Antarctic marine mammals have been conducted on the Southern elephant seal (Mirounga leonina) (Wilkinson and Bester 1988; Burton and van den Hoff 2002; Engelhard 2002; Engelhard et al. 2002a; Engelhard et al. 2002c). Burton and Van den Hoff (2002) looked at indirect effects of human activities, such as competition with fisheries, seal mortality through discarded fishing gear and pollutants in the ocean on Southern elephant seal populations. In doing so, opportunistic observations were made of the behavioural response of 14 male elephant seals to helicopter operations on Macquarie Island (54°30'S, 158°57'E). The only discernible response from the seals was increased head-lifting during helicopter operations (Burton and van den Hoff 2002). Wilkinson and Bester (1988) showed that research activities on Marion Island (64°52'S, 37°51'E) did not have any deleterious effects on Southern elephant seals breeding there. In this case, the measure of disturbance was the overall abundance of adult cows, weaned pups and dead pups at disturbed versus undisturbed sites.

The research by Engelhard et al. (2002; 2002a; 2002b; 2002c) is by far the most comprehensive study on the effects of human activity on the Southern elephant seal conducted to date. Their studies examined endocrinological, clinical-chemical, haematological, immunological, behavioural and mass-related parameters to investigate the impact of people on female seals and their pups during lactation. This research showed that there was no significant difference in the level of stress
hormones between mothers and pups in areas of high and low human presence (Engelhard et al. 2002b), no significant difference in mother-pup pairs in clinical chemistry and blood composition (Engelhard et al. 2002c), no difference in the haematological parameters for the pups (Engelhard et al. 2002c), and no significant difference in mass-related parameters of weaned pups (Engelhard et al. 2002a). The only evidence of an effect of human activity was a threefold increase in alertness among adult females in the presence of humans (Engelhard et al. 2002a).

From the above examples it is clear that human activity is capable of eliciting changes in the behaviour and physiology of Antarctic animals. The Weddell seal lives under and on the fast ice, which also represents a platform upon which people travel, work and explore as tourists. The species is therefore directly exposed to pedestrian visits by scientific research station staff and commercial tourists, to handling for scientific purposes, and to aircraft operations and over-snow vehicle traffic. Most of these interactions occur during the austral spring and summer when the seals are hauled out on the ice to breed and to moult and the number of people visiting and living in Antarctica is increased (Tedman et al. 1985; Hall 1992; Stonehouse 1992). During breeding, the energy demands on both lactating seals and their pups are substantial (Pond 1977; Ofstedal et al. 1987; Hastings et al. 1999), suggesting the seals may therefore be at their most vulnerable to disturbance from human activity at this time.

1.2 Guidelines for wildlife management

Scientific investigations into the effects of human activity on wildlife often aim to provide detailed information for the management of human-wildlife interactions (e.g. Shackley 1996; Weisenberger et al. 1996; Conomy et al. 1998; Higginbottom 2004a). In most cases, wildlife management involves the development of guidelines, and, even though specific guidelines vary with species and geographic location, the aims are ostensibly the same, to minimise disturbance caused by human activity (see for example Australian Government Department of the Environment and Heritage 2002; Kirkwood et al. 2003; Australian Antarctic Division 2004c).

The development of guidelines requires a practical definition of what constitutes disturbance and the level of disturbance deemed acceptable. Both of these factors depend on the goals of management, safety aspects, social expectations, legal requirements and ethical considerations (e.g. Claridge 1997; Moscardo 2001; Kirkwood et al. 2003; Higginbottom 2004a, b). For example, managers wishing to
minimise disturbance to wildlife might define disturbance as 'any' visible change in behaviour, while managers wishing to minimise disturbance to wildlife as well as maximise visitor satisfaction might define disturbance as a change in behaviour that has a significant biological consequence for the animal (i.e. adverse effects on reproductive success or survival). Thus, changes that have no biological consequence for the animal are considered acceptable. Both scenarios highlight the role of scientific study on the effects of human activity on wildlife and its importance in assisting managers in determining separation distances to maintain from the wildlife, and which behaviours have adverse biological consequence for the wildlife.

1.2.1 Guidelines for managing human-Weddell seal interactions
Interactions with wildlife in Antarctica are broadly governed by the Antarctic Treaty 1959 and associated agreements, collectively known as the Antarctic Treaty System (Rothwell and Davis 1997). In 1991, the Protocol on Environmental Protection to the Antarctic Treaty (The Madrid Protocol) was adopted by the Antarctic Treaty Consultative Parties to ensure the protection of the Antarctic environment and its dependent and associated ecosystems. The protocol applies to tourism and both governmental and non-governmental activities in the Treaty Area and is intended to “ensure that these activities do not have adverse impacts on the Antarctic environment, or in its scientific value and aesthetic values” (p. 118).

The Protocol contains a number of guiding principles relevant to minimising disturbance to Antarctic wildlife. For example, recommendation XVIII-Ia – Protect Antarctic Wildlife (p. 118), which governs general human activity around wildlife states:

“Do not use aircraft, vessels, small boats or other means of transport in ways that disturb wildlife, either at sea or on land.

Do not feed, touch, or handle birds or seals, or approach or photograph them in ways that cause them to alter their behaviour. Special care is needed when animals are breeding and moulting.”

Similarly, Article VI (Protection of native fauna) of the Antarctic Treaty Handbook states that:

“Each participating Government shall take appropriate measures to minimise harmful interference within the Treaty Area with the normal living conditions of any native mammal or bird, or any attempt at such harmful interference...” (US Department of State 2002).
In this case, harmful interference is suggested as occurring when aircraft or vehicles are operated in a manner, which would disturb concentrations of birds and seals, or where people on foot disturb bird or seal colonies. In neither the Protocol, nor the Treaty itself, is disturbance defined.

Within this framework, Antarctic Treaty Nations, and users operating in accordance with the Antarctic Treaty, such as the International Association of Antarctic Tour Operators (IAATO), which is a member organisation founded to advocate, promote and practice safe and environmentally responsible private-sector travel to the Antarctic (IAATO 2004a), must develop specific codes of conduct to manage on-ground activities. IAATO and many of the Treaty Nations with scientific research stations in Antarctica, such as Australia, New Zealand and France, have generated specific guidelines for interactions with wildlife (see Harris 2001; Australian Antarctic Division 2002b, 2004a, c). However, these guidelines, with the exception of pedestrian approaches to Adélie penguins and aircraft over-flights to emperor penguin chicks in Australian Antarctic Territory (AAT), are not based on rigorous scientific testing. At best the guidelines are based on anecdotal reports and observations of animals responding to different types of human activity.

Within the AAT, the Australian Antarctic Division (AAD) has developed guidelines relevant to managing human activity around Weddell seals (see Table 1.1). However, no scientific research has yet been conducted to investigate the effect of pedestrian and over-snow vehicle activity on the species, and determine the adequacy of the guidelines. Accordingly, it is not known, for example, how resilient or sensitive Weddell seal are to different types of human activities.

The AAD guidelines stipulate that the minimum approach distances are a guide only and that if the activity is disturbing the wildlife then greater distances should be maintained (Australian Antarctic Division 2004a). However, once again, no definition of disturbance is offered. Similarly, IAATO guidelines are intended to:

"avoid harmful impacts on marine wildlife populations by ensuring that the normal pattern of daily and seasonal activity of the animals are maintained in the short and long term" and specify that certain behaviours/actions should be prevented, which include: "disruption of reproductive and social behaviours" (IAATO 2005 pp. 1 & 3).

Further, the IAATO guidelines state that:

"any seal response other than a raised head should be avoided" (IAATO 2005 pp. 1 & 3).

Again, it is not clear what is meant by disturbance.
Even though the Madrid Protocol does not offer a specific definition of disturbance, recommendation XVIII-Ia states that approaches to wildlife must not elicit changes in behaviour (Rothwell and Davis 1997). Given that both the AAD and IAATO comply with the Madrid Protocol, 'disturbance' could be interpreted to mean any change in the visible behaviour of seals. For the purpose of this study, then, disturbance is defined as a change in visible behaviour.

Table 1.1 Minimum separation distances (m) from Weddell seals for human activity in the Australian Antarctic Territory (data from Australian Antarctic Division 2002a, b; Australian Government Department of the Environment and Heritage 2002; Australian Antarctic Division 2004c; IAATO 2005).

<table>
<thead>
<tr>
<th></th>
<th>On foot/ ski</th>
<th>Quad or skidoo</th>
<th>Tracked vehicle</th>
<th>Small boat</th>
<th>Aircraft</th>
</tr>
</thead>
<tbody>
<tr>
<td>Australian Antarctic Division</td>
<td>Adult females with pup and lone pups</td>
<td>15</td>
<td>150</td>
<td>250</td>
<td>50*</td>
</tr>
<tr>
<td></td>
<td>Lone adults</td>
<td>5</td>
<td>150</td>
<td>250</td>
<td>50*</td>
</tr>
<tr>
<td>International Association of Antarctic Tour Operators</td>
<td>All</td>
<td>5-10</td>
<td>30#</td>
<td>300 (vertical)#</td>
<td></td>
</tr>
</tbody>
</table>

* distance applies to seals in the water, on ice floes and onshore,
† all wildlife including seals.
# in water (specified for cetaceans only)

1.3 The aims of this study

The aims of this study were to measure the effects of human activity on Weddell seals, with a view to verify existing guidelines in regards to Weddell seals in the Australian Antarctic Territory, and make recommendations as appropriate. To achieve this, I conducted experiments to measure the behavioural response of Weddell seals to pedestrian approaches and over-snow vehicle operations. The study also aimed to investigate the effect of pedestrian approaches on Weddell seal physiology and to develop sound/distance profiles of vehicles commonly used in the AAT to determine whether vehicle noise has the potential to affect the Weddell seal.

The five specific objectives of this study, each the subject of a chapter of the thesis, were:
(i) to determine the immediate behavioural responses of lactating Weddell seals and their pups to pedestrian approaches;

(ii) to investigate the temporal nature of the behavioural responses of lactating Weddell seals and their pups to repeated exposure to pedestrian activity;

(iii) to determine whether the heart rate of lactating seals (on the ice) varied with respect to behaviour, (e.g. during rest or travel) and, further, to determine whether heart rate changed in response to pedestrian approaches;

(iv) to determine the immediate behavioural response of lactating Weddell seals to over-snow vehicle operations;

(v) to measure the noise generated by the commonly used Antarctic vehicles in the AAT, to develop an assumed detection threshold for Weddell seals and to determine whether vehicle noise affects the vocal behaviour of Weddell seals underwater.

1.4 Study site

The study was conducted at two locations in East Antarctica, Long Fjord, Vestfold Hills (68°35'S, 77°58'E) and Penny Bay, Windmill Islands (66°25'S, 110°40'E) (Figure 1.1 & 1.2). These locations are near the permanent Australian research stations of Davis and Casey, respectively. Fieldwork for the study was completed in three stages during the summers of 2000/01 and 2002/03 at the Vestfold Hills and 2001/02 at the Windmill Islands.

Five breeding colonies, all within 10 km of each other, were studied in the Vestfold Hills and one colony was studied in the Windmill Islands (Figures 1.1 & 1.2). Each colony contained between 20 and 40 cow-pup pairs and was readily accessible to people from nearby research stations. However, the colonies in the Vestfold Hills received more visitors per season than the Windmill Islands colony, as the Vestfold Hill colonies were located on common thoroughfares for people traveling to scientific and recreation areas from Davis Station. The average summer population at Davis Station is approximately 80 people, while at Casey Station this number is 55. Davis Station is approximately 15 km from the closest colony used in this study, while Casey Station is located approximately 25 km from the Windmill Islands colony. Seals in the Vestfold Hills have been subject to tagging and resighting studies (Green et al. 1995; Lake et al. 1997) during each summer from 1973/74 to 2000/01. No such studies have been conducted in the Windmill Islands.
Figure 1.1 Map of a section of the Vestfold Hills showing the location of the five Weddell seal colonies used in this study. Other symbols in the legend of this map relate to the locations of acoustic experiments, where Site A was used to generate the sound/distance profile for the quad, Hagglund and pedestrian. Site B was used to generate the sound/distance profile for the helicopter. Site C was used to generate the sound/distance profile for Twin Otter, and Site D was used to generate the sound/distance profile for the Twin Otter and the Zodiac.
1.5 Study species

1.5.1 General description

The Weddell seal is an Antarctic seal in the family Phocidae. It is the most southerly breeding mammal and the only mammal that regularly inhabits the fast ice areas of the Antarctic continent (Bonner 1999). The species has a circumpolar distribution, but can also be found on some sub-Antarctic Islands, with occasional sightings as far north as South Australia and New Zealand. The northern-most breeding population of Weddell seals is on South Georgia Island (54°30'S, 37°00'W) (Kooyman 1981c; Bonner 1999).
Weddell seals are semi-gregarious, polygamous, non-migratory and show strong fidelity to breeding sites (Stirling 1969, 1971; Kaufman et al. 1975; Bartsh et al. 1992). The seals haul-out on the ice for two main purposes: to breed and to moult.

Females haul-out on the fast ice to give birth to a single pup between September and November each year, with the specific timing increasing with latitude (Stirling 1969). Females remain close to their pups for the first 12 days post-partum, and then spend increasing periods of time in the water (Thomas and DeMaster 1983). Pups enter the water about two weeks after birth and are weaned after 6-7 weeks (Elsner et al. 1977; Tedman et al. 1985). Ovulation occurs at the end of lactation and copulation occurs underwater where males hold territories (Bertram 1940; Cline et al. 1971). Implantation is delayed until January/March when the seals have moulted and have resumed normal foraging activity (Stirling 1969; Miller 1991).

Both male and female Weddell seals haul out to moult between January and March each year. Unlike some other pinnipeds, hair replacement in Weddell seals occurs gradually allowing the seals to enter the water to forage (Wartzok 1991). The number of seals hauled out on the ice varies with time of day, with numbers peaking in the early afternoon when the sun is at its highest elevation and air temperatures are at a maximum (Green and Burton 1988; Bartsh et al. 1992; Bornemann et al. 1998). High skin temperatures are conducive to hair growth (see Wartzok 1991).

Weddell seals have large, well-developed eyes, capable of vision both in-air and underwater. Pinnipeds lack S-cones in their eyes so that they cannot see colour and therefore respond to brightness cues rather than hues (Schusterman et al. 1981; Peichl et al. 2001). However, they have a rod-saturated retina and a well-developed tapetum making the eye well adapted to low light conditions, such as those experienced underwater (Lavigne et al. 1977). Vision underwater in the Weddell seals is emmetropic (i.e. normal vision), but in-air is myopic and astigmatic (imperfect vision - near-sightedness).

The pinniped auditory system is adapted to hear both aquatic and airborne sounds, and is directional (Repenning 1972; Richardson et al. 1995; Kastak and Schusterman 1998). All pinnipeds studied to date show greater sensitivity to underwater sounds than to airborne sounds as a result of having a modified external meatus (the passage leading from the outside of the head to the eardrum) (Schusterman et al. 1981; Kastak and Schusterman 1999). Aural communication underwater is important in pinnipeds because the other senses of sight, smell and touch, have limited use in the
underwater environment (Ray and deCamp 1969). Most phocid calls are between 0.1 kHz and 15 kHz, but calls have been recorded as high as 40 kHz (Wartzok and Ketten 1999). The source levels of these calls in water is in the order of 130 dB re: 1 μPa, however, levels as high as 193 dB re: 1 μPa have been reported for the trills of Weddell seals (Thomas and Kuechle 1982a; Thomas and Kuechle 1982b; Richardson et al. 1995).

There is no specific data on the hearing ability of Weddell seals, but audiogram determinations and other psychophysical and anatomical studies indicate that all phocids are likely to have similar underwater hearing abilities (Terhune and Turnbull 1995). Of the phocid species tested, the upper limit of effective hearing is likely to be 60 kHz underwater and 20 kHz in air, although in-air sensitivity deteriorates as frequency decreases below 2 kHz (Richardson et al. 1995).

1.5.2 Behaviour
The behaviour of Weddell seals has been studied since the early 1900s, when Edward Wilson made a general study of the Weddell seal’s habitat (Kooyman 1969). Since then, the behaviour of the species has been extensively documented, with research investigating several aspects of behaviour, including diving (Kooyman 1967; Kooyman 1975), hunting (Davis et al. 1999), under-ice orientation and movement (Kooyman 1981a; Wartzok et al. 1989), cow-pup interactions (Tedman and Bryden 1979), colony behaviour (Kaufman et al. 1975; Bartsh et al. 1992), social behaviour and acoustics (Ray 1967), reproductive behaviour (Braun Hill 1987; Testa et al. 1987) and territorial behaviour (Kaufman et al. 1975; Bartsh et al. 1992). As the present study focuses on lactating females and their pups, the following description of behaviour focuses on the behaviours displayed during the lactation period.

During lactation, female Weddell seals spend most of their time hauled out on the ice where they nurture their pup. They also conserve energy whilst hauled out, and spend most of their time resting, as has been observed for most pinnipeds (Wartzok 1991). For the first two to three weeks post-partum, Weddell seal cows rarely enter the water (~1-3 times in total) and then only briefly. After that, the cows spend increasing periods of time in the water as the pup matures and learns to swim (Kaufman et al. 1975).

Weddell seals have a reputation of being docile, approachable and unafraid of humans (e.g. Stirling 1956; Kooyman 1981c), however both males and females can be aggressive towards intruders (both humans and conspecifics), particularly in the
vicinity of breathing holes and when their pups are present (King 1964; Smith 1966; Stirling 1969; Cline et al. 1971). Although anecdotal reports are few, upon the approach of humans, some seals have been seen to charge, change their body position, (e.g. roll onto their sides), vocalise, snap their jaws, move between the approacher and their pup and raise a flipper (similar to the threat posture of harbour seals) and flee over the ice or into the water (Ray and deCamp 1969; Kaufman et al. 1975; Siniff et al. 1977). Weddell seal cows have also been observed to bite their own pup in response to approaching humans (Kaufman et al. 1975). Instances of intense apparent tenacity and defence of a pup, even a dead pup, have also been described (Siniff et al. 1977). The pups themselves are generally reported to be inquisitive, but can act aggressively towards people, biting them if touched (Kaufman et al. 1975).

Responses to conspecifics include vocalisations, and snapping at and biting of adults and pups (Smith 1966; Kaufman et al. 1975). Females will snap their jaws at the approach of a male Weddell seal, but if persistent, she will roll over or move away (Smith 1966; Cline et al. 1971). The approach of a male seal is known to cause greater disturbance than the approach of either a female or pup (Kaufman et al. 1975). Females have also been observed to saw the ice with their teeth in response to conspecifics, which has resulted in this act being described as a displacement behaviour (Kaufman et al. 1975). Displacement behaviours are behaviours that are irrelevant to the situation in which they occur (Allaby 1999) and are conducted to focus attention away from the aversive stimulus to reduce anxiety (Harvey et al. 1984). However, others have suggested that ice-sawing is not a displacement behaviour and is only conducted by adult females to remove the steep edge of a tide crack to enable their pup to haul-out onto the sea ice (Lugg 1966) or to loosen the ice to enable ingestion of water (Stirling 1971).

Behaviours observed and quantified during this study are defined in the following chapters. From initial observations of the seals, 12 behaviours were identified (with the exception of a few occurrences, I noticed that all Weddell seals were resting on their sides rather than on their stomachs. However, this difference in body posture did not seem to be significant). The terms used to describe these behaviours are original, with the exception of comfort, defined in the Oxford Dictionary of Zoology (Allaby 1999), and ice-sawing described by Kaufman et al. (1975).
1.5.3 Physiology

Much of the research on the physiology of the Weddell seal has focussed on the physiology of diving. These studies have investigated the aerobic dive limit (e.g. Burns and Castellini 1996), oxygen transport (Davis and Kanatous 1999) and heart rate (HR) of the species (Kooyman and Campbell 1972). Other studies have investigated the basic biochemistry of Weddell seal blood (Murphy et al. 1982; Schumacher et al. 1992), plasma levels of hormones during apnea (Zenteno-Savin and Castellini 1998) and temperature regulation (Elsner et al. 1977). No research has been conducted on the physiological response of Weddell seals when exposed to human activities, however existing information on the HR of Weddell seals provides a useful background from which to examine HR responses to human stimuli.

The HR of Weddell seals during diving behaviour have been shown to be considerably lower (bradycardia) than during rest. For example Hill et al. (1987) recorded decreases of between 35 and 40 beats per minute (bpm) from resting HR to diving HR and Zapol et al. (1977) recorded decreases of 41 bpm from resting HR to diving HR. Heart rate during rest onshore has been recorded at 56 and 60 bpm for adults and 123 bpm for pups (Ray and Smith 1968; Zapol et al. 1977). Kooyman and Campbell (1972) recorded the HR of adult seals during sleep in ice holes as well as before, during and after dives. Heart rate was found to vary with respiration, with eupneic HR during rest averaging 64 beats per minute (bpm) compared to apnoeic HR averaging 34 bpm. The average HR during and after dives was 85 bpm. In another study, Hill et al. (1987) recorded HR during recovery after a dive of > 20 minutes duration at 98 bpm.

1.5.4 Vocal behaviour during the breeding season

The Weddell seal is a particularly vocal pinniped (Thomas and Kuechle 1982b; Evans et al. 2004); with somewhere in the order of 30-55 call types grouped into approximately 13 broad categories (Thomas and Stirling 1983; Pahl et al. 1997). Research on Weddell seal vocal behaviour is extensive, covering a number of different topics including, the proportional use of underwater calls (Pahl et al. 1996), patterns of underwater calls (Thomas et al. 1988), rates of calls (Serrano and Terhune 2001; Terhune et al. 2001), repertoire and geographic variation in underwater calls (e.g. Thomas and Stirling 1983), responses to playback experiments (Watkins and Schevill 1968; Thomas et al. 1983) and in-air call sequences (Terhune et al. 1994a).
Vocalisations are made by both sexes in-air and underwater throughout the year, and have even been recorded from sleeping seals (Stirling 1971). Diurnal and seasonal patterns in vocal behaviour have been identified, with the diurnal pattern depending on the time of year, with a peak-calling rate in November (Green and Burton 1988). A link between vocalisation and breeding has been proposed by Schusterman (1981), where the peak calling rate corresponds with the breeding season and the number of vocalisations decreases significantly thereafter (Thomas et al. 1987; Green and Burton 1988).

Males are more vocal than females and pups during the breeding season when they are communicating with breeding females as well as establishing, and vigorously defending, underwater territories (Thomas and Kuechle 1982b). Females, in contrast, are particularly vocal after the birth of their pup (Poulter 1968) and most of their vocal behaviour on the ice is associated with mother-pup interactions (Thomas 1979). Airborne vocalisations of pinnipeds in general appear to be associated with social organisation (Evans 1967).

A complete understanding of the vocal behaviour of the Weddell seal has not yet been established. In playback experiments of their own sounds, seals responded differently to each of the sounds played to them, implying that the various sounds had different meanings for them (Watkins and Schevill 1968). However, due to the short duration of the experiments this finding was difficult to prove definitively. Thomas et al. (1983) did however propose interpretations for a number of the vocalisations recorded in their study. The ‘Trill’, which is male-specific, was associated with territorial advertisement, territorial defence, dominance and warning. The ‘Chug’ was associated with aggressive behaviour, the ‘Mew’ was associated with high intensity threat behaviour and the ‘Growl’ and the ‘Grunt’ were associated with low intensity threat behaviours (also supported by Thomas and Kuechle (1982b) and Watkins and Schevill (1968)). In addition, Rouget (2004) proposed that the ‘Whistle descending’ (WD) call has a submissive function and might be used as a means of defense.

### 1.5.5 Colony behaviour

During the austral spring, female Weddell seals haul-out to give birth to a pup on the fast ice. They form colonies around tide-cracks, which facilitate access to the water (Tedman and Bryden 1979). The characteristics of these colonies are determined by
the stability of the fast ice, the availability of breathing holes and proximity to food resources (Stirling 1969).

Spacing of cow-pup pairs within the colony affects the movement of both cows and pups. Spacing is believed to be the result of cows occupying vacant sites as close as possible to tide cracks at the time of haul-out (Kaufman et al. 1975). Although the species is generally not regarded as territorial, cows maintain small ‘zones of interference’ with a radius of 3 m or less (e.g. Mansfield 1958; Ray and deCamp 1969; Stirling 1969; Smith and Burton 1970). These zones are maintained via mutual avoidance, vocal signals and attacks on intruders (Kaufman et al. 1975). Manipulative experiments show that females maintained at high colony densities experience a much higher rate of interactive stress, (i.e. interactions with conspecifics, as evidenced by fresh wounds), than those at low densities (Siniff et al. 1977). According to Tedman and Bryden (1979) territorial behaviour is based on pup defence and not on the space on the ice per se. This suggests that the ‘zone of interference’ is actually the space that the cow and pup occupy, and not a true territory.

As the breeding season progresses, spacing between cow-pup pairs within the colony reduces as seals move towards tide cracks because their pups are entering the water more often (Tedman and Bryden 1979). The distance between individual seals further decreases outside of the breeding season, which is evident in large groups of seals consisting of juveniles, adult males and females that form in January through to March to moult (Stirling 1971).

1.6 Response parameters used in this study

There are two types of immediate responses to human activity that can be measured in human-wildlife interaction studies; 1) a change in behaviour and 2) a change in physiology, indicated by parameters such as HR, respiratory rate, adrenal state or body temperature. Other parameters, such as reproductive success (e.g. Hunt 1972; Safina and Burger 1983) or population stability (e.g. Young 1990; Woehler et al. 1991) have also been measured to determine the effects of human activity on wildlife (see for example Fetterolf 1983; Safina and Burger 1983; Giese 1996), however, these parameters do not reflect the direct and immediate responses of wildlife as readily as do parameters such as behaviour or physiology.
1.6.1 Behaviour

Behaviour is the external expression of an animal’s response to stimuli from its internal or external environment (Hinde 1982) and appears to be the most common response measured in human-wildlife interactions studies. Behavioural observations made in both the absence and presence of human activity can reveal whether an animal performs or suppresses particular behaviours in response to human activity (Toates 1995). The behaviour can also reveal how an individual animal, and even a species, perceives a specific stimulus (i.e. whether it is of positive, negative or neutral consequence). Behavioural changes in response to human activity may also be taken as indicators of physiological changes that an animal is experiencing. For example, if an animal flees from a stimulus (e.g. a predator), sympathetic activity is increased, which in turns results in an increase in HR and cardiac output. Blood sugar is increased to support prolonged activity and blood flow to the skeletal muscle is increased to enable greater speed, agility and endurance (Gabrielsen and Smith 1995).

Changes in behaviour, such as increased vigilance, aggression or locomotor activity, can result in increased energy expenditure for adult seals and may reduce energy intake for pups if behaviours such as suckling are interrupted. For example, Kovacs (1990) found that tourist approaches to lactating harp seals caused the seals to enter the water. Those that remained in the colony did not subsequently provide their pups with normal care and females became more aggressive and occasionally clawed and bit their pup, causing injury. In a study of grey seals (Halichoerus grypus) by Fogden (1971), the presence of researchers in the colony also resulted in adult seals entering the water, with the long-term consequence of almost half of the pups (13 pups, 46%) being deserted by their mothers. In this case, crowding at the beach due to pups waiting for the return of their mother, resulted in increased aggression between seals, which in turn decreased the time spent suckling and was even thought to prevent suckling from occurring.

The advantages of measuring behaviour in the context of human-wildlife interaction studies include:

(i) the ability to measure the response of the animal to the stimulus with little or no interference to the animal, because it is possible to observe and record behaviour from a distance and from a (largely) hidden location. Behavioural results are therefore less likely to be confounded by methodology, and more likely to be a true reflection of an animal’s response.
(ii) compared to anatomical or physiological measurements, behavioural observations are relatively inexpensive to obtain because equipment costs, such as a video camera or a pair of binoculars and a notebook, are minimal.

(iii) behaviour can be defined and quantified with relative accuracy and, as behaviour is readily observable, visitors to breeding wildlife can be educated as to which behaviours to look for when approaching seals so that disturbance is minimised.

1.6.1.1 Limitations with behavioural responses
Although behavioural responses can provide complex information on how a stimulus is perceived and therefore whether the human activity is affecting an animal, it is not necessarily the most sensitive response parameter. In some animals, underlying physiological changes have been recorded without there being any visible behavioural signs (e.g. Wilson et al. 1991; Giese 1998). For example, significant increases in HR of Adélie penguins were measured in response to an approaching person. At a distance of 15 m, penguin HR increased significantly, yet no behavioural signs of disturbance were visible (Giese 1998). Significant increases or decreases in physiological parameters may have significant consequences for reproductive success or energy conservation in wildlife. For example, increases in neurogenic amines and corticosteroids (involved in the activation of the nervous system) may increase the potential for short-term survival, but depress the growth and skeletal development of young birds and can cause weight loss, reduced reproductive capabilities and increased vulnerability to disease in adults (Siegel 1980). Therefore, a person conducting an activity may believe that there is no consequence, based on the absence of a behavioural response, when in fact the activity is detrimental to the animal.

A further limitation of only measuring the behavioural responses of wildlife to human activity, is that it may be difficult to identify behavioural changes that are of biological significance, i.e. changes that have consequences for the survival or reproductive success of the animal. For example, suckling time in young elephant seal pups is correlated with lactational pup growth, i.e. weaning mass (Engelhard et al. 2002a), which in turn is correlated with survival (McMahon et al. 2000). The ability to link changes in behaviour with reproductive success or survival provides vital information for the management of human-wildlife interactions. Behaviours
that affect survival, for example, could be identified and relayed to visitors so that they are aware of the behaviours that should be avoided.

By contrast, HR for example, that is recorded as increasing or decreasing during exposure to a stimulus, can be linked to the metabolic rate and energy expenditure of an animal and therefore to fitness (Fedak 1986; Williams et al. 1991; Butler et al. 1992; Woakes et al. 1992; Hofer and East 1998).

Finally, behaviour can sometimes be misinterpreted, leading to incorrectly concluding that the human activity does or does not elicit a change in behaviour. For example, a displacement behaviour, which is executed to focus attention away from an aversive stimulus to reduce the anxiety aroused by the stimulus (Harvey et al. 1984; Kortmulder 1998; Allaby 1999), could be wrongly interpreted as a maintenance behaviour, i.e. a behaviour conducted to maintain body condition.

1.6.2 Physiology

Physiological data often provides the first indication that a response to a stimulus has occurred and often provides more detailed information about the magnitude and potential consequences of the response than do changes in behaviour alone (Jones and Faure 1981; Withers 1992; Hofer and East 1998). The measurement of physiological parameters allows the identification of subtle changes at an autonomic level (Jones and Faure 1981; Withers 1992), which can occur in the immune, cardiovascular, endocrine or metabolic systems. The most common physiological response parameters measured in human-wildlife interaction studies are changes in hormone levels, body temperature and HR.

The measurement of physiological parameters typically involves the extraction of biological samples or the attachment of specialised sensors. In the context of human-wildlife interaction studies, this poses a problem, as subsequent exposure to human activity is likely to be affected by physiological sampling. Therefore, the physiological response parameter utilised in human-wildlife interaction studies and the methods used to collect this information must ensure that methodological interference is minimised.

Hormone analysis (adrenocortical responses) requires serial blood collection requiring restraint of seals on multiple occasions, usually before, during and after exposure to the stimulus. This alone can cause considerable physiological change in wildlife. In birds, for example, capture and handling results in a rapid increase of glucocorticosteroids, usually within 5-10 minutes, and reaches a maximum within
30-60 minutes (Wingfield 1994). Similar results on the effect of handling on glucocorticoid levels were found in female Southern elephant seals, with moderate changes in cortisol levels occurring during the 45 minute sampling period following restraint, with average peaks of cortisol occurring 23 minutes after anaesthetic administration (Engelhard et al. 2002b). The increase in glucocorticosteroids during capture and handling, and the ongoing effects following handling, can potentially mask any increases in the corticosteroids related to subsequent exposure to human activity. Corticosteroids in faeces and urine may be used to indicate responsiveness to stimuli (Wingfield et al. 1997), and thereby remove the need to handle animals, however, baseline levels of corticosteroids must first be established using invasive sampling methods. In the context of studies to examine responses to particular human disturbance stimuli, the animal may not defecate or urinate for hours after exposure to the stimulus and may experience other forms of stress that could further elevate corticosteroid levels, thereby confounding the results. Furthermore, only certain 'stressors’ have been found to increase corticosterone concentrations (Harvey et al. 1984).

To measure internal body temperature the animal must swallow a temperature logger (Wildlife Computers 1997). Thus, the animal must be restrained and usually anaesthetised in order to insert the logger into the stomach, again this can cause changes in the physiological state of the animal and confound results. Stomach temperature may also be affected when the animal consumes food, and in the case of Weddell seals, if they consume ice during exposure to the human activity. There may also be a delayed temperature change following exposure to the stimulus (see Boyd and Sladen 1971; Regel and Pütz 1997), making it difficult to correlate precisely with particular human activities, especially in situations where an approach by a person for example, tests the response of the animal at various distances as they approach.

Heart rate was considered to be the most sensitive, practical and efficient parameter to measure in this study. Although the attachment of an external HR recorder also requires anaesthesia, it is possible to include a drug with amnesic properties in the anaesthetic regime to reduce the chance of the animal associating humans with any discomfort caused by anaesthesia. Heart rate has been shown to be a sensitive indicator of the general physiological condition of an animal (Thompson et al. 1968) and changes in HR have been interpreted as an indicator of stress in other species (e.g. Thompson et al. 1968; Syme and Elphick 1982; Culik and Wilson 1991; Bevan et al. 1994). Also, changes in HR have instantaneous onset with exposure to
stimuli, unlike changes in body temperature and hormone levels, for which there is often a delayed response (Thompson et al. 1968; Boyd and Sladen 1971; Perry 1973; Regel and Pütz 1997). Relative to other parameters, HR can therefore provide an immediate measure of a physiological change.

1.6.2.1 Limitations with heart rate
Heart rate can provide information about wildlife responses at an autonomic level and if precautions are made to minimise methodological interference, HR can be a valuable parameter in studies of the effects of human activity on seals. However, it is still possible that the activity of attaching a HR monitor does have an effect on the response of the seal during subsequent controlled exposures. The biological significance of increases and decreases in HR is not always clear, particularly when HR is measured alone and not in the context of behaviour and the general physiological state of the animal. Furthermore, in managing to avoid negative effects of human activity, the acceptable level of change in HR is therefore an arbitrary one, and if set incorrectly, may lead to an incorrect interpretation of results, with possible negative consequences for the wildlife.

1.6.3 Behavioural and heart rate responses
Based on the advantages and limitations of both response parameters, it is apparent that a more comprehensive understanding of the nature of an animal’s response to a stimulus can be achieved when both behaviour and HR are measured concurrently. Behavioural changes can be related to changes in HR and vice versa in order to better understand the responses of an animal to human activity. The inadequacy of one parameter can be compensated by the strength of the other, which will enhance interpretation of the full response of the wildlife to the stimulus.

1.7 Outline of thesis
In this thesis I examine and measure the effects of a range of human activities on lactating Weddell seals and their pups (Chapter 2-6) then briefly summarises these findings in Chapter 7, where I also discuss wildlife management guidelines, the implications of the results from my study on existing guidelines, suggest modifications to these guidelines and provide a method to enhance wildlife management guidelines.

With the exception of the general introduction (this chapter) and the general discussion (Chapter 7), all chapters are self-contained and have been written as
scientific papers. As a consequence, there is some repetition between chapters in the introduction and methodology. The abstracts and reference lists for each paper have been removed and combined into one thesis abstract and reference list.

I am the senior author on each paper in this thesis, with the exception of the anaesthetics paper in Appendix 4. I have been responsible for the organisation and execution of field seasons, laboratory and data analysis and the presentation of publications. Dr M. Giese (supervisor) was involved with the initial experimental design; both Dr Giese and Dr M. Hindell (supervisor) have made contributions to each of the papers in terms of discussion on content and critically reading drafts of the papers. Dr J. Terhune (supervisor) made contributions to Chapter 6 in terms of data analysis, discussion on content and critically reading drafts. Dr S. Wotherspoon has made significant contributions to statistical analyses in Chapters 2 and 5.
2 The Behavioural Responses of Lactating Weddell Seals and their Pups to Pedestrian Approaches
2.1 Introduction

Behavioural studies examining the response of wildlife to human activity, particularly in the context of wildlife tourism, are becoming increasingly common. Studies have been conducted on a wide range of species and human activities, for example, the effects of tourists on skis or snow shoes approaching woodland caribou (*Rangifer tarandus caribou*) (Duchesne et al. 2000), the response to pedestrians of Adélie penguins (*Pygoscelis adeliae*) (Woehler et al. 1994; Giese 1998), the influence of tourist boat operations and swimmers on bottlenose dolphins (*Tursiops truncates*) (Constantine 2001; 2004) and responses of various seal species to people and boats (e.g. Kovacs and Innes 1990; Cassini 2001; Boren et al. 2002). These studies suggest that human activity can result in significant changes in the behaviour of wildlife and have provided information for the management of human-wildlife interactions.

The response of wildlife to human activity can be influenced by a number of factors, which can be separated into (i) stimulus related factors and (ii) factors inherent to the animal. In the context of pedestrian activity, stimulus related factors include group size (i.e. number of people), visitor behaviour and approach distance (e.g. Cassini 2001; Boren et al. 2002). Factors inherent to the animal can include, its age, degree of previous exposure to the stimulus, stage of breeding, distance from shelter and location within a breeding group (e.g. Richardson et al. 1995; Lelli and Harris 2001; Beale and Monaghan 2004).

Pinnipeds are a group of animals that are commonly exposed to human activity, particularly with the growth of pinniped focused tourism (Birtles et al. 2001; Kirkwood et al. 2003). There have been a number of studies investigating the response of seals to pedestrian and watercraft activity, which have highlighted the various factors that affect an animals' response. For example, a study on tourist disturbance on New Zealand fur seals (*Arctocephalus forsteri*) found that the four most important factors affecting the behavioural response of the seals to human activities were, function of the site (breeding vs. haul-out), gender of the seals, level of previous exposure the seals had to the stimulus and approach type (Boren et al. 2002). In this study, fur seals at an undisturbed site showed higher levels of avoidance/aggression and responded more often than did seals at disturbed sites. In addition, approaching seals on land appeared to affect the animals more than approaches by kayaks and boats (Boren et al. 2002). In other pinniped studies, tourist behaviour has been shown to be an important factor in response, for example,
both South American fur seals (*Arctocephalus australis*) (Cassini 2001) and female
harp seals (*Phoca groenlandica*) (Kovacs and Innes 1990) can be approached closer if people approach slowly and calmly.

Breeding Weddell seals (*Leptonychotes weddellii*) are the most visited marine mammal in the Antarctic because they are the only species that inhabits the fast ice and are therefore readily and easily accessible to people (Bonner 1999). Weddell seals also have a reputation as having a docile nature (e.g. Stirling 1956; Kooyman 1981c), largely because they appear to tolerate relatively close approaches by people, even during the breeding season.

Adult female Weddell seals haul-out on the fast ice to give birth to a pup; which they nurture for 6-7 weeks (Wilson 1907; Tedman *et al.* 1985). Lactating cows form colonies around tide-cracks, which allow the animals ready access to the water (Tedman and Bryden 1979). The cows maintain small ‘zones of interference’ around themselves, of a radius of 3 m or less (e.g. Mansfield 1958; Ray and deCamp 1969; Stirling 1969; Smith and Burton 1970). These zones are maintained through mutual avoidance, vocal signals and attacks on intruders (Kaufman *et al.* 1975). Manipulative experiments show that females maintained at high colony density experience a high rate of interactions with conspecifics (as evidenced by fresh wounds) (Siniff *et al.* 1977). Pedestrian activity around or in pupping colonies has the potential to cause changes in behaviour, such as movement of the seals within the colony, which increase interactions between cows, in turn affecting cow-pup interactions with potential consequences for energy conservation and the time available for suckling.

Measures to protect Weddell seals and Antarctic wildlife in general, exist under the Antarctic Treaty System (Kimball 1999) and specific guidelines to minimise disturbance to wildlife have been established by the International Association of Antarctic Tour Operators (IAATO) (IAATO 2004a), which is an organisation founded to advocate, promote and practice safe and environmentally responsible private-sector travel to the Antarctic, and various nations with Antarctic research stations (e.g. Australian Antarctic Division 2004a). These guidelines are largely based on anecdotal reports and in the case of the Weddell seal the guidelines are not based on scientific studies. Given that other Antarctic wildlife, namely Adélie penguins and emperor penguins (*Aptenodytes forsteri*), and other pinniped species have been shown to be sensitive to human activity (e.g. Kovacs and Innes 1990;
Giese 1998; Giese and Riddle 1999; Cassini 2001; Boren et al. 2002) determining whether Weddell seals are affected by human activity is vital for the effective management of human-Weddell seal interactions.

The aim of this study then, was to provide a scientific basis for a review of existing guidelines used in the Australian Antarctic Territory and for the tourism industry. Experiments, which were designed to expose Weddell seals to the type of pedestrian activity they currently experience, were therefore conducted to measure the immediate behavioural response of lactating Weddell seals and their pups to pedestrian approaches, and the factors affecting response.

2.2 Methods

2.2.1 Study sites, number of seals and stimuli examined
The study was conducted on lactating Weddell seals and their pups at two sites in East Antarctica: near Davis in Long Fjord, Vestfold Hills (68°35'S, 77°58'E) during the summer of 2000/2001, and near Casey at Penny Bay, Windmill Islands (66°25'S, 110°40'E) during the summer of 2001/2002. Both colonies contained on average 40 cow-pup pairs. Although both colonies are readily accessible to humans, seals in the Vestfold Hills colony (Colony A) receive on average more visitors per season than those in the Windmill Islands colony (Colony B) because the former is located in a thoroughfare area and is closer to the Antarctic research station, Davis (~ 10 km away). The seals in Colony A have also been subject to tagging and re-sighting studies from 1973 to 2001 (Green et al. 1995) and thus have potentially more experience with people than do the seals in the Windmill Islands, that have not been tagged.

In total, the behaviour of 52 lactating Weddell seals with pups and 41 lone pups was recorded (Table 2.1). Single and group approaches to cow-pup pairs were conducted within a 19 and 15 day period for Colony A and Colony B respectively. Single person approaches to lone pups were conducted within a seven and five day period for Colony A and Colony B respectively.

2.2.2 Approach experiments
Pedestrian approaches were designed to closely resemble the actual pedestrian activity that the seals in this part of Antarctica experience. Therefore, three different approach experiments were conducted, (i) an approach to a cow-pup pair by a single person, (ii) an approach to a cow-pup pair by a group of five people and (iii) an
approach to a lone pup by a single person (Table 2.1). The experiments incorporated four approach distances: 20, 15, 10 and 5 m. The 15 m distance, was recommended by the Australian Antarctic Division (AAD) guidelines at the time of the study as being suitable for approaches to breeding Weddell seals and pups (2004a) and the 5 and 10 m distances were recommended by IAATO (2005). As the efficacy of these guidelines has never been tested, one distance greater than the existing limits was included (i.e. 20 m). All three experiments also examined the effect of posture of the approacher, i.e. whether people stood or crouched in front of the seals.

Table 2.1 The number of cow-pup pairs used in each colony approached by a single person, a group of five people, and both the single and group of people. The number of lone pups approached by a single person is also presented.

<table>
<thead>
<tr>
<th>Colony</th>
<th>Approach type</th>
<th>Single</th>
<th>Group</th>
<th>Single + Group</th>
<th>Lone pups</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vestfold Hills</td>
<td></td>
<td>6</td>
<td>1</td>
<td>19</td>
<td>15</td>
</tr>
<tr>
<td>(Colony A)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Windmill Islands</td>
<td></td>
<td>0</td>
<td>22</td>
<td>4</td>
<td>26</td>
</tr>
<tr>
<td>(Colony B)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Seals were selected such that experimental approaches would not affect other seals in the immediate vicinity. Cows with pups greater than one week old, determined from body size or observations of pup births, were selected for cow-pup approaches (Bryden et al. 1984). The lone pup approaches were conducted towards the end of the pupping season, as this was when they were more likely to be by themselves. The pups were therefore close to weaning age (6-7 weeks) (Tedman et al. 1985). Seals were given an identification number at the beginning of the season (painted on the hair) with peroxide hair-dye (Bristol Myers Squibb, Rydalmere Australia). One person quietly approached each seal (wearing camouflaged clothing) and applied the dye while the seal was asleep to avoid the seal responding and thereby invalidating the results. Although seals sometimes responded, their response was short-term. Given that each seal was treated the same, and no aggressive responses were observed, all dyed seals were experimentally approached.

Each approach consisted of a pre-approach recording of 30 minutes, the approach (approximately eight minutes) and a post approach recording of 10-20 minutes. The pre-approach recording period functioned as a control, in which behaviour in the absence of human activity was recorded. The approach consisted of either a single person or a group of five people walking directly towards the seal, starting from a
distance of at least 60 m. At 30 m, the approacher notified the observer, with the use of a handheld radio, who was recording the behaviour of the seal and the approach distance on Hi8 digital video camera. The observer was out of sight, behind rafted ice or rocks, and between 5-30 m from the seals (Figure 2.1). At a distance of 20 m from the seals the approachers stopped for one minute, then continued walking towards the seals, stopping again at 15, 10 and 5 m. At both the 10 and 5 m distances, the approachers spent an extra minute in a crouched position. People retreated along the same approach path without stopping. Post approach recordings commenced once the people were out of view of the seal, and were made to enable the time taken for the resting behaviour of seals to return to pre-approach levels to be calculated. The speed of all approaches was constant and the appearance of the approachers was standardised, i.e. dark coloured pants and a standard-issue red top.

For the cow-pup pairs that were exposed to both single person and group approaches, the order in which each approach was conducted was randomised to avoid any bias associated with previous exposure to approach experiments. All approaches were made between 08:00 and 19:30 on days with winds < 25 knots (measured at 2 m above ground level using a Speedtech Instrument Weathermate®).

For each approach, the following co-variates were recorded: the distance of the focal seal to the nearest conspecific, the distance of the seal to water (being a potential refuge), the approach angle i.e. the part of the seal that the approach was directed at, and whether the pup was exposed to the approacher, i.e. whether the pup was between the cow and the approacher.

Figure 2.1 A group approach to a cow-pup pair showing the observer filming the behaviour of the cow from behind rafted ice and the approaching group from a distance of > 60 m.
2.2.3 Analysis

Behaviour was quantified using The Observer (version 5.0 Noldus Information Technology 2003), a software package specifically designed for integrated behavioural analyses.

Eleven behavioural categories were initially identified: rest, comfort, look, attack, ice-sawing, eat ice, vocalise, interact, travel, pup bump, and shift position (Table 2.2). Vocalise, pup bump and shift position were classified as event behaviours, i.e. they were instantaneous, and were measured as frequency of occurrence per minute (Altmann 1974). The other behaviours were classified as state behaviours that had an appreciable duration, and were measured in minutes as the proportion of time of the recording that the seal spent performing the behaviour (Altmann 1974). Look, interact, attack and vocalise were further categorised in terms of ‘to whom’ the behaviour was directed (Table 2).

All data were tested for normality and homogeneity of variance using exploratory analysis and residual plots (Quinn and Keough 2002). Non-parametric statistical methods were used where transformations were not found to improve variables to meet the assumptions of the parametric statistical tests.
Table 2.2 Categories and description of Weddell seal behaviour.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Classified as</th>
<th>To whom the behaviour is directed</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rest</td>
<td>State</td>
<td>N/A</td>
<td>Lying still, no sign of activity, eyes closed.</td>
</tr>
<tr>
<td>Comfort</td>
<td>State</td>
<td>N/A</td>
<td>Included scratching, yawning, grooming and stretching. These behaviours increase the physical comfort of the animal (Allaby 1999).</td>
</tr>
<tr>
<td>Look</td>
<td>State</td>
<td>Pup, conspecific, surroundings, bird or approachers.</td>
<td>Involved the seal looking. The seal's body position was not taken into account, that is, no distinction was made between lying still and raising the head.</td>
</tr>
<tr>
<td>Attack</td>
<td>State</td>
<td>Pup, conspecific, surroundings, bird or approachers.</td>
<td>Agonistic behaviour, which included lunging or charging, biting and snapping of jaws.</td>
</tr>
<tr>
<td>Ice sawing</td>
<td>State</td>
<td>N/A</td>
<td>Short duration behaviour consisting of incomplete and often slow swings of the head from side to side where the upper jaw makes contact with the ice or snow (Kaufman et al. 1975).</td>
</tr>
<tr>
<td>Eating ice</td>
<td>State</td>
<td>N/A</td>
<td>Ingesting snow or ice. Often seen after ice-sawing.</td>
</tr>
<tr>
<td>Vocal</td>
<td>Event</td>
<td>Pup, conspecific, surroundings, bird or approachers.</td>
<td>The seal vocalised. Vocalisations were not differentiated.</td>
</tr>
<tr>
<td>Interact</td>
<td>State</td>
<td>Pup or conspecific.</td>
<td>Unlike 'attack', this category included behaviours such as the cow placing her fore flipper on the pup and the cow and pup nuzzling together.</td>
</tr>
<tr>
<td>Travel</td>
<td>State</td>
<td>N/A</td>
<td>Purposeful movement involving the seal moving from one location to another.</td>
</tr>
<tr>
<td>Pup bump</td>
<td>Event</td>
<td>N/A</td>
<td>Cow responded to the pup touching her, usually when the pup was moving around her body. The cow shifted the affected part, for example, her head, out of the pup's way.</td>
</tr>
<tr>
<td>Shift position</td>
<td>Event</td>
<td>N/A</td>
<td>Seal altered its posture by rolling or shifting part of its body. Did not include purposeful movement as described in 'travel'.</td>
</tr>
</tbody>
</table>

2.2.3.1 Comparison between colonies
Mann-Whitney U tests (Quinn and Keough 2002) were used to compare the behaviour of the cows during the group approach and of the pups during the lone pup approaches from the two study sites. The five most commonly occurring behaviours: rest, comfort, looking-at-approacher (LA), looking-at-surroundings (LS) and shifting position were compared. Sequential Bonferroni corrections were used to correct for possible inflation of Type II errors due to multiple tests (Quinn and Keough 2002). Behaviour of the seals approached by a single person was not compared due to the small sample size at Colony B.
On the basis that the behaviour of seals exposed to the group and lone pup experiments from Colony A and Colony B was indistinguishable (Appendix 1), these data were pooled to produce final sample sizes of 29, 46 and 41 animals for the single, group and lone pup approaches respectively.

2.2.3.2 Determination of commonly occurring behaviours
The most common behaviours recorded during the approach for each of the three experiments were identified by calculating the percentage of seals that performed each behaviour (Appendix 2).

2.2.3.3 Comparison between stages of the approach
Friedman rank tests (Zar 1999) were used to compare the duration and frequency of the five most commonly occurring behaviours before, during and after pedestrian approaches for each of the three experiments.

2.2.3.4 Significance of recorded variable in determining approach distance
Looking-at-approacher was the behaviour that, in both the single person and group approach experiments, was consistently different before, during and after pedestrian approaches, and was therefore used for further analysis.

Two statistical methods were employed to investigate the effects of the co-variates on approach distance: a linear regression (LR) and a proportional odds regression model (PORM) (McCullagh and Nelder 1989). However, data from the lone pup approaches was not analysed in this way because of the small percentage of pups that responded to the approacher. Therefore, lone pup data was only explored descriptively and graphically for this analysis.

The linear regression model related the distance of approach at which the seal responded to the distance to the nearest conspecific and the distance to water, allowing the relations to differ with approach type and pup exposure. The limitation of this method was that it focused on the distance that people could approach a seal before it responded, and not the different posture of the approachers, i.e. standing versus crouching.

The proportional odds regression model treated the stages of approach as a set of ordered categories, for example, 15 m, 10 m standing and 10 m crouching. Body posture, standing and crouching, at the 10 and 5 m distances were therefore separated into two distinct categories.
Where a linear regression models the mean distance of approach that is reached before a seal will respond, proportional odds regression models the odds that a stage of approach is reached before a seal will respond. If $\Pr(\text{stage} \leq j)$ is the probability that the seal will respond to the approacher before stage $j$, then the odds the seal will respond to the approacher before stage $j$ are simply:

$$\frac{\Pr(\text{stage} \leq j)}{1 - \Pr(\text{stage} \leq j)}.$$

The proportional odds model assumes there is a linear relationship between the log odds and the predictors as follows:

$$\log\left(\frac{\Pr(\text{stage} \leq j)}{1 - \Pr(\text{stage} \leq j)}\right) = \alpha_j + \beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_m x_m.$$  

Here, the $\alpha_j$ are intercepts that determine “baseline” odds that an individual will respond before a given stage of approach, and the $\beta_i$ are regression coefficients that describe the effect of the predictors $x_1, x_2, \ldots, x_m$. The key assumption of the proportional odds model is that the values for $\beta_i$ are independent of $j$, that is, the effect of the predictors is consistent across all stages.

To interpret these results, the model was presented in terms of three sets of contour maps (see 2.3.2.3) where the cumulative probability of an outcome exceeds a given threshold probability. Three thresholds, 0.2, 0.5 and 0.8 were chosen to represent the stage (distance and body posture from the seals) at which one can be 20%, 50% and 80% confident respectively, that the seals will have responded. Two maps represent the group approaches and two maps represent the single approaches to distinguish between pup exposures. The conditions of the contours were: the distance to water (range 0-30 m in 5 m increments) and distance to a conspecific (range 0-50 m in 10 m increments).

### 2.2.3.5 Calculation of the time taken to return to rest

Behavioural data was arc-sin transformed to improve normality and homogeneity of variances. A Multivariate Analysis of Variance (MANOVA) was conducted to determine whether the behavioural response profile of the cows differed over the approach experiments for the single and group approaches. On the basis that there was no significant difference in the profile of the cows that were approached by a single person and a group of people ($F = 0.502, p = 0.921$), the data were pooled to increase the sample size for this analysis. The data from the lone pup approaches were not further analysed because of the small sample size.
To determine when post approach resting levels (i.e. the percentage of time the seal spent resting) returned to pre-approach resting levels, the post approach period was first divided into five minute sections. Helmert style contrasts of each post approach period and the average pre-approach resting levels were then tested by MANOVA. The first five minute time interval post approach in which the seals' resting level statistically matched the pre-approach resting level was taken to indicate the time interval at which the approachers no longer had an affect on the behaviour of the seals. This time was however, an underestimate, because of the limited power of the test.

2.3 Results

2.3.1 Determination of commonly occurring behaviours and comparison of seal behaviour before, during and after pedestrian approaches

The most common behaviours recorded during each of the three experiments were resting (100% of seals), comfort (single = 96.55%, group = 89.13%, pup = 87.80%), looking-at-approacher (single = 62.07%, group = 76.09%, pup = 39.02%), looking-at-surroundings (single = 41.38%, group = 65.22%, pup = 34.15%) and shift position (single = 55.17%, group = 45.65%, pup = 19.51%) (Appendix 2).

Comparisons before, during and after the pedestrian approach for each experiment showed that the percentage of time that seals spent looking-at-approacher was significantly higher during the approach than during any other phase. Cows approached by the group also spent less time resting and more time looking-at-surroundings during the approach. Lone pups spent significantly less time performing comfort behaviour during the approach than during post approach observations (Table 2.3).
Table 2.3 Results of the Friedman test (mean ± st. dev) comparing the most commonly occurring behaviours observed during the single person approach to the cow-pup pair, the group approach to the cow-pup pair and the single person approach to the lone pup across the three stages of approach (pre-approach, approach and post approach). Values of p < 0.05 are in bold. If a significant effect was found, the Wilcoxon signed rank test was applied for post-hoc comparisons. Symbols '<' and '>' indicate significant increase or decrease in the % of seals performing the behaviour between stages; symbol '=' indicates no significant difference (see Appendix 3 for statistical values).

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Pre-approach</th>
<th>Approach</th>
<th>Post approach</th>
<th>χ²</th>
<th>p</th>
<th>Post hoc test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Single approach to cow-pup n=29</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rest (% of time)</td>
<td>92.57 ± 6.22</td>
<td>85.26 ± 16.61</td>
<td>88.90 ± 12.59</td>
<td>4.62</td>
<td>0.099</td>
<td></td>
</tr>
<tr>
<td>Comfort (% of time)</td>
<td>5.46 ± 4.20</td>
<td>4.45 ± 5.05</td>
<td>8.62 ± 10.13</td>
<td>2.97</td>
<td>0.227</td>
<td></td>
</tr>
<tr>
<td>Looking-at-Approacher (% of time)</td>
<td>0.00 ± 0</td>
<td>7.01 ± 11.13</td>
<td>0.00 ± 0</td>
<td>36.00</td>
<td>&lt; 0.0001</td>
<td>A &gt; Pre, A &gt; Post, Pre = Post</td>
</tr>
<tr>
<td>Looking-at-Surroundings (% of time)</td>
<td>0.83 ± 1.88</td>
<td>1.07 ± 2.15</td>
<td>1.35 ± 3.70</td>
<td>0.32</td>
<td>0.85</td>
<td></td>
</tr>
<tr>
<td>Shift position (freq. of occur min/hr)</td>
<td>0.12 ± 0.19</td>
<td>0.24 ± 0.33</td>
<td>0.26 ± 0.34</td>
<td>2.26</td>
<td>0.322</td>
<td></td>
</tr>
</tbody>
</table>
Table 2.3 continued

<table>
<thead>
<tr>
<th>Group n=46</th>
<th>Pre-approach</th>
<th>Approach</th>
<th>Post approach</th>
<th>χ²</th>
<th>P</th>
<th>Post hoc test</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean ± st. dev</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pre-approach</td>
<td>92.51 ± 6.22</td>
<td>82.98 ± 16.53</td>
<td>88.93 ± 14.35</td>
<td>13.91</td>
<td>0.001</td>
<td>A &lt; Pre</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>A &lt; Post</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Pre = Post</td>
</tr>
<tr>
<td>Post-approach</td>
<td>82.98 ± 16.53</td>
<td>6.36 ± 6.95</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
<td>0.135</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Post-hoc</td>
<td>6.36 ± 6.95</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
<td>0.135</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Pre = Post</td>
</tr>
<tr>
<td>Rest (% of time)</td>
<td>6.66 ± 5.21</td>
<td>3.52 ± 3.67</td>
<td>6.36 ± 6.95</td>
<td>4.0</td>
<td>0.001</td>
<td>A &gt; Pre</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Pre = Post</td>
</tr>
<tr>
<td>Comfort (% of time)</td>
<td>0.00 ± 0</td>
<td>9.48 ± 12.76</td>
<td>0.00 ± 0</td>
<td>70.0</td>
<td>&lt; 0.0001</td>
<td>A &gt; Pre</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Pre = Post</td>
</tr>
<tr>
<td>Looking-approacher (% of time)</td>
<td>0.21 ± 0.33</td>
<td>1.90 ± 3.72</td>
<td>0.59 ± 1.38</td>
<td>11.77</td>
<td>0.003</td>
<td>A &gt; Pre</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Pre = Post</td>
</tr>
<tr>
<td>Looking-at-surroundings (% of time)</td>
<td>0.10 ± 0.15</td>
<td>0.22 ± 0.38</td>
<td>0.17 ± 0.30</td>
<td>0.28</td>
<td>0.868</td>
<td>Pre = Post</td>
</tr>
<tr>
<td>Shift position (freq. of occur min/hr)</td>
<td>0.00 ± 0</td>
<td>2.71 ± 5.36</td>
<td>0.00 ± 0</td>
<td>28.0</td>
<td>&lt; 0.0001</td>
<td>A &gt; Pre</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Pre = Post</td>
</tr>
<tr>
<td>Pup n=39</td>
<td>Pre-approach</td>
<td>Approach</td>
<td>Post approach</td>
<td>χ²</td>
<td>P</td>
<td>Post hoc test</td>
</tr>
<tr>
<td></td>
<td>Mean ± st. dev</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rest (% of time)</td>
<td>80.73 ± 15.96</td>
<td>79.72 ± 24.81</td>
<td>71.71 ± 25.47</td>
<td>5.282</td>
<td>0.071</td>
<td>A = Pre</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>A &lt; Post</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Pre = Post</td>
</tr>
<tr>
<td>Comfort (% of time)</td>
<td>18.04 ± 14.91</td>
<td>15.23 ± 18.56</td>
<td>24.69 ± 22.23</td>
<td>13.12</td>
<td>0.001</td>
<td>A &gt; Pre</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Pre = Post</td>
</tr>
<tr>
<td>Looking-at-approacher (% of time)</td>
<td>0.00 ± 0</td>
<td>2.71 ± 5.36</td>
<td>0.00 ± 0</td>
<td>28.0</td>
<td>&lt; 0.0001</td>
<td>A &gt; Pre</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Pre = Post</td>
</tr>
<tr>
<td>Looking-at-surroundings (% of time)</td>
<td>0.79 ± 1.18</td>
<td>1.16 ± 3.0</td>
<td>1.81 ± 3.01</td>
<td>3.127</td>
<td>0.001</td>
<td>A &gt; Pre</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Pre = Post</td>
</tr>
<tr>
<td>Shift position (freq. of occur min/hr)</td>
<td>0.49 ± 0.13</td>
<td>0.06 ± 0.15</td>
<td>0.11 ± 0.20</td>
<td>2.375</td>
<td>0.001</td>
<td>A &gt; Pre</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Pre = Post</td>
</tr>
</tbody>
</table>

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2.3.2 LA Response

The percentages of seals that responded by looking-at-approacher during the single, group and lone pup approaches were 62%, 76% and 39% respectively. There was no clear pattern in the percentage of lone pups that responded to the approachers at each of the stages of the approach (Figure 2.2a). Similarly, there was no evidence of a difference in the duration of response across the stages of approach for lone pups (Figure 2.2b).

Only one cow (of the 52 cows approached) showed a stronger response than looking-at-approacher. This individual attacked both her pup and the approachers. When approached by a single person to the 10 m distance the cow attacked her pup (biting and shaking it), when the person approached to the closer distance of 5 m the cow charged the approacher with an open gape. When approached by a group of people, the cow attacked her pup when people were at the 15 m distance, and again, when the group was 5 m away, again charging the group with an open gape.

![Figure 2.2a](image1) ![Figure 2.2b](image2)

**Figure 2.2a** The percentage of pups responding at each of the stages of approach. **b)** The percentage of time spent responding ± SE during each stage of the approach. The 's' signifies that the person was standing and the 'c' signifies that the person was crouching. Note: The 30 m distance and the retreat have been removed because the time spent at the 30 m distance and retreating was considerably shorter than at the other distances.
2.3.2.1 **Significance of recorded variables in determining approach distance (cow/pup pairs)**

Exploratory analysis of the recorded co-variates in relation to the distance at which the seal first responded indicated that approach type (single or group), distance to conspecific, and pup exposure were important (Figure 2.3-2.5). Distance to water was included in the model to investigate whether it may function as a refuge to which seals could retreat when presented with a negative stimulus on the ice.

If the effects of the other co-variates were ignored, a two-samples t-test showed that the distance at which the seals responded was dependent on pup exposure ($t = 3.262, df = 46, p = 0.002$). However, given the highly discrete nature of the data, the assumptions of normality required by a t-test were likely to be violated, therefore a permutation test (Good 2000), was also performed. This test also showed strong evidence of a difference in pup exposure with the distance of approach (probability of 0.005).
Figure 2.3 The percentage of cows looking at the single person (n=29) and the group of people (group size = 5 people) (n=46) at each of the distances of the approach.
Figure 2.4 The percentage of cows looking at the approachers, irrespective of approach type (single versus group), when the pup was directly exposed to the approachers (i.e. pup was between the cow and the people) and when not exposed (i.e. cow was between the pup and the approachers).
2.3.2.2 Significance of recorded variables in determining approach distance using linear regression

An initial regression model was used to relate the distance at which the cows first responded to the distance each cow was from the nearest conspecific, the distance the cow was from water, whether or not the pup was exposed and the type of approach (single and group). All three-way interactions between approach type, pup exposure and either distance to conspecific or distance to water were included. Stepwise model selection, based on the Akaike’s information criterion (AIC) (Quinn and Keough 2002), was used to select the most parsimonious model. The final model included all the main effects; approach type, pup exposure, distance to conspecific and distance to water, and two-way interactions between approach type and distance to water ($p = 0.003$), approach type and distance to conspecific ($p = 0.003$), and pup exposure and distance to water ($p = 0.009$). The model therefore showed that the seals’ response differed with the approach type and that the relevance of distance to water differed with pup exposure.

The responses of some individual cows and the related co-variates strongly influenced the results of the regression model. However, deleting these observations
and refitting the model did not alter the major conclusions of the model, therefore they were retained in the data set.

As there were significant interactions between approach type and distance to water and approach type and distance to conspecific, the model was refitted to the single approach experiment and to the group approach experiment separately, to simplify the interpretation of the model.

When the model was refitted to the single approach data alone, there was no evidence that pup exposure or distance to water influenced the distance that a single person could approach a cow before she responded (pup exposure $t = -1.766$, $df = 15$, $p = 0.098$, and distance to water $t = 1.54$, $df = 15$, $p = 0.143$). The lack of a significant difference between interactions may be attributed to the decreased sample size compared to the combined dataset. If, for consistency with the combined analysis (i.e. single and group data set) these terms were retained, inspection of the 95% confidence intervals for the regression coefficients showed that:

(i) irrespective of the exposure of the pup, for every 1 m the cow was closer to the water, the single person could approach between -0.2 m and 1.4 m closer before the cow responded. Thus, a single person could approach to a closer distance before the cow responded when the cow was closer to the water.

(ii) when the pup was exposed, then a single person could approach between -10.4 m and -16.6 m closer before the cow responded, while if the pup was not exposed, a single person could approach between -1.1 m and 12.2 m closer before the cow responded. Therefore, a single person could approach to a closer distance before the cow responded when the pup was not exposed.

When the model was refitted to the group approach data alone, distance to the nearest conspecific had significant effects on the distance at which the cows first responded ($p < 0.001$) and a significant interaction occurred between pup exposure and distance to water ($p = 0.005$). Inspection of the 95% confidence intervals for the regression showed that:

(i) irrespective of pup exposure, for every 1 m the cow was closer to a conspecific, the distance to which the group could approach decreased by between 0.3 m to 0.7 m before the cow responded. Thus, the group could get closer when the cow was closer to a conspecific.
(ii) When the pup was exposed, for every 1 m the cow was further from the water, the distance to which the group could approach increased by between 0.5 m and 1.3 m before the cow responded. Thus, the group could get less close when the cow was further from the water.

(iii) When the pup was not exposed, for every 1 m the cow was further from the water, the distance to which the group could approach decreased by between 0.6 and -0.6 m before the cow responded. What is indicated here is that there is no evidence that the distance the group could approach was related to the distance to the water when the pup was not exposed.

2.3.2.3 Significance of recorded variables in determining stage of approach using proportional odds regression

The proportional odds regression model related the stage of approach at which the seals first responded to the distance the cow was from the nearest conspecific, the distance the cow was from water, pup exposure and the type of approach (single and group). As with the linear regression, stepwise model selection based on the AIC was used to select the most parsimonious model. The final model included all of the main effects and the two-way interactions between approach type and distance to conspecific ($t = 3.167$), approach type and distance to water ($t = -2.903$) and distance to water and pup exposure ($t = -2.597$).

While it is possible to interpret the model coefficients, the fitted model is more easily understood through its predictions. The reason for this is the complicated nature of the proportional odds model. Figure 2.6 presents the contour maps that show the closest stage of approach that the approachers could reach before 80% of cows were predicted to respond for specific combinations of the co-variates. For example, when a cow was 15 m from the water and 30 m from a conspecific and the pup was not exposed, 80% of cows were predicted to respond when the group was somewhere between 20 m and 15 m from the pair. If the cow was 20 m from a conspecific and still 15 m from the water, then the group could approach to 10 m and crouch down (Figure 2.6a) before the cow responded. Similarly, Figures 2.7 and 2.8 show the stage of approach that could be reached before 50% and 20% of cows responded.

The results of the proportional odds model for the cumulative probability for the 0.8 threshold showed that when a pup was not exposed, the distance the cow was from water had little effect on the stage of approach that the group could reach before
the cow responded. The distance that the cows were from a conspecific did, however, affect the stage of approach. Contrariwise, for an approach by a single person the distance to water did have an effect on the stage of approach, but the distance the cow was from a conspecific did not (Figure 2.6c). When the pup was exposed, irrespective of approach type, both distance to water and distance to a conspecific influenced the stage of approach that could be reached before 80% of cows were predicted to respond. The effect of distance to water, however, was counter-intuitive, in that it was reversed. A single person could approach to a closer stage when the cow was closer to the water while a closer approach by the group required the seals to be further from the water (Figure 2.6b & d).

The contour maps from Figures 2.6-2.8 show the stage of approach for specific combinations of the co-variates at the three different cumulative probability thresholds. That is, the stage of approach that both the single person and the group of people could reach before 80%, 50% and 20% of cows were predicted to respond. For example, 80% of cows with pups that were not exposed and were lying 15 m from the water and 10 m from a conspecific were predicted to respond to an approach by a single person when the person was somewhere between 15 m and 10 m from the seals (Figure 2.6d). This stage of approach increased to approximately 20 m when the percentage of cows that were predicted to respond was decreased to 50%, and the stage of approach was further increased to between 30 m and 20 m when the percentage of cows that were predicted to respond was decreased to 20% (Figure 2.7d & 2.8d).
Figure 2.6 The contour maps generated through the proportional odds regression model for the 0.8 predictability threshold. The maps illustrate the closest stage of approach that could be reached before 80% of cows were predicted to respond for specific combinations of the co-variates. The ‘s’ represents the body posture of standing and ‘c’ represents the body posture of crouching. The dotted lines provide an example of how to use the maps, so, in figure (a) for example, the stage of approach the group could reach before 80% of cows, whose pups are not exposed and are lying 15 m from the water and 20 and 30 m from a conspecific, are predicted to respond occurs at the intersection of the dotted lines (10 m crouching and standing at 15 m, respectively).
Figure 2.7 The contour maps generated through the proportional odds regression model for the 0.5 predictability threshold. The maps illustrate the closest stage of approach that could be reached before 50% of cows were predicted to respond for specific combinations of the co-variates. The 's' represents the body posture of standing and 'c' represents the body posture of crouching. The dotted lines in figure (d) provide an example of how to use the maps, so, the stage of approach a single person could reach before 50% of cows, whose pups are exposed and are lying 15 m from the water and 10 m from a conspecific, are predicted to respond occurs at 20 m. Compare with Figure 2.6d and Figure 2.8d for the 0.8 and 0.2 thresholds.
Figure 2.8 The contour maps generated through the proportional odds regression model for the 0.2 predictability threshold. The maps illustrate the closest stage of approach that could be reached before 20% of cows were predicted to respond for specific combinations of the co-variates. The ‘s’ represents the body posture of standing and ‘c’ represents the body posture of crouching. The dotted lines in figure (d) provide an example of how to use the maps, so, the stage of approach a single person could reach before 20% of cows, whose pups are exposed and are lying 15 m from the water and 10 m from a conspecific, are predicted to respond occurs between 20 and 30 m. Compare with Figure 2.6d and Figure 2.7d for the 0.8 and 0.5 thresholds.
2.3.3 Time taken to return to rest

A MANOVA, combining the data from both single person and group approach experiments, showed evidence of a change in the duration of resting behaviour during the approach experiment ($F = 2.193, p = 0.032$). The contrast revealed that cows spent significantly less time resting, compared to pre-approach resting levels (92.7% of time), when the approachers were between 10 m standing and 5 minutes post approach. It should be recognised that at the 15 m distance, resting levels first fell to an indistinguishable level, that is, compared to pre-approach levels. Resting levels returned to those recorded prior to approaches 5 minutes after the approach (Table 2.4).

Table 2.4 Summary results of the Contrast analysis showing the significance of the percentage of time spent resting during the pre-approach compared to each stage of the approach, irrespective of approach type, starting with the final 5 minutes of the post approach. Significant results at the 0.5 alpha level are in bold. Combined n=71.

<table>
<thead>
<tr>
<th>Contrast with Pre-approach (mean = 92.6)</th>
<th>Mean (% of time resting)</th>
<th>F test</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>5-10 min post approach</td>
<td>89.6</td>
<td>0.854</td>
<td>0.360</td>
</tr>
<tr>
<td>0-5 min post approach</td>
<td>88.3</td>
<td>4.612</td>
<td>0.037</td>
</tr>
<tr>
<td>Retreat</td>
<td>84.3</td>
<td>3.685</td>
<td>0.061</td>
</tr>
<tr>
<td>5 m crouching</td>
<td>82.2</td>
<td>4.464</td>
<td>0.040</td>
</tr>
<tr>
<td>5 m standing</td>
<td>72.8</td>
<td>13.39</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>10 m crouching</td>
<td>86.0</td>
<td>3.801</td>
<td>0.057</td>
</tr>
<tr>
<td>10 m standing</td>
<td>82.6</td>
<td>4.673</td>
<td>0.039</td>
</tr>
<tr>
<td>15 m</td>
<td>85.6</td>
<td>1.041</td>
<td>0.313</td>
</tr>
<tr>
<td>20 m</td>
<td>89.1</td>
<td>2.230</td>
<td>0.634</td>
</tr>
<tr>
<td>30 m</td>
<td>85.4</td>
<td>0.082</td>
<td>0.776</td>
</tr>
</tbody>
</table>

2.4 Discussion

Guidelines for human-wildlife interactions often aim to minimise disturbance to wildlife and simultaneously ensure viewer satisfaction and safety (see for example Australian Government Department of the Environment and Heritage 2002; Kirkwood et al. 2003; Australian Antarctic Division 2004c). In most cases however, guidelines, including those tested in this study (i.e. the AADs and IAATOs), recommend one distance per type of approach per species, and in some cases breeding status, to guide visitors and reduce wildlife disturbance (e.g. Australian...
Government Department of the Environment and Heritage 2002; Australian Antarctic Division 2004a; 2004c; IAATO 2005). Often, such guidelines have been purposely developed to increase the probability of the guidelines being adhered to, as guidelines that are too complex may be less likely to be remembered, influencing compliance. However, the approach of setting generic guidelines does not always allow for differences in the sensitivity of individual animals to human activity or the animal related factors that can affect an animal’s response. Where such ‘blanket’ guidelines are set conservatively, they may minimise the likelihood of wildlife being affected by human activity, but this may come at the cost of visitor satisfaction. Alternatively, guidelines designed to maximise visitor satisfaction, for example by allowing close approaches to breeding animals, may result in greater wildlife disturbance. Irrespective of how they are set; such guidelines are not always maximally effective.

This study has shown that the behavioural responses of lactating Weddell seals and lone pups to pedestrian approaches can be influenced by a number of factors, namely, (i) the type of approach, i.e. single versus group, (ii) the distances of the focal seal to water and to the nearest conspecific and (iii) whether pups are exposed to the approacher. These associations have implications for the development of sensitive management guidelines that aim to minimise disturbance to the seals while providing a satisfying viewing experience for visitors.

2.4.1 General behavioural effects of approach experiments
The approach of a single person or a small group of people to 5 m from Weddell seals resulted in most cows and some lone pups becoming alert. Some individuals showed no sign of a behavioural response, suggesting that approaches to 5 m were relatively insignificant. Weddell seals are, however, known to react strongly to approaching people (for example, Kaufman et al. 1975), and I recorded one instance of a lactating cow attacking her pup and charging at the approachers. Although just one animal in the sample responded in this manner, the result suggests that pedestrian approaches can elicit extreme responses, albeit rarely, that may have adverse consequences for the pup.

Generally, however, the response looking-at-approacher was the only behaviour indicative of a response to the stimuli tested. Alert behaviour, often described as vigilance, and defined as the “readiness of an animal to detect certain specified events that occur unpredictably in its environment” (Allaby 1999 p.566), is often reported as a response to human activity (e.g. Yorio and Boersma 1992; Conomy et
In Weddell seals, alertness in response to pedestrians suggests that the approach of people represented an unpredictable stimulus that warranted monitoring.

The number of people (group size) approaching and observing wildlife has been shown to affect the behaviour and even the breeding success of wildlife. For example, an increase in the number of observers resulted in a decrease in the time that woodland caribou (*Rangifer tarandus caribou*) spent foraging and resting/ruminating (Duchesne *et al.* 2000). An increase in the number of boats observing bottlenose dolphins (*Tursiops truncatus*) also resulted in a decrease in resting behaviour (Constantine *et al.* 2004). In a study of kittiwakes (*Rissa tridactyla*) and guillemots (*Uria aalge*), an 8.5% increase in the number of visitors resulted in a 22% and 13% nesting failure rate for the two species respectively, while halving the number of visitors resulted in a nesting failure of 4.4% and 12.8% respectively (Beale and Monaghan 2004).

In the current study, the response of Weddell seals indicated that the number of people approaching the seals determined the stage of approach at which the seals responded, and the percentage of cows that responded. During group approaches, cows also spent more time looking-at-surroundings and less time resting. Although resting levels increased once the approachers were out of sight, the seals remained alert during this period. This response was not apparent during single approach experiments, which may indicate that the cows considered an approach by a group to be of greater concern, requiring increased vigilance.

Responses of wildlife to human activity have also been shown to differ according to the age of an animal. Adult female New Zealand fur seals, for example, are known to enter the sea when exposed to pedestrians or small boats, while pups hide among the rocks (Boren *et al.* 2002). The percentage of Weddell seals in this study that responded to an approaching person was lower for lone pups than for lactating cows. This suggests that the pups perceived the approach of the person differently to the cows, perhaps because of differences in age, and therefore lack of previous exposure to human activity. Female Weddell seals return to the same pupping colonies to give birth each year (e.g. Cline *et al.* 1971; Thomas and DeMaster 1983; Thomas and Stirling 1983) and the colonies used in this study have been subject to intermittent visits by station personnel since the establishment of the two scientific research stations during the 1950s (Australian Antarctic Division 2004b). This prior exposure may mean that the cows had learned to become vigilant when subject to
pedestrian approaches (see Chapter 3 for behavioural responses to cumulative exposure). The pups in this study, on the other hand, had only received exposure to pedestrian activity during the experimental period, and may not have developed an association with people.

Alternatively, the lower percentage of lone pups (compared to lactating cows) responding to the single approach may have been related to factors such as the distance the pups were from water and the distance they were from a conspecific. Both of these factors had an effect on how close people could approach before eliciting a response from lactating cows (see 2.4.2). Unfortunately, the percentage of lone pups that responded to the approach was small, making it impossible to verify whether these factors influenced the results.

Lone pups spent significantly more time performing comfort behaviours, i.e. scratching, yawning, grooming and stretching following the approach than during the approach. Changes in comfort behaviours are not typically described in responses of pinnipeds to human activity (for example Born et al. 1999; Cassini 2001; Boren et al. 2002; Engelhard et al. 2002a; Cassini et al. 2004; Orsini 2004). Rather, responses are described as vigilance activities and escape behaviour. However, in a study on the impact of tourism on harp seals, comfort behaviours were described for pups (Kovacs and Innes 1990). Contrary to the results in the current study, harp seals reduced their comfort behaviour both during tourist approaches and for one hour after the tourists had retreated (Kovacs and Innes 1990).

The increase in comfort behaviours following approaches in the present study may be the result of those pups that were looking-at-approacher during the approaches, actively conducting behaviours to increase their overall comfort levels following exposure to the approacher. Even if this were the case, approaches by a single person appear to affect the behaviour of the pups for only short time periods following exposure.

2.4.2 Factors affecting response and stage of approach

The two statistical methods employed to determine the distance, or stage of approach, before the cows responded provided the same qualitative results. While the coefficients of the PORM are relatively difficult to interpret, the predictions expressed through the contour maps provide clear information that is immediately usable by any visitors on site. This method also provides additional information about the significance of some animal and stimulus related factors that affect seal
behaviour, which means that managers are in a better position to develop more effective guidelines. The PORM also has the advantage of distinguishing between the effects that body posture of the approacher (stand versus crouch) has on seal response. Determining whether or not body posture has an effect on the likelihood of response can be used as a management tool to minimise disturbance to wildlife, yet increase visitor satisfaction. For example, if crouching at 10 m does not elicit an alert response but standing at 10 m does, then people can be informed that they can approach to 10 m as long as they crouch down.

Cows adopted a different strategy when approached by a group of people than when approached by a single person. For a cow approached by a single person, the importance of distance to water and distance to another seal differed according to whether or not her pup was exposed. For cows approached by a group, the closeness of other seals, irrespective of pup exposure, was important, but distance to water was only perceived to be important to cows when their pups were exposed. These results will therefore be discussed as four scenarios, (i) a single approach to a cow-pup pair where the pup is exposed, (ii) a single approach to a cow-pup pair where the pup is not exposed, (iii) a group approach to a cow-pup pair where the pup is exposed and (iv) a group approach to a cow-pup pair where the pup is not exposed.

**Scenario 1 - Single approach to a cow-pup pair where the pup is exposed**

Both the distance to water, and to a conspecific influenced response, with cows positioned near the water allowing closer approaches and cows positioned closer to a conspecific allowing closer approachers. This suggests that seals regarded water as a place to escape to and therefore that they perceived the approacher to be a potential threat. Proximity to shelter (equivalent to water for the seals) has been identified in other studies as an important factor affecting the distance from a stimulus at which an animal responds. For example, grey squirrels (*Sciurus carolinensis*) characteristically seek shelter in a tree when attacked (Dill and Houtman 1989). The distance at which squirrels flee when exposed to a predator, increases when the distance from the tree is increased (Dill and Houtman 1989). No seals in this study entered the water, indicating that the effort associated with entering the water, or the consequences of spending time in the water instead of being hauled out on the ice, may have been greater than the perceived threat of the approaching person. This suggests that while the approaching person warranted monitoring and preparedness to
respond further, the approacher was not perceived by the cows to be particularly threatening.

In other studies, vigilance behaviour has been correlated with proximity to a conspecific, where vigilance behaviour was related to predator detection/vulnerability and foraging success (e.g. Robinson 1981; Roberts 1988; Barnard 2004). Predator detection is increased when animals are closer together because of the increase in the number of eyes watching for predators. This also means that each individual can spend less time vigilant and more time for other fitness enhancing behaviours, such as foraging and resting. Since Weddell seals do not feed on the ice, foraging activity will not be influenced by group vigilance, however, vulnerability to predators may be. Even though Weddell seals do not have any land-based predators (e.g. Lindsey 1937; Ray and deCamp 1969) they may display an innate avoidance and vigilance response to humans, which are a relatively novel stimulus in the environment of a Weddell seal. Vulnerability to predators decreases with increased proximity to conspecifics because of the dilution factor, where risk of capture is diluted by the presence of conspecifics (Barnard 2004). Furthermore, the probability of an individual being taken by a predator decreases with an increase in group size because there are more eyes to detect a predator. Therefore, the closer the seals are to each other, the more ‘at ease’ they may feel, and so allow an intruder (in this case a pedestrian) to approach more closely before responding.

Scenario 2 - Single approach to a cow-pup pair where the pup is not exposed

As with scenario 1, the response of cows was influenced by distance to water, however, under this scenario, the distance to a conspecific was not important. The reasons why the distance to conspecific is important when the pup is not protected from the stimulus and not when the pup is protected, is however, not clear.

Scenario 3 – Group approach to a cow-pup pair where the pup is exposed

Both the distance to a conspecific and the distance to the water influenced response in Weddell seals when approached by a group of people. Cows closer to another seal could be approached more closely than cows further from conspecifics. The importance of distance to water in this result is, however, counter-intuitive. When cows were further away from the water, people could approach more closely before a response was evident. In this scenario, there is no obvious explanation for the cows responding at a later stage of approach (closer distance) the further they were from the water. This may simply be an artefact of the dataset, i.e. limited sample size and
therefore the inability to examine three-way interactions, and may be clarified with additional sampling.

**Scenario 4 – Group approach to a cow-pup pair where the pup is not exposed**

Under this scenario, the distance to a conspecific influenced response in Weddell seals when approached by a group of people. Again, cows closer to another seal could be approached more closely than cows further from conspecifics. However, the stage of approach that the group could reach before the seals responded was not influenced by distance to water. This suggests that the seals did not consider the water as a place of escape to be relevant. The reasons for this are not clear, particularly because an increase in people can equate to an increase in predation risk (which the results of this study suggest), and an increase in predation risk can result in an increase in escape behaviour. For example, two heron species (*Egretta* spp.) are known to be more likely to flee when birdwatchers are present in larger groups (Burger and Gochfeld 1998).

**Summary of response and factors influencing response**

In all but one scenario, the proximity of the cow to a conspecific was important in determining the stage of approach that people could reach before seals responded. The reason this factor was not important when a single person approached a cow where her pup was not exposed, is not clear. The proximity of water in affecting seal responses was also inconsistent, but results nonetheless indicated that distance to water could influence Weddell seal response. The influence on response (of the cow) of the position of the pup is not obvious and therefore does not allow specific ‘pup exposure’ oriented guidelines to be developed. However, taking both distance to conspecifics and distance to water into account appears likely to improve the ability of visitor guidelines to ensure minimal disturbance to Weddell seals, while allowing visitors to approach seals closely.

**2.4.3 Time to recovery**

In this study, significant decreases in cow resting behaviour occurred when people were 10 m or closer to seals, and did not return to pre-approach levels until five minutes after the completion of the approach. This indicates that although a significant change in behaviour occurred, it was of short duration. Other studies of the response of pinnipeds to human activity have also shown that behaviour returns to pre-disturbance levels soon after the disturbance is removed. For instance, the alert behaviour of lactating Southern elephant seals (*Mirounga leonina*) returned to
pre-disturbance levels immediately after the departure of humans (Engelhard et al. 2002a) and attendance behaviour of lactating harp seals returned to normal levels almost immediately after the departure of tourists (Kovacs and Innes 1990).

An interruption to resting behaviour, or any other behaviour, may not have immediate negative consequences for the animal, however, there may be cumulative effects of interruptions in behaviour that are, as yet, unclear. Wildlife is often subjected to on-going human activity. For instance, some penguin colonies on the Antarctic Peninsula receive up to 3,000-4,000 visitors within a three month season (IAATO 2004b). Therefore, understanding how the responses of animals change when interruptions are repeated will also be important in developing guidelines that reduce both the short and long-term consequences of visitation (see Chapter 3).

2.4.4 Implications for management

Generic, or ‘blanket’ guidelines, which are commonly employed for the management of human-wildlife interactions, may not be maximally effective at minimising disturbance to all individuals, unless the guidelines are set conservatively at a level that causes no visible response. However, guidelines that ensure no disturbance to wildlife run the risk of failing to achieve visitor satisfaction (e.g. Australian Government Department of the Environment and Heritage 2002; IAATO 2005).

The blanket guideline set by the AAD for people approaching Weddell seals with pups and pups on their own was 15 m at the time of this study, although this distance has recently been increased to 20 m (Australian Antarctic Division 2002a, 2004a). The AAD acknowledges that this distance is a guide only and stipulates that if human activity is disturbing the wildlife, then greater distances should be maintained (Australian Antarctic Division 2004a). No definition of disturbance is provided by the AAD, however, it is reasonable to interpret disturbance to mean ‘a change in behaviour’ as the AAD complies with recommendation XVIII-Ia – Protect Antarctic Wildlife, of the Madrid Protocol (Rothwell and Davis 1997 p. 118), which states: “Do not feed, touch, or handle birds or seals, or approach or photograph them in ways that cause them to alter their behaviour…” (Rothwell and Davis 1997 p.118).

The blanket guideline set by IAATO for approaches to Weddell seals on foot is 5-10 m (IAATO 2005). IAATO also complies with the Madrid Protocol, and has specified separation distances that should prevent disruption to reproductive and social behaviours, but that do allow the seal to raise its head. However, a strict
interpretation of the results of the current study indicate that adherence to the IAATO guidelines would elicit at least short-term changes in Weddell seal behaviour.

Disturbance in this study has been defined as 'a change in behaviour', suggesting that approaches to 20 m result in some seals being disturbed. Strict interpretation of existing guidelines, those of both the AAD and IAATO, show that they are not effective at preventing a change in all Weddell seal behaviour. The Weddell seal responses reported here imply that a separation distance of more than 30 m would need to be employed if no change in seal behaviour is the desired outcome for managers controlling visits to lactating Weddell seals and pups close to weaning.

Given that many management guidelines aim to minimise disturbance to wildlife and maximise visitor satisfaction, large separation distances, designed to prevent any visible change in behaviour are not necessarily the best solution, especially in cases where an increase in separation distance raises logistic problems relating to safety for example. It is at this point that managers may need to adopt less strict definitions of disturbance and accept some behavioural change of wildlife exposed to visitation. One approach to this is to reconsider the definition of disturbance in relation to whether changes in behaviour have significant biological consequences for the animals. Thus, changes in behaviour that have no biological consequence to the animal may be considered acceptable, but behavioural changes that have adverse effects on reproductive success or survival are not. A threefold increase in alertness of lactating Southern elephant seals during visits by researchers, for example, was found to have no measurable effect on the weaning mass of pups or on mother-pup behaviour (Engelhard et al. 2002a). The authors therefore concluded that the human activity investigated in their study was unlikely to result in a decrease in fitness of the seals. Thus, the change in behaviour could be considered acceptable because there was no fitness cost demonstrated.

Studies investigating the biological consequence of short-term, seemingly innocuous changes in behaviour are limited, specifically those that correlate short-term changes in behaviour to long-term effects. Those that are able to link short-term changes in behaviour to long-term effects, or an absence of, should not, however, be taken to imply that similar species or stimuli will result in the same outcome. Thus in the case of the Weddell seals in this study, an increase in alertness could have long-term consequences for pup mass and possibly survival.
An alternative management option to balance the pressure of minimising disturbance to wildlife and maximising visitor satisfaction and safety is to allow a certain percentage of animals in a colony/population to show a change in behaviour. Approaches to a distance that elicits a response in some individuals (i.e. a small percentage of animals) will enable a closer approach (increase in visitor satisfaction), but ensure protection for most individuals (who show no change in behaviour).

Ultimately the decision to change the definition of disturbance or to allow a specific number of individuals to be disturbed depends on a number of factors, including the goals of management, legal requirements, social expectations, safety aspects and ethical considerations (e.g. Claridge 1997; Moscardo 2001; Kirkwood et al. 2003; Higginbottom 2004a, b). Nevertheless, scientific research, as in the present case, can provide the information required for either management option.

Management guidelines can be tailored for the species in question, by understanding and incorporating the factors that affect their response, to further increase visitor satisfaction and prevent/minimise disturbance to wildlife. This study has shown that there are a number of factors that influence the point at which a lactating Weddell seal responds behaviourally to an approach by a single person and a group of people. Many of the factors can be incorporated into guidelines, for example by using the PORM method of analysis, so that visitors in the field can determine which seal they can make the closest approach to without causing significant changes in the natural behaviour of the wildlife. In addition, the PORM method of analysis allows wildlife managers to control the percentage of individuals in a colony/population that are likely to respond by providing visitors with the appropriate contour map, i.e. specific predictability threshold.

Although both managers and tour operators may consider the use of contour maps impractical, because it requires additional education and that tourists assess each situation before approaching, the use of these maps allows closer approaches (increased satisfaction), because the approacher can determine which animal is least likely to respond for any combinations of the factors influencing its behaviour.

Furthermore, the PORM method of analysis has broader applications than Weddell seals in the Antarctic. It can be used for any species, focus on any behaviour and can incorporate other stimulus and animal related factors. The generation of species specific and stimulus specific contour maps (guidelines) can therefore make
substantial contributions to minimising disturbance during human-wildlife interactions.
3 The Short and Long-term Behavioural Responses of Lactating Weddell Seals and their Pups to Pedestrian activity
3.1 Introduction

In the context of studies investigating the responses of wildlife to human activity, the short-term, or immediate behavioural reactions to novel stimuli, or to stimuli that are encountered at irregular intervals, have been documented for a number of species. For example, Giese and Riddell (1999) report on the behavioural responses of emperor penguin (Aptenodytes forsteri) chicks to the single passage of a helicopter and Erwin (1989) reports on the flush distance (i.e. the distance at which a bird flies up off its nest) of various species of nesting water birds to a single approach by two people. However, wildlife is often subjected to on-going human activity, creating a need to understand how prolonged and repeated exposure influences the nature of wildlife response. Such information provides insight into the possible cumulative effects of repeated human activity on wildlife, which is essential if interactions are to be sustained over the long-term.

At some point after repeated exposure to the same stimulus, an animal will no longer perceive the stimulus as novel, and may alter its response accordingly (Manning and Stamp Dawkins 1992). The nature of the response, and the way this changes, depends on a variety of factors, including how the stimulus is perceived, (e.g. whether it is of positive, negative or neutral consequence), the state of the animal (e.g. its health, age and stage of breeding) and the environment in which the animal experiences the stimulus (Petrinovich 1973; Manning and Stamp Dawkins 1992; Constantine 2001).

There are five categories into which the behavioural responses of wildlife to a repeated stimulus can be placed. (i) Attraction, which is the strengthening of an animal’s response as a result of positive reinforcement, and is often manifested as physical movement towards the stimuli (Knight and Cole 1991); (ii) avoidance, which is an aversion to negative consequences associated with a stimulus (Knight and Cole 1991; Allaby 1999); (iii) sensitisation, which is an increased responsiveness to the stimulus over time (Richardson et al. 1995; Allaby 1999); (iv) habituation, which is the gradual waning of a response as a result of repeated stimulation, where the stimulus lacks significant consequences for the animal (Hinde 1970); and (v) tolerance, which occurs when an animal remains in the vicinity of the stimulus because there is no option to leave (Richardson et al. 1995). However, special care must be taken not to misinterpret a lack of response as an instance of tolerance, because the stimulus might simply have been too weak to warrant a measurable reaction. Nevertheless, each of these response types demonstrates that the animal has
recognised a stimulus, has learnt something of its consequences, and has changed its behaviour accordingly (Manning and Stamp Dawkins 1992).

The type of behavioural response elicited by a stimulus is of considerable practical concern when attempting to manage human interactions with wildlife populations. Knowing which response is elicited by a particular stimulus allows management strategies to be developed that are appropriate and effective at minimising disturbance over the long-term.

In Antarctica, especially during the austral spring and summer, many animal species receive visits from both tourists and personnel working at scientific research bases. Many of these visits occur at wildlife breeding areas, as these offer reliable opportunities to view animals, often resulting in the same sites receiving multiple visits. For example, of the 150 sites visited by tourists on the Antarctic Peninsula since 1989, the majority of these visits were concentrated at < 35 sites, with a small number of those sites receiving 3,000-4,000 visitors each season (IAATO 2004b).

Weddell seals (Leptonychotes weddellii) are one species that receives multiple visits from humans, primarily because females haul-out to give birth on the fast ice, which is readily accessible from research bases and offers a platform for human travel. In addition, the species has a reputation of being unafraid of humans (e.g. Stirling 1956; Kooyman 1981c) and is therefore targeted by visitors in the hope of getting close to breeding animals and their young. The aim of this study was to investigate whether the behavioural responses of lactating Weddell seals and their pups change with repeated exposure to pedestrian activity over a short-time period and a longer-time period, to better inform management of human-Weddell seal interactions.

3.2 Methods

3.2.1 Study sites

The study was conducted during the Weddell seal pupping season (October-December) in Long Fjord, Vestfold Hills (68°35'S, 77°58'E, 2000) and Penny Bay, Windmill Islands (66°25'S, 110°40'E, 2001) East Antarctica.

3.2.2 Experimental design

Two experiments were conducted. Experiment 1 (short-term exposure), was designed to measure the changes in behaviour of lactating Weddell seals to a highly controlled and predictable stimulus over a short time period (within a few hours).
Seals were exposed to repeated approaches by a single person, simulating the kind of exposure that the individual seals might experience during a visit by a tour group or by station personnel. The age of the pups was unknown, however, based on body size and observations of births, approaches were restricted to cows with pups older than one week (Bryden et al. 1984). Experiment 2 (long-term exposure), compared the behaviour of seals (adult females and pups) in a colony exposed to relatively unpredictable pedestrian activity throughout the pupping season (several weeks), to that of seals in a colony not exposed to human activity. Once again, this experiment was designed to simulate the type and level of exposure the seals might receive during an entire pupping season.

### 3.2.2.1 Experiment 1: Short-term exposure

The experiment testing the short-term effects of repeated exposure to human activity was conducted in Penny Bay. Ten direct approaches by a single person were successively made to the same cow-pup pair over a period of approximately 1.4 hours, with each approach separated by 10 minutes. For each approach, the person stopped at a distance of 5 m from the pair for one minute and then crouched for a further minute, simulating a visitor crouching to take a photograph, before standing and retreating along their approach path to an area out of sight of the seals (behind rafted ice). All experiments were conducted between 09:00 and 18:00 (local time). Eighteen pairs of seals were approached. The approacher, using a Hi8 Digital video camera, filmed the behaviour of the cows during the approach. The responses that were quantified were (i) whether the seal looked at the approacher and (ii) the proportion of time that this behaviour was expressed. For each approach, the person walked at a constant pace and wore the same clothing (black pants and a standard-issue red top).

### 3.2.2.2 Experiment 2: Long-term exposure

The experiment testing the long-term effects of repeated exposure to pedestrian activity was conducted in Long Fjord using two seal colonies, located approximately 4.5 km apart and out of sight of each other. The seals, both cows and pups, in the experimental colony were exposed to daily pedestrian activity during the pupping season, in the form of pedestrian activity within the colony, which included approaches to read flipper tags (attached in previous years) and experimental pedestrian approaches conducted by the research group. Each cow-pup pair received up to two experimental approaches (5 m from the seals) throughout the pupping season. The seals in the control colony were not exposed to any human activity.
At the end of the pupping season, a scan sample (Altman 1974) of the behaviour of all seals (cows and pups) in response to a single person slowly walking through each colony, approaching each seal to a distance of 5 m, was conducted. These approaches were made between 18:00 and 19:30 (local time). At the experimental colony, several cows were in the water at the time of the walk through, (indicated by the presence of nine lone pups hauled out on the ice, which was approximately half of the pups observed at the start of the pupping season). Therefore, another walk through and scan sample was conducted on the following day at this colony to ensure that the responses of as many individuals as possible were assessed. Both cows and pups spend increasing periods of time in the water towards the end of the pupping season (Thomas and DeMaster 1983), which means it is highly probable that different individuals are on the ice at any given time, and that different individuals were observed on the second day of sampling.

The scan sample was conducted by an observer positioned out of sight of the seals on a high vantage point on rocky outcrops overlooking the colonies (~25 m high and 10-100 m from the seals). Behaviour was scored using 11 categories (Table 3.1).
Table 3.1 Categories and descriptions of Weddell seal behaviour used in the long-term exposure experiment.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>To whom the behaviour is directed</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rest</td>
<td>N/A</td>
<td>Lying still, no sign of activity, eyes closed.</td>
</tr>
<tr>
<td>Comfort</td>
<td>N/A</td>
<td>Included scratching, yawning, grooming and stretching.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>These behaviours increase the physical comfort of the animal (Allaby 1999).</td>
</tr>
<tr>
<td>Alert</td>
<td>Pup, conspecific, surroundings, bird or approachers.</td>
<td>Involved the seal looking. The seal's body position was not taken into account, that is, no distinction was made between lying still and raising the head.</td>
</tr>
<tr>
<td>Attack</td>
<td>Pup, conspecific, surroundings, bird or approachers.</td>
<td>Agonistic behaviour, which included lunging or charging, biting and snapping of jaws.</td>
</tr>
<tr>
<td>Ice sawing</td>
<td>N/A</td>
<td>Short duration behaviour consisting of incomplete and often slow swings of the head from side to side where the upper jaw makes contact with the ice or snow (Kaufman et al. 1975).</td>
</tr>
<tr>
<td>Eating ice</td>
<td>N/A</td>
<td>Ingesting snow or ice. Often see after ice-sawing.</td>
</tr>
<tr>
<td>Vocal</td>
<td>Pup, conspecific, surroundings, bird or approachers.</td>
<td>The seal vocalised. Vocalisations were not differentiated.</td>
</tr>
<tr>
<td>Interact</td>
<td>Pup or conspecific.</td>
<td>Unlike 'attack', this category included behaviours such as the cow placing her fore flipper on the pup and the cow and pup nuzzling together.</td>
</tr>
<tr>
<td>Travel</td>
<td>N/A</td>
<td>Purposeful movement involving the seal moving from one location to another.</td>
</tr>
<tr>
<td>Pup bump</td>
<td>N/A</td>
<td>Cow responded to the pup touching her, usually when the pup was moving around her body. The cow shifted the affected part, for example, her head, out of the pup's way.</td>
</tr>
<tr>
<td>Shift position</td>
<td>N/A</td>
<td>Seal altered its posture by rolling or shifting part of its body. Did not include purposeful movement as described in 'travel'.</td>
</tr>
<tr>
<td>Suckling</td>
<td>N/A</td>
<td>Pup sucking the teat</td>
</tr>
</tbody>
</table>

3.2.3 Analysis

All data were examined for normality and homogeneity of variance using residual plots and exploratory data analysis (Quinn and Keough 2002). Non-parametric statistical tests were used in cases where transformations were insufficient to meet the assumption of the parametric statistical tests. All data are presented as means ± 1 standard error.

Behaviour was quantified using The Observer (version 5.0, Noldus Information Technology 2003). For both the short and long-term experiment, the response looking at the approacher was classified as a state behaviour (i.e. having an
appreciable duration) and was calculated in terms of the proportion of time the seal spent responding (Altmann 1974).

3.2.3.1 Experiment 1: Short-term exposure
Regression analysis was used to describe the relationship between the percentage of seals that responded and the number of approaches they had been exposed to. Friedman tests were used to determine whether response time decreased with the number of approaches.

3.2.3.2 Experiment 2: Long-term exposure
G-tests were used to determine whether the proportion of cows and pups performing each of the observed behaviours differed between colonies during the experimental walk through.

3.3 Results
3.3.1 Experiment 1: short-term exposure
Lactating Weddell seals exposed to repeated approaches over a short-time period showed a change in behaviour with successive approaches. The proportion of seals responding decreased in an approximately linear fashion, from 67% of seals (12 of 18) responding during the first approach to 18% of seals (3 of 17) responding during the tenth approach ($R^2 = 0.398, F = 5.291, df = 9, p = 0.050$) (Figure 3.1a). The proportion of time spent responding also differed significantly across the ten approaches, with a decrease in the percentage of time spent looking at the approacher with repeated exposure (Friedman test, $\chi^2 = 36.078, df = 9, p = <0.001$). The duration of the response during approach numbers 3-10 was considerably shorter than during the first two approaches (Figure 3.1b).
Figure 3.1a) The percentage of adult female Weddell seals (n=18) responding to the approacher during each of the 10 approaches, b) mean duration of time spent responding to the approacher during each of the approaches.
3.3.2 Experiment 2: long-term exposure

The percentage of cows responding to a 5 m approach by a single person in both the experimental and control colony was similar. Alert behaviour was displayed by 83% of cows in the experimental colony compared to 80% of cows in the control colony. No significant differences were seen between colonies in terms of the percentage of seals displaying any other behaviour, notably resting and vocal behaviour, during the approach (Table 3.2).

Comparisons between the behaviour of the pups from the experimental and control colonies revealed that 88% of pups were alert in the experimental colony compared to 11% in the control colony when exposed to the approacher. Significantly more pups were resting in the control colony than in the experimental colony during the approach (Table 3.2). However, there was no significant difference between colonies in the percentage of pups performing comfort behaviours (Table 3.2). No other behaviours were observed from pups in response to the approacher.

Table 3.2 G-test statistics of the percentage of cows and pups from the experimental and control colonies performing each of the observed behaviours in response to an approach. Significant differences in bold.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>% of seals</th>
<th>G test statistic</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Experimental</td>
<td>Control</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cows</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rest</td>
<td>0</td>
<td>20</td>
<td>1.726</td>
<td>1</td>
</tr>
<tr>
<td>Alert</td>
<td>83</td>
<td>80</td>
<td>0.027</td>
<td>1</td>
</tr>
<tr>
<td>Vocal</td>
<td>17</td>
<td>0</td>
<td>1.537</td>
<td>1</td>
</tr>
<tr>
<td>Pups</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rest</td>
<td>53</td>
<td>85</td>
<td>4.013</td>
<td>1</td>
</tr>
<tr>
<td>Alert</td>
<td>47</td>
<td>10</td>
<td>5.811</td>
<td>1</td>
</tr>
<tr>
<td>Comfort</td>
<td>0</td>
<td>5</td>
<td>0.694</td>
<td>1</td>
</tr>
</tbody>
</table>

3.4 Discussion

The responses of Weddell seals to repeated pedestrian activity was investigated at two temporal scales, short and longer-term, and across two different patterns, regular frequency and irregular frequency of exposure.
3.4.1 Short-term exposure

Lactating Weddell seals in the Penny Bay colony showed a reduction in alert behaviour to repeated approaches by a single person over a period of 1.4 hours. This was manifest both as a decrease in the percentage of seals that responded to the approacher, and as a decrease in the mean time spent responding. Of the five different ways in which changes in behaviour in the presence of a repeated stimulus can be described (i.e. attraction, avoidance, sensitisation, habituation or tolerance), the change in behaviour observed in cows from this study is probably best explained as habituation, because the response of the seals waned with repeated approaches (Hinde 1970). After the initial, relatively long duration in response evident during the first two approaches, the duration of response decreased significantly.

Typically, during approaches 3-10, the seals simply looked up at the approacher and thereafter resumed 'normal' behaviour, suggesting that the seals had adjusted their response. This rapid waning of response may indicate that the stimulus was not particularly strong or meaningful to the seals. The speed with which a response wanes is dependent on the strength of the stimulus and/or the frequency of exposure (Hinde 1970; Petrinovich 1973). For example, the mobbing behaviour of chaffinches (Fringilla coelebs) has been shown to diminish more slowly with a strong stimulus (live owl), than with a weak stimulus (stuffed owl), suggesting that it takes an animal a longer period of time to 'learn' that a strong stimulus is ultimately not harmful. Other studies have shown that the greater the frequency of stimulation, the more rapid is the resulting habituation (see Petrinovich 1973). Frequent exposure should result in the recognition of the stimulus and the adjustment of behaviour more quickly. In the current study, the interval between approaches to Weddell seals was relatively short (10 minutes), and is therefore likely to have been a key factor in the rate with which the seals showed signs of habituating.

Habituation tends to be stimulus specific, such that habituation to a particular stimulus does not necessarily mean that animals will habituate to other stimuli or that if habituation does occur, that the rate of waning would occur over the same time frame (Hinde 1970). Further, the rate of recovery (i.e. re-establishment of the normal response after the stimulus is removed) is variable, again depending on the strength and type of stimulus (Hinde 1970). Recovery can occur rapidly, and completely, or can take considerable lengths of time. Alternatively, recovery may not occur at all
and the animals’ response to subsequent exposure may continue to be affected (Hinde 1970).

In the case of Weddell seals, habituation to a particular stimulus during one breeding season should therefore not be taken to imply that the seals remain habituated between seasons, as they disperse during non-breeding periods into environments where they will have little or no interaction with humans (Testa 1994). However, individual seals may habituate more readily on subsequent exposures, as habituation becomes more and more rapid with a series of habituation sessions (Petrinovich 1973). Thus although the speed at which an animal habituates to a stimulus increases with exposure, it is important to treat each stimulus independently and to devise appropriate management practices accordingly.

Both the weakness and the frequency of the stimulus are therefore factors that can be exploited from a management perspective. The immediate implication of the stimulus being weak is that there appears to be no obvious harm in approaching the seals in the manner with which the approaches were conducted.

There are examples in the literature where managers deliberately expose certain wildlife colonies to human activity and prohibit access to others, as a means of managing the effects of visitation. For example, of the five colonies of otariids at Cabo Polonio in Uruguay, visits are restricted to one colony only (Cassini 2001), and access to certain breeding seabird colonies across Antarctica is restricted to permit holders through the designation of Antarctic Specially Protected Areas (Australian Antarctic Division 2004b). The logic behind such strategies appears to be that most animals (or colonies) will be ‘protected’ from exposure to human activity at the expense of a small number of individuals. While such an approach has many advantages, particularly where species are highly sensitive to disturbance yet the pressures for visitation are intense, there is seldom sufficient information on the long-term effects of visitation to be certain that undesirable and irreversible consequences will not occur to those animals receiving frequent visits. It is possible, for instance, that animals, which have previously demonstrated habituation to human activity, may begin to exhibit other learned responses, such as sensitisation, because frequent exposure to human activity is no longer considered to be of neutral consequence.
3.4.2 Long-term exposure

3.4.2.1 Adult females

Despite the apparent habituation to frequent, predictable pedestrian approaches over the short-term (Penny Bay colony), seals exposed to less frequent exposure over the longer-term (Long Fjord colony) did not show signs of habituation. A similarly high percentage of seals (80 and 83\%) became alert during the approach at the control and experimental colonies respectively.

Adult females in both colonies may have responded to the approach of a single person in the same manner, *i.e.* becoming alert, because the seals had already developed an association with human activity prior to our experiment, where the learned response was to become vigilant in readiness for further response. This might then suggest that the seals had already become sensitised to human activity. If so, the extent to which sensitisation had occurred is unknown, although it would appear to be fairly mild as there was no evidence of escape or agonistic behaviours.

The additional ‘sporadic’ exposure that the seals in the experimental colony received during this experiment did not, however, appear to alter the perception of humans that the seals already had, evident by the similarity in the percentage of seals that were alert between colonies. Boren *et al.* (2002), in a study on New Zealand fur seals (*Arctocephalus forsteri*) showed that previous exposure to approaches by people and boat activity was the most important factor in determining whether or not the seals were likely to respond to subsequent human activity. New Zealand fur seals from areas experiencing high levels of tourism responded less often, responded at closer distances and responded less dramatically than did seals at study areas that were rarely visited. In the present study, Weddell seals in Long Fjord have been intermittently exposed to human activity since the establishment of the Australian Antarctic research station, Davis, in 1957 (Australian Antarctic Division 2004b). The seals have been exposed to human activity in the form of recreational visits and vehicle drive-bys and also to scientists who have been tagging Weddell seal pups, and subsequently checking flipper tags, each spring/summer since 1973 (Green *et al.* 1995). Given that breeding adult females show strong site fidelity to pupping areas, it is highly probable that individual seals in this study had already received various levels of exposure to human activity before this experiment was conducted (Stirling 1969; Cline *et al.* 1971). Habituation, one form of response, can remain expressed for considerable lengths of time or even indefinitely (Hinde 1970), which means that
the response of an animal may continue to be affected for considerable lengths of
time. In the current study, previous exposure to human activity may therefore have
confounded the results. It was not possible to find a colony of Weddell seals in the
Vestfold Hills that had not been exposed to some sort of human activity and was
therefore completely naïve. However, repetition of the study in other localities in
Antarctica, that receive little or no visitation, could demonstrate whether previous
exposure is a significant factor in the seals' response.

In terms of managing visits to Weddell seals in the Vestfold Hills, there is no
evidence that justifies restricting visits to one colony in order to minimise
disturbance of the greater population.

3.4.2.2 Pups
For the Long Fjord colonies, comparisons between pups that were exposed to
pedestrian activity over the pupping season and pups that had no experience with
humans should provide a clearer picture of the effects of long-term exposure to
pedestrian activity, as pups have no previous familiarity with humans.

In this study, the percentage of pups that were alert during the pedestrian approach
in the experimental colony was significantly higher than in the control colony. This
suggests that the pups in the experimental colony may have become sensitised to
pedestrian activity, i.e. their response became greater with repeated exposure. The
results therefore suggest that infrequent visits over the pupping season have an effect
on behaviour.

Although it could be argued that restricting visits to one colony is the most
appropriate management strategy to minimise disturbance to the greater population, it
must first be determined whether the change in behaviour has any negative
consequences. If a vigilant response to infrequent visits results in adverse
consequences, then it may be more appropriate to 'disturb' one colony only and
attempt to induce habituation by increasing the number of visits so that the pups can
learn that an approaching person does not represent a threat. If successful, the
approaching person would no longer represent a threat and only a small proportion of
pups would have had to learn, and change their behaviour, so that people could visit
the seals. If there were no adverse consequences to the pups becoming alert
infrequently over the pupping season, then it may be more appropriate to manage
visits such that each pup in the Vestfold Hills is only visited a few times over the
entire pupping season rather than attempting to induce habituation (with the possibility that habituation is unsuccessful and that the effect of the increase in visits is detrimental to the pups).

3.4.3 Conclusion

The initial response of most lactating Weddell seals to an approaching person was to become alert. Regular approaches by a single person over a short time period provided a good basis for learning, where, in this case, the frequency of approaches was sufficient for stimulus recognition, yet weak enough for cows to recognise that the stimulus posed no threat. However, irregular approaches over a longer-time period, where the human stimulus was variable, did not result in habituation. Although previous exposure to human activity may have confounded the results of the adult female experiment, the effect of irregular exposure on the behaviour of pups indicated that the pups had become sensitised to pedestrian activity.

It is difficult to recommend a management strategy for pedestrian interactions with lactating Weddell seals and their pups from this study, largely because of the lack of knowledge as to the biological significance of the seals becoming alert and the lack of knowledge about the effects of human activity over much longer time periods than examined here. However, it is possible to identify two different management strategies that could be adopted; (i) minimise changes in behaviour to all individuals by sending visitors out at irregular intervals over the entire pupping season and to all colonies. This strategy would therefore allow only a few visits to each seal. (ii) Designate one specific colony for visitation, and in doing so protect all other colonies from pedestrian activity. This strategy would accept that the behaviour of the exposed seals is likely to be affected in the short-term, with longer-term responses unclear. Either approach should involve monitoring the responses of cows and pups to determine whether there are any longer-term effects of visits on the seals.
Onshore Heart Rate and Behaviour of Lactating Weddell Seals in the Presence and Absence of People
4.1 Introduction

Human activity in the vicinity of wildlife can cause changes in the behaviour and physiology of animals. Vigilance of woodland caribou (*Rangifer tarandus*), for example, can increase in response to ecotourists (Duchesne *et al.* 2000), while faecal glucocorticoid levels, a measure of physiological stress, are known to be higher in wolves (*Canis lupus*) during periods of heavy snowmobile activity (Creel *et al.* 2002). These, and similar studies highlight the need to manage human activity in order to minimise any negative effects on wildlife.

To demonstrate that an animal has responded to human activity, there must be a quantifiable change in the state of the animal that can be related to exposure to a particular human stimulus. Behavioural observations measure the external expression of an animals' response to a stimulus (Hinde 1982). However, they provide little or no information about the underlying physiological changes that may be occurring at the autonomic level, such as changes in heart rate (HR), respiratory rate, body temperature and adrenal state. Physiological changes are often the first, and sometimes the only response manifest in the presence of a stimulus (Jones and Faure 1981; Withers 1992; Hofer and East 1998). The identification of potentially unseen physiological changes can therefore provide a more complete understanding of the effects of human activity on wildlife than can behavioural observations alone.

Physiological parameters commonly measured in studies of human-wildlife interaction are HR, body temperature and hormone levels (e.g. Culik *et al.* 1990; Regel and Pütz 1997; Giese 1998). Of these, HR is the most practical and efficient parameter to measure from wildlife in situ, for a number of reasons. Firstly, HR has been shown to be a sensitive indicator of the general physiological condition of an animal (Thompson *et al.* 1968) with changes in HR having instantaneous onset with exposure to a stimulus (Thompson *et al.* 1968; Perry 1973). By contrast, delays have been recorded between exposure to a stimulus and changes in body temperature (see Regel and Pütz 1997) and glucocorticosteroid levels in birds, the latter of which usually increase 5-10 minutes after capture and handling of an animal, with maximum levels occurring 30-60 minutes later (Wingfield 1994). These delays make it difficult to establish cause and effect relationships in human-wildlife interactions.

Secondly, the method of attaching a HR monitor to wildlife can involve less interference than measuring other physiological parameters, such as hormone levels.
Hormone analysis typically requires serial blood collection, so investigator activity is likely to confound subsequent results. Although hormone levels can be measured from faecal and urine samples (Wingfield et al. 1997), it is necessary to obtain baseline levels from blood samples. Thirdly, changes in HR have been interpreted as an indicator of stress in other species (e.g. Thompson et al. 1968; Syme and Elphick 1982; Culik and Wilson 1991; Bevan et al. 1994).

Current methods of measuring the HR of marine mammals include surgical implantation of loggers, and external attachment of loggers. Although both techniques require that the animal be anaesthetised, surgical implantation requires incisions and for some species, requires the animal to be anaesthetised a second time to remove the logger, making this method less suitable for use in human-wildlife interaction studies because of extra handling. Reducing methodological interference increases the ability to identify and measure a ‘true’ response should there be one, of an animal exposed to human activity.

Guidelines pertaining to interactions with wildlife in Antarctica have been developed by the International Association of Antarctic Tour Operators (IAATO) (IAATO 2005), which is a member organization founded to advocate, promote and practice safe and environmentally responsible private-sector travel to the Antarctic, and by many individual countries with scientific research stations in the region, for example Australia (Australian Antarctic Division 2004a). However, the majority of these guidelines are not based on the results of scientific studies investigating the responses of wildlife to human activity, and may therefore not be effective at minimising disturbance.

Weddell seals (Leptonychotes weddellii) inhabit areas close to some scientific research stations in Antarctica and are therefore regularly exposed to approaches by people on foot, over-snow vehicle drive-bys and aircraft operations. In particular this is the case during the austral spring and summer when female Weddell seals haul-out onto the fast ice to give birth and nurture their pup (Tedman et al. 1985). Although it has been demonstrated that Weddell seals can modify their behaviour in response to these activities (Chapter 2, 3 and 5), their physiological responses to human activity are unknown.

Establishing a link between HR and behaviour, and relating behavioural responses to changes in HR, can greatly enhance our understanding of the responses of Weddell
seals to human activity. Such information can be used to develop more sensitive, and therefore more effective guidelines for human-Weddell seal interactions. Therefore, the aims of this study were to describe the on-ice HR of lactating Weddell seals, to determine whether the HR of seals hauled out varied with different behaviours, and to determine whether the close approach of a single person and a group of people on foot elicited a change in HR.

4.2 Methods

4.2.1 Study sites and number of seals
The study was conducted in Long Fjord, Vestfold Hills, East Antarctica (68°35'S, 77°58'E) during the summer of 2002/2003 on lactating Weddell seals. Ten adult female seals were anaesthetised using gas anaesthesia (Appendix 4), fitted with a Wildlife Computers™ heart rate recorder and given an identification number, painted on the hair with peroxide hair-dye (Bristol Myers Squibb, Rydalmere Australia).

4.2.2 Measuring heart rate
The HR recorder used consisted of three components: (i) a HR processor and transmitting unit (8 cm x 12 cm x 3 cm, 46 g), (ii) a logging unit (4 cm x 6 cm x 2 cm, 60 g) and (iii) two electrode pads (6 cm diameter) (Figure 4.1). Both the processing unit, which was programmed to record the time between successive heart beats, and the logging unit, were first fixed with plastic cable ties to separate Velcro™ strips (10 x 5 cm). The two strips were then glued, using Araldite K268 Ciba Geigy, 2-5 cm apart onto the hair along the dorsal midline of the seal to ensure good communication between the two components (Wildlife Computers 1997) (Figure 4.1). Attachment of the logging units to the Velcro enabled the units to be easily retrieved from the seals by cutting through the cable ties. The electrode pads consisted of a copper coin soldered to a waterproof electrical cable (~60 cm) leading to the processor unit. The coins were covered on one side with acrylic sheeting (20 mm thick) in a dome shape for protection against the ice and so that the electrode pad could be glued onto the hair of the seal. The skin directly under the coin was shaved and coated with a thin layer of electrode gel to enhance conductivity. The electrode pads were glued slightly offset to the dorsal midline, one towards the anterior end of the seal and one towards the posterior end. The exact distance of separation between the electrode pads was dependent on the strength of the received
signal (evident by a Polar® heart-rate receiver placed next to the processor unit during gluing) (Figure 4.1).

Heart rate recorders were retrieved following the completion of two pedestrian approaches (see below) and no units were attached for more than five days. The electrode pads and Velcro™ strips were not removed, but left to fall off during the moult.

Heart rate data were downloaded and expressed as beats per minute (bpm) by diving the time interval by 60 seconds, enabling HR to be matched to specific behaviours recorded during subsequent approach experiments. The HR data were filtered to remove anomalously high readings (> 150 bpm) resulting from false triggering by muscle activity and from seawater penetration between the electrode and the seal’s skin when the seal was in the water. The upper and lower limits of HR, although conservative estimates, were based on (i) resting HR recorded from Weddell seals onshore, at 56 and 60 bpm (Ray and Smith 1968; Zapol et al. 1977), and HR recorded during apnea while asleep at 45 bpm (Kooyman and Campbell 1972); (ii) limited HR data from other pinniped species onshore, recorded as low as 37 bpm during apnoeic periods of rapid eye moment (REM) sleep in Northern elephant seals (Mirounga angustirostris) (Castellini et al. 1994a) to 120 bpm for harbour seals (Phoca vitulina) (Pasche and Krog 1980); (iii) previous findings that HR during activity can increase two to threefold in mammals (Phoades and Pflanzer 1992; Withers 1992); and (iv) the low frequency of occurrence of HR > 150 and < 30 bpm from this study.
4.2.3 Measuring behaviour
Seal behaviour was recorded during a series of approach experiments (see below) using Hi8 Digital video cameras mounted 5-30 m from the seals, but out of sight of the animals (i.e. behind rafted ice or rocks). Seal behaviour was later entered into The Observer (Version 5, Noldus Information Technology 2003), a software program designed for integrated behavioural analyses.

Eleven behavioural categories were identified: rest, look, interact, vocalise, attack, travel, shift position, comfort, pup bump, eat ice and shift snow (see Table 4.1 for descriptions). Vocalise, pup bump and shift position were classified as event behaviours (Altmann 1974) and were quantified as frequency of occurrence per minute. Because event behaviours were record as a 'moment' in time, the HR data point immediately after the event occurred was used. The remaining eight behaviours were classified as state behaviours (Altmann 1974) and were quantified as the proportion of the total observation time spent performing that behaviour.
Look, interact, attack and vocalise were further categorised in terms of ‘to whom’ the behaviour was directed (Table 4.1).

Given the short durations of many of the observed behaviours recorded during the approach experiments, non-resting behaviours were pooled (see Table 4.1) to form a new category ‘active’, so that HR during resting behaviour could be compared to HR during activity when testing for effects of pedestrian approaches.

**Table 4.1 Categories and descriptions of Weddell seal behaviour used in this study.**

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Classified as</th>
<th>To whom the behaviour is directed</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rest</td>
<td>State</td>
<td>N/A</td>
<td>Lying still, no sign of activity, eyes closed.</td>
</tr>
<tr>
<td>Comfort</td>
<td>State</td>
<td>N/A</td>
<td>Included scratching, yawning, grooming and stretching. These behaviours increase the physical comfort of the animal (Allaby 1999).</td>
</tr>
<tr>
<td>Look</td>
<td>State</td>
<td>Pup, conspecific, surroundings, bird or approachers.</td>
<td>Involved the seal looking. The seal’s body position was not taken into account, that is, no distinction was made between lying still and raising the head.</td>
</tr>
<tr>
<td>Attack</td>
<td>State</td>
<td>Pup, conspecific, surroundings, bird or approachers.</td>
<td>Agonistic behaviour, which included lunging or charging, biting and snapping of jaws.</td>
</tr>
<tr>
<td>Ice sawing</td>
<td>State</td>
<td>N/A</td>
<td>Short duration behaviour consisting of incomplete and often slow swings of the head from side to side where the upper jaw makes contact with the ice or snow (Kaufman et al. 1975).</td>
</tr>
<tr>
<td>Eating ice</td>
<td>State</td>
<td>N/A</td>
<td>Ingesting snow or ice. Often seen after ice-sawing.</td>
</tr>
<tr>
<td>Vocal</td>
<td>Event</td>
<td>Pup, conspecific, surroundings, bird or approachers.</td>
<td>The seal vocalised. Vocalisations were not differentiated.</td>
</tr>
<tr>
<td>Interact</td>
<td>State</td>
<td>Pup or conspecific.</td>
<td>Unlike ‘attack’, this category included behaviours such as the cow placing her fore flipper on the pup and the cow and pup nuzzling together.</td>
</tr>
<tr>
<td>Travel</td>
<td>State</td>
<td>N/A</td>
<td>Purposeful movement involving the seal moving from one location to another.</td>
</tr>
<tr>
<td>Pup bump</td>
<td>Event</td>
<td>N/A</td>
<td>Cow responded to the pup touching her, usually when the pup was moving around her body. The cow shifted the affected part, for example, her head, out of the pup's way.</td>
</tr>
<tr>
<td>Shift position</td>
<td>Event</td>
<td>N/A</td>
<td>Seal altered its posture by rolling or shifting part of its body. Did not include purposeful movement as described in ‘travel’.</td>
</tr>
</tbody>
</table>
4.2.4 Approach experiments

Two approach experiments were conducted on each seal that was fitted with a HR recorder; a single approach and a group approach. The first approach was made 24 hrs after anaesthesia (to ensure the seal was fully recovered) and the second at least 48 hrs after anaesthesia. The order in which the seals were exposed to each approach type was randomised to avoid any bias associated with previous exposure to either approach type. Both approaches were designed to closely resemble the type of pedestrian activity that the seals are currently exposed to from station personnel or commercial tourist visits. The approaches consisted of a pre-approach recording of 30 minutes, the approach (approximately eight minutes in duration) and a post approach recording of 20 minutes. The pre-approach recording functioned as a control, and the post approach recording enabled the time taken for HR to return to pre-approach levels to be calculated. The approach consisted of either a single person or a group of five people walking towards the seal, starting from a distance of at least 60 m. The approachers stopped for one minute at 20 m from the seal, and again when at 15, 10 and 5 m. At both the 10 and 5 m distances, the approachers spent an extra minute crouching before continuing the approach. This approach style was designed to simulate a person crouching to take a photograph. The approachers then retreated and the post approach recording commenced once people were out of view of the seal. The speed of the approach was kept constant and the appearance of the approachers was standardised, i.e. dark coloured pants and a standard-issue red top.

The effect of an approach by a single person and a group of five people on HR during rest and HR during activity was tested by a two-factor ANOVA. Data were examined for normality and homogeneity of variance using residual plots and exploratory statistics and log transformations were made where necessary (Quinn and Keough 2002).

4.3 Results

The amount of HR data retrieved was limited due to difficulties experienced with the HR recorders. The very low temperatures, the abrasive nature of the ice and the behaviour of the seals resulted in extensive electrode cable breakage, and therefore only six monitors returned usable data, with an average of 37 hours of HR data recorded per seal (range approx. ¼ of a day to five days) (Table 4.2). Only one HR
recorder, however, logged HR during the approach experiments (Seal 2). This was due to cable breakage in the 24 hour period between attachment and exposure to the pedestrian or because of poor conductivity between the skin and the electrode. (Further research into other methods of recording HR would greatly enhance sample sizes).

Table 4.2 The total duration of recorded heart rate per seal.

<table>
<thead>
<tr>
<th>Seal</th>
<th>Total duration of recorded HR (hh:mm:ss)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>43 hr, 27 min, 10 s</td>
</tr>
<tr>
<td>2</td>
<td>122 hr, 00 min, 50 s</td>
</tr>
<tr>
<td>3</td>
<td>15 hr, 05 min, 53 s</td>
</tr>
<tr>
<td>4</td>
<td>09 hr, 35 min, 09 s</td>
</tr>
<tr>
<td>5</td>
<td>28 hr, 22 min, 34 s</td>
</tr>
<tr>
<td>6</td>
<td>09 hr, 21 min, 47 s</td>
</tr>
<tr>
<td>Mean</td>
<td>37 hr, 01 min, 06 s</td>
</tr>
<tr>
<td>St dev.</td>
<td>43 hr, 00 min, 33 s</td>
</tr>
</tbody>
</table>

4.3.1 General patterns in onshore heart rate

Over a period of five days, the HR of Seal 2 showed a clear diurnal pattern. The lowest HRs, with an average of 54.4 bpm, were recorded between 21:00 and 01:00 (local time), then increased to more than 75 bpm between 05:00 and 10:00, followed by a linear decrease throughout the rest of the day (Figure 4.2). As the experimental approaches were made between 09:00 and 18:00, this decrease in HR throughout the day needed to be taken into account when interpreting HR during the approaches. This correction used the standardised residuals from a linear regression on HR and time (between 10:00 and 17:00) (Figure 4.3).
Figure 4.2 Mean heart rate per hour (bpm) ± 1 SE recorded over 5 days for Seal 2.

Figure 4.3 Mean heart rate per hour (bpm) ± 1 SE averaged over the 5½ days of recorded heart rate for Seal 2 showing the change in HR over 24 hours and the regression line (HR=79.39−1.27xh) used to calculate the standardised residuals in order to correct the HR data to remove the time of day effects.
All six seals showed a broadly similar pattern in HR (Figure 4.4), and in all cases, there was a wide range of HR's recorded between 30 bpm and 75 bpm. Discontinuous records of on-shore HR were primarily due to seals entering the water. Heart rate data from Seals 1, 2, 4 and 6 all showed the diurnal pattern as described in Figures 4.2 and 4.3.

Figure 4.4 Complete time series of heart rate (bpm) for each of the six seals. The vertical dashed lines through the 12:00 functions to align the graphs according to the time of day.

Mean HR recorded over 24 hours from Seals 1 and 2 (the only two seals for which continuous HR was recorded over 24 hours) showed the same distinct pattern of decreasing HR during the day with the lowest mean HR recorded at 16:00 and 01:00 for Seal 1 and Seal 2 respectively, and the highest mean HR recorded at 23:00 and
05:00 for Seal 1 and Seal 2 respectively. Mean HR, calculated separately for the period of highest and lowest recorded HR, was lower for Seal 1 than for Seal 2 (lowest - 50 & 53 bpm respectively, highest - 67 & 73 bpm respectively) (Figure 4.5). The time of day that HR started to decrease varied between individuals (Seal 1 at approximately 07:00 and Seal 2 at approximately 10:00), however, the period of time that HR remained relatively stable was similar between seals (Seal 1 - 7 hrs and Seal 2 - 5 hrs) (Figure 4.5). Intra seal variation was also evident as seen in (Figure 4.9) where HR was significantly higher during the group approach experiment than during the single approach experiment ($F = 508.77, df = 1, p = 0.028$).

![Figure 4.5](image)

**Figure 4.5** Mean heart rate per hour (bpm) ±1 SE for Seal 1 (black circle) and Seal 2 (grey circle) during a 24-hr period.

Heart rate and behaviour were recorded simultaneously for Seal 2 only, and although mean HR of Seal 2 was similar during each of the 10 state behaviours recorded (Table 4.3 & 4.4), graphical presentation of HR per behaviour (1½ -3½ minute intervals) showed distinct patterns in both HR during resting behaviour and
when the seal was looking in the water, i.e. the seal had its head immersed in water (Figure 4.6). During rest, the HR exhibited either a cyclic pattern (Figure 4.6ai) or a relatively stable pattern (Figure 4.6aii). Lag analysis revealed an eight second cycle in HR with a maximum HR of 83 bpm and a minimum HR of 33 bpm (Figure 4.7). Heart rate when the seal was looking into the water also showed a distinct cyclic pattern (Figure 4.6c) but of a longer duration. This was evident in two of four periods for which the behaviour continued for durations of ≥1 minute. The cycle had a period of 60 seconds with an amplitude of 25 bpm (maximum HR of 102 bpm and a minimum HR of 77 bpm, Figure 4.8). The remaining eight behaviours did not show any distinct patterns with respect to HR.
Table 4.3 Summary statistics of the heart rate (bpm) data recorded from Seal 2 during the three stages of the single approach experiment for each of the observed behaviours. ‘% of time’ is the proportion of the total time spent performing each of the state behaviours and the ‘freq of occur.’ is the frequency of occurrence of event behaviours calculated as the number of times the behaviour was recorded per minute. Because event behaviours were record as a 'moment' in time, the HR data point immediately after the event occurred was used.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Pre-recording Duration 30 mins 55 secs</th>
<th>Approach Duration 8 mins 40 secs</th>
<th>Post recording Duration 20 mins 8 secs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean Median 95% CI Range % of time Freq. of occur.</td>
<td>Mean Median 95% CI Range % of time Freq. of occur.</td>
<td>Mean median 95% CI Range % of time Freq. of occur.</td>
</tr>
<tr>
<td>Rest</td>
<td>58.1 60.0 57.6-58.7 30.0-115.4 95.51 N/A</td>
<td>58.7 60.6 57.6-59.8 30.6-113.2 81.86 N/A</td>
<td>58.2 59.4 57.5-59.0 30.0-117.6 92.01 N/A</td>
</tr>
<tr>
<td>Comfort</td>
<td>59.7 62.2 56.7-63.2 30.3-83.3 3.64 N/A</td>
<td>56.2 58.3 53.7-58.8 30.0-75.0 15.65 N/A</td>
<td>57.5 59.4 54.8-60.3 30.9-83.3 6.87 N/A</td>
</tr>
<tr>
<td>Look pup</td>
<td>59.1 58.0 52.1-67.7 42.0-80.0 0.58 N/A</td>
<td>- - - - - -</td>
<td>62.8 65.2 47.9-77.8 43.2-75.9 0.49 N/A</td>
</tr>
<tr>
<td>Look surrounding</td>
<td>59.0 58.8 43.3-74.5 52.6-65.2 0.13 N/A</td>
<td>38.8 38.8 -0.8-78.5 35.7-42.0 0.64 N/A</td>
<td>60.5 60.6 58.5-62.5 57.7-63.2 0.63 N/A</td>
</tr>
<tr>
<td>Look approacher</td>
<td>- - - - - -</td>
<td>54.7 57.7 43.2-66.2 35.5-67.4 1.85 N/A</td>
<td>- - - - - -</td>
</tr>
<tr>
<td>Interact pup</td>
<td>61.0 61.0 33.0-89.0 58.8-63.2 0.13 N/A</td>
<td>- - - - - -</td>
<td>- - - - - -</td>
</tr>
<tr>
<td>Vocalise pup</td>
<td>45.2 46.2 33.2-57.3 30.5-66.7 N/A 0.26</td>
<td>- - - - - -</td>
<td>56.1 56.1 56.1 56.1 N/A 0.05</td>
</tr>
<tr>
<td>Pup bump</td>
<td>58.6 62.5 51.2-66.1 36.6-74.1 N/A 0.46</td>
<td>- - - - - -</td>
<td>- - - - - -</td>
</tr>
</tbody>
</table>

Note: N/A means calculation not possible because of the method in which the behaviour was recorded.
Table 4.3 continued.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Pre-recording Duration 30 mins 55 secs</th>
<th>Approach Duration 8 mins 40 secs</th>
<th>Post recording Duration 20 mins 8 secs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Median</td>
<td>95% CI</td>
</tr>
<tr>
<td>Shift position</td>
<td>61.2</td>
<td>66.3</td>
<td>46.3-76.1</td>
</tr>
<tr>
<td>Active</td>
<td>58.9</td>
<td>61.5</td>
<td>56.4-61.3</td>
</tr>
</tbody>
</table>

Note: N/A means calculation was not made because the calculation was not applicable to that behaviour.
Table 4.4 Summary statistics of the heart rate (bpm) data recorded from Seal 2 during the three stages of the group approach experiment for each of the observed behaviours. ‘% of time’ is the proportion of the total time spent performing each of the state behaviours and the ‘freq of occur.’ is the frequency of occurrence of event behaviours calculated as the number of times the behaviour was recorded per minute. Because event behaviours were recorded as a 'moment' in time, the HR data point immediately after the event occurred was used.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Pre-recording (Duration 29 mins 54 secs)</th>
<th>Approach (Duration 9 mins 31 secs)</th>
<th>Post-recording (Duration 20 mins 34 secs)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Median</td>
<td>95% CI</td>
</tr>
<tr>
<td>Rest</td>
<td>63.7</td>
<td>65.9</td>
<td>63.0-64.5</td>
</tr>
<tr>
<td>Comfort</td>
<td>63.6</td>
<td>65.2</td>
<td>62.1-65.1</td>
</tr>
<tr>
<td>Look pup</td>
<td>62.6</td>
<td>66.3</td>
<td>59.8-65.4</td>
</tr>
<tr>
<td>Look surrounding</td>
<td>59.9</td>
<td>63.8</td>
<td>52.4-67.4</td>
</tr>
<tr>
<td>Look water</td>
<td>64.9</td>
<td>66.7</td>
<td>64.2-65.6</td>
</tr>
<tr>
<td>Look approacher</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Shift snow</td>
<td>62.6</td>
<td>65.2</td>
<td>60.5-64.8</td>
</tr>
<tr>
<td>Eat ice</td>
<td>66.3</td>
<td>66.7</td>
<td>65.1-67.6</td>
</tr>
</tbody>
</table>

Note: N/A means calculation not possible because of the method in which the behaviour was recorded.
Table 4.4 continued.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Pre-recording</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th>Approach</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th>Post recording</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Duration 29 mins 54 secs</td>
<td>Duration 9 mins 31 secs</td>
<td>Duration 20 mins 34 secs</td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Mean</td>
<td>Median</td>
<td>95% CI</td>
<td>Range</td>
<td>% of time</td>
<td>Freq. of occur.</td>
<td>Mean</td>
<td>Median</td>
<td>95% CI</td>
<td>Range</td>
<td>% of time</td>
<td>Freq. of occur.</td>
<td>Mean</td>
<td>Median</td>
<td>95% CI</td>
<td>Range</td>
<td>% of time</td>
</tr>
<tr>
<td>Interact pup</td>
<td>65.6</td>
<td>66.2</td>
<td>64.0-67.1</td>
<td>37.7-76.9</td>
<td>5.08</td>
<td>N/A</td>
<td>65.4</td>
<td>65.2</td>
<td>63.3-67.5</td>
<td>63.2-69.0</td>
<td>1.09</td>
<td>N/A</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Travel</td>
<td>64.1</td>
<td>64.5</td>
<td>61.2-67.0</td>
<td>39.7-85.7</td>
<td>0.86</td>
<td>N/A</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Vocalise pup</td>
<td>62.8</td>
<td>67.4</td>
<td>56.8-68.8</td>
<td>33.7-75.0</td>
<td>N/A</td>
<td>0.6</td>
<td>65.9</td>
<td>65.9</td>
<td>64.1-67.7</td>
<td>61.2-70.6</td>
<td>N/A</td>
<td>0.84</td>
<td>65.9</td>
<td>65.9</td>
<td>65.9</td>
<td>65.9</td>
<td>N/A</td>
</tr>
<tr>
<td>Pup bump</td>
<td>57.7</td>
<td>61.6</td>
<td>48.7-66.7</td>
<td>34.9-65.9</td>
<td>N/A</td>
<td>0.2</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Shift position</td>
<td>64.6</td>
<td>65.2</td>
<td>61.1-68.1</td>
<td>32.8-87.0</td>
<td>N/A</td>
<td>1.41</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Active</td>
<td>64.5</td>
<td>65.9</td>
<td>64.0-65.0</td>
<td>31.4-115.4</td>
<td>N/A</td>
<td>68.51</td>
<td>63.8</td>
<td>64.5</td>
<td>62.6-65.0</td>
<td>32.4-82.2</td>
<td>22.16</td>
<td>N/A</td>
<td>62.3</td>
<td>63.2</td>
<td>60.2-64.3</td>
<td>32.6-69.8</td>
<td>3.7</td>
</tr>
</tbody>
</table>

Note: N/A means calculation was not made because the calculation was not applicable to that behaviour.
Figure 4.6 Examples of heart rate (bpm) against time for each of the state behaviours recorded from Seal 2 on the 16/11/02 during a(i) rest, showing the cyclic HR pattern and a(ii) rest, showing the stable HR pattern, b) comfort activities, c) look water, d) look pup, e) look surrounding, f) look approacher, g) shift snow, h) eat ice, i) interact with pup, and j) travel. The breaks between data points occur because the seal was performing other behaviours at that particular time.
Figure 4.7 Autocorrelation function (ACF) of the heart rate (bpm) recorded from Seal 2 during resting behaviour in the absence of human activity showing a cycle in HR occurring every eight seconds (1 lag = 2 seconds). The lag is a transformation in the ACF that brings past values of a series into the current case. The case prior to the current case is a lag of 1. Solid lines indicate the lower and upper 95% confidence intervals.

Figure 4.8 Autocorrelation function (ACF) of the heart rate (bpm) recorded from Seal 2 during 'look water' behaviour, i.e. the seal has its head immersed in water, showing half a cycle, where the peak and trough of the cycle (3-19 lag number) result in a difference of 16 lags. This corresponds to a 32 second time period resulting in a 60 second cycle of heart rate. The lag is a transformation in the ACF that brings past values of a series into the current case. The case prior to the current case is a lag of 1. Solid lines indicate the lower and upper 95% confidence intervals.
4.3.2 Heart rate during approaches
There was no evidence of a significant effect of a single person approach or a group approach on the HR of Seal 2. This was demonstrated by a comparison of time-corrected HR data testing for differences between experiments (single and group), stage of approach (pre-recording, approach and post recording) \( F = 0.278, df = 2, p = 0.782 \) and behaviour (rest or active) stage of approach \( F = 0.61, df = 1, p = 0.621 \). However, a significant increase in HR was recorded during the group approach when compared to the single person approach \( F = 508.77, df = 1, p = 0.028 \) (Figure 4.9).

4.3.3 Behaviour during approaches
The behaviours displayed by Seal 2 during the three stages of the single approach experiment did not appear to change with stage of approach (Figure 4.10, Table 4.3). The seal spent > 80% of her time resting during each stage of the approach. However, changes in behaviour were evident during the group approach, with the greatest difference found in the percentage of time spent resting. This increased sequentially from the pre-approach recording (31%), to the approach (78%) to the post approach recording (97%). The seal also spent time looking in the water during the pre-approach recording (39%) but not during the approach or the post approach recording. The time spent performing the remaining state behaviours did not appear to change between the stages of the approach, with the exception of looking at approacher (Figure 4.10, Table 4.4).
Figure 4.9 Time corrected heart rate data (bpm) (time corrected to remove the effect of the natural decrease in HR during the day) of Seal 2 showing HR ± 1 SE during resting and active behaviour for the three stages of approach for both single and group approach experiments.
Figure 4.10 The proportion of time Seal 2 spent performing each of the state behaviours during the three stages of the approach (pre-approach, during approach and post approach) for (a) the single approach experiment and (b) the group approach experiment. LP = look pup, LS = look surroundings, LA = look approachers, LW = look water, IP = interact pup, SN = shift snow and EI = eat ice.
4.4 Discussion
Heart rate is regulated by the efferent neurons of the autonomic nervous system, which is divided into the parasympathetic and sympathetic nervous systems (Withers 1992). The nerves of the parasympathetic system influence organs to conserve and restore energy, particularly during quiet, calm activities, corresponding to decreases in HR (Withers 1992; Solomon et al. 1999). Conversely, the nerves of the sympathetic system operate to stimulate organs and to mobilise energy, especially in response to stress and vigorous activity, which results in an increase in HR (Withers 1992; Solomon et al. 1999). During stress, sympathetic stimulation also results in an increase in blood pressure, pupillary dilatation, elevation in blood glucose and free fatty acid concentrations, and an increase in arousal state (Cunningham 2002). The increase in arousal state prepares the animal to respond behaviourally, either by fighting or taking flight, commonly known as the ‘fight or flight’ reaction (Cannon 1963). The behavioural state of an animal therefore has a direct relationship with HR.

However, physical and emotional stressors can also result in an increase in HR without a concomitant change in behaviour (Dressen et al. 1990; Giese 1998; Solomon et al. 1999). During stress, the adrenal gland secretes the hormones epinephrine and norepinephrine, which results in an increased HR (Withers 1992). Therefore, if an animal is presented with a negative stimulus, an increase in HR may occur. Research on sheep, starlings, penguins and albatrosses, for example, have illustrated that HR can be interpreted as an indicator of stress (Thompson et al. 1968; Syme and Elphick 1982; Culik and Wilson 1991; Bevan et al. 1994).

4.4.1 Onshore heart rate
In this study, observations of the HR of six lactating Weddell seals revealed a daily periodicity in HR. Circadian rhythm of HR has been shown to be affected by endogenous and exogenous factors, and to occur in many different species, including humans (Krauchi and Wirz-Justic 1994), hamsters (Hashimoto et al. 2004), rats (van den Buuse 1994; Lemmer et al. 1995) and sea bream (Aissaoui et al. 2000). Changes in HR reflected in the circadian rhythm of an animal are partly determined by the biological clock, which in mammals is located in a small suprachiasmatic nucleus of the hypothalamus and its effector control is mediated by the nervous system and ultimately by genes and proteins (Withers 1992; Sherwood et al. 2005). Changes in HR are also based on exogenous factors, such as physical activity, body temperature
and, in some animals, food intake (Minors and Waterhouse 1981; Withers 1992). In the case of Weddell seals, the activity pattern, namely haul-out behaviour, seems to be driven by a circadian rhythm based on changes in solar radiation (Bornemann et al. 1998) and air-temperature (Lake et al. 1997). However, Bornemann et al. (1998) proposed that the principal ‘zeitgeber’ of the Weddell seals ultradian (semicircadian) rhythm of behaviour is actually the tide. Behavioural observations of lactating Weddell seals onshore have shown that the seals are relatively inactive, spending 92.7% of their time resting (Chapter 2), as is the case for other pinnipeds (for example, grey seals (Halichoerus grypus) Anderson and Harwood 1985), suggesting that activity does not fully explain the periodicity in HR seen here. Furthermore, HR recorded during the various forms of behaviour indicate that the circadian HR rhythm of the seals is more likely to reflect endogenous processes and not activity levels.

Similar results have been reported in Tamar wallabies (Macropus eugenii), where long-term changes (e.g. hours) in HR occurred in the absence of activity (e.g. Dressen et al. 1990). Reite and Short (1981) found relatively long-term day-to-day changes in the HR of pigtailed monkeys (Macaca nemestrina), with no significant relationship to day-to-day variability in activity.

The timing of the circadian rhythm of Weddell seals varies between individuals by as much as 5.2 hours (n=5) (Bornemann et al. 1998), which is consistent with the difference in timing of the HR cycles recorded from the present study. Intra-specific variation in physiological parameters is well known in vertebrates (Spicer and Gaston 1999). Moreover, variation within individuals also occurs, as was evident of the HR of Seal 2. Heart rate was higher during the hour of the group approach experiment than during the hour of the single approach experiment. There was no difference, however, in the daily HR between the two days of recording or over the five days of recording. The difference in HR was not related to the approach type or the behaviours observed, as HR did not change in the presence of the approacher irrespective of approach type, nor did it change with different behaviours conducted, therefore the difference is likely to be related to other factors, one of which could be the physical and/or emotional state of the animal. For example, the seal may have been more agitated during the hour of the group approach (the group approach was conducted 25 hours after the single approach) or her body temperature may have been elevated resulting in an overall higher HR. This pronounced intra-seal variation in HR highlights the importance of obtaining baseline data at a fine scale (e.g. at least
hourly for Weddell seals, and for a larger sample of individual seals) before HR can be used as a proxy for stress in human-wildlife interactions studies.

4.4.2 Heart rate in relation to behaviour

The HR for Seal 2 did not increase during activity compared to rest, suggesting that the active behaviours were not of sufficient vigour to elevate HR above resting rates. This may be partly related to the high degree of variability in HR during resting behaviour and during active behaviour (Rest: range = 31.4-84.5 bpm and 30.0-115.4 bpm for group and single pre-approach respectively, and Active: range = 31.4-115.4 bpm and 30.3-83.3.7 bpm for group and single pre-approach respectively). Many of the active behaviours, for example, comfort, shift snow and interact pup, occurred for short time periods (< 2 minutes). The increased activity level may simply not have been of sufficient vigour to result in an increase in HR. Many of these behaviours do not require the expenditure of much energy, for example, comfort behaviours, which include scratching and stretching, and can be conducted by Weddell seals while resting. The HR recorded during travel, which in this study was the most physically demanding behaviour observed, was not elevated relative to HR recorded during the other behaviours. The most likely explanation for this was the short duration (29.9-71.4 seconds) of the behaviour and therefore the lack of an increase in metabolic rate.

Changes in HR may not have been the best metric to use when comparing behaviours, however, patterns in HR, in particular during rest and when the seal was looking into the water, were more telling. Both of these behaviours can involve periods of eupnea and apnea, which are known to affect HR (Harrison and Ridgway 1972; Kooyman and Campbell 1972; Kenny 1979; Castellini et al. 1994a). Although it was not possible to distinguish between sleeping and resting behaviour, in humans, HR differs during times of sleep versus being awake while resting (see Veerappan et al. 2000). In a qualitative study of sleeping and waking patterns in Weddell seals, inspection of HR patterns within sleeping periods of an adult female (non-lactating) Weddell seal and a female pup show similar patterns to human patterns classifiable as REM and Slow-Wave (delta) sleep, with intermediate stages in the non-REM portions (Shurley et al. 1969). Kooyman and Campbell (1972) recorded the HR of adult seals during sleep in ice holes and found HR to vary with respiration, where eupneic HR during rest averaged 64 bpm compared to apnoeic HR, which averaged 34 bpm. This suggests that different HR patterns occur during sleep. In Northern elephant seal pups (Mirounga angustirostris) several cycles of apnea and eupnea can
occur during a single sleep episode (Castellini et al. 1994a). Heart rate during REM sleep was irregular and during apnea the HR was relatively stable and similar to the minimum value recorded during eupneic HR (Castellini et al. 1994a; Castellini et al. 1994b; Ware 1998). In hooded seals (Cystophora cristata) and harbour seals (Phoca vitulina) resting on land, HR during apnea has been shown to be significantly lower than during eupnea (Pasche and Krog 1980). Studies such as these indicate that different patterns in resting HR can occur in seals, and can be explained by breath holding. The two different patterns in HR observed during resting behaviour in this study are therefore likely to reflect two different resting states.

In the present study, the cyclic pattern in HR during look water was most probably the result of breath holding. There was no evidence of the dive response, i.e. a decrease in HR, which is probably because the seal had no intention of diving (see Kooymann and Campbell 1972; Kooymann 1981b). There was however, evidence of a longer HR cycle suggesting that respiratory rate decreased. Hence, the HR pattern was different to that observed during resting behaviour. Therefore, the only measurable change in HR during this behaviour was the length of the period of the cycle.

4.4.3 Approach experiments
The HR of Seal 2 did not vary with the approach to 5 m by a single person or a group of people. This indicates that the stimuli tested did not activate the sympathetic nervous system of the seal, which is stimulated under conditions of fright or vigorous activity (Cannon 1963). The seal did, however, respond behaviourally, indicating that the approachers were considered to be of interest.

It would be imprudent to generalise from the results gained from a single seal about the physiological responses of Weddell seals to pedestrian approaches. Due to the lack of research on the effect of human activity on HR in pinnipeds, comparisons cannot be made to establish whether the response of Seal 2 are representative of the species or pinnipeds in general. Further research is therefore required. Experiments with stronger stimuli may be needed to substantiate the relationship between HR and stress in Weddell seals.

4.4.4 Conclusion
This study has revealed periodicity in the onshore HR of lactating Weddell seals at two quite different temporal scales: a daily periodicity related to haul-out behaviour, and the shorter cycles seen during rest and look water, which were likely to be related
to respiration (eupnea and apnea). Some degree of individual variation was apparent in the time of day at which HR was at its maximum and minimum. Therefore, care needs to be exercised when using HR as a proxy for stress.

The absence of a change in HR with the approach of a single person or a group of people to a distance of 5 m may suggest that there is no immediate physiological HR change associated with close approaches to lactating Weddell seals, but further research involving more individuals must first be conducted to clarify this.
5 The Behavioural Response of Lactating Weddell Seals to over-snow vehicles
5.1 Introduction

Human activity in Antarctica is primarily focused on scientific research, its logistic support and tourism. All of these involve travel over land or ice by foot, over-snow vehicles, or light aircraft. These forms of transport, with the exception of pedestrians, are often large, brightly coloured, and generate varying levels of noise; all factors which have the potential to negatively affect wildlife. Previous studies on marine mammals and seabirds have shown that vehicular activity (encompassing all forms of transport) can cause changes in behaviour, including vocal behaviour, and physiology, such as heart rate and body temperature (e.g. Regel and Pütz 1997; Giese 1998; Constantine 2001; van Parijs and Corkeron 2001). Emperor penguin (Aptenodytes forsteri) chicks for example, are known to become more vigilant during the approach of a helicopter (Giese and Riddle 1999), and beluga whales (Delphinapterus leucas) will change their vocal behaviour during small motorboat and ferry activity (Lesage et al. 1999). Polar bears (Ursus maritimus) are also known to alter their behaviour in the presence of vehicles (Dyck and Baydack 2004). Despite these studies, the effects on wildlife of vehicle activity are still poorly understood.

The behavioural response of an animal to a vehicle depends on a number of factors associated with both the stimulus and the animal. For example, the physical structure of the vehicle (i.e., its size and shape), its speed of travel, operating distance, the manner in which it is driven, and the level and frequency of sound generated, can all influence the degree and nature of an animal’s response (e.g. Richardson et al. 1995; Richardson and Würsig 1997; National Research Council 2003). A large vehicle generally elicits stronger responses than a small one, an increase in speed often results in higher noise levels (McCauley and Cato 2003) and a fast moving vehicle may seem more threatening to wildlife (Dill 1974). Another important factor is the constancy of the sound level generated by the vehicle (Myrberg 1990; Richardson et al. 1995).

Factors inherent to the animal that will influence responses to vehicles include its gender, phase of breeding, and age. Adult female Atlantic walruses (Odobenus rosmarus), for example, are reported as often being the only members of a colony to show vigilance behaviour in the presence of aircraft at terrestrial haul-outs (Salter 1979). Similarly, adult female New Zealand fur seals (Arctocephalus forsteri) approached by pedestrians and small boats will respond by entering the sea, while adult males will stay in the colony to fight (Boren et al. 2002). Pups in this study
responded differently again, and fled from the vehicles to hide among the rocks (Boren et al. 2002).

Managing vehicular activity around wildlife in Antarctica is currently achieved in a variety of ways. The Antarctic Treaty system, for example, has measures and conventions that protect wildlife from disturbance from vehicles, prohibiting the operation of vehicles in a manner that disturb concentrations of seals and birds (Kimball 1999). Further, many individual Antarctic Treaty Nations have established their own guidelines to minimise vehicle disturbance to Antarctic wildlife (e.g. Australian Antarctic Division 2002a), as has the International Association of Antarctic Tour Operators (IAATO) (IAATO 2004a), which is an organisation founded to advocate, promote and practice safe and environmentally responsible private-sector travel to the Antarctic.

However, for most Antarctic wildlife, there has been little, if any, research to verify the accuracy and effectiveness of existing guidelines, which is further exacerbated by the fact that these guidelines are mostly based on anecdotal reports. In particular, the guidelines for the Weddell seal (Leptonychotes weddellii) have not been examined, yet this species receives the highest level of exposure to vehicular activity on the continent than any other pinniped. Weddell seals are the only pinniped to breed and moult on the fast ice upon which humans travel, and at a time when human activity in the region is at its peak. The aim of the study was to verify the existing guidelines for travel around Weddell seals adopted by one Treaty Nation; Australia, by measuring the immediate behavioural responses of lactating Weddell seals to over-snow vehicles.

5.2 Methods

5.2.1 Study site, number of seals and stimuli used
The study was conducted on lactating Weddell seals and their pups over a 17-day period during November 2001 at Penny Bay, Windmill Islands, East Antarctica (66°25'S, 110°40'E). Fifteen cow-pup pairs were exposed to drive-bys of a 4-wheeled, all-terrain vehicle (known as a 'quad' bike, Honda TRX350) and 12 pairs were exposed to drive-bys of a tracked all-terrain vehicle (known as a 'Hagglund', Mercedes Benz BV206D). Five cow-pup pairs were exposed to the passage of both a quad and a Hagglund.
5.2.2 Drive-by experiments

The drive-bys were designed to closely resemble the type of vehicle activity that Weddell seals in the Australian Antarctic Territory (AAT) currently encounter, and incorporated three treatments: drive-by distance, vehicle type and travel speed. The distances were based on the current guidelines recommended by the Australian Antarctic Division (AAD) for travel in the vicinity of Weddell seals and were, for a quad: 150 m, and for a Hagglund: 250 m (Australian Antarctic Division 2004b). As the efficacy of these guidelines has never been tested, distances that were less than and greater to existing limits were also included (Table 5.1). One drive-by for both types of vehicles at the same speed was conducted at 250 m from the seals so that comparisons of seal responses between vehicle types could be made.

Table 5.1 Distance from the seal and speed of travel used in the drive-by experiments. Distances in bold represent the current Australian Antarctic Division guidelines for travel in the vicinity of Weddell seals.

<table>
<thead>
<tr>
<th>Distance</th>
<th>Speed of travel (km hr⁻¹)</th>
<th>Quad</th>
<th>Hagglund</th>
</tr>
</thead>
<tbody>
<tr>
<td>Closest distance</td>
<td>15</td>
<td>50 m</td>
<td>100 m</td>
</tr>
<tr>
<td>Middle distance</td>
<td>15 &amp; 45 - quad</td>
<td>150 m</td>
<td>250 m</td>
</tr>
<tr>
<td></td>
<td>15 &amp; 25 - Hagglund</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Furthest distance</td>
<td>15</td>
<td>250 m</td>
<td>400 m</td>
</tr>
</tbody>
</table>

Cow-pup pairs were selected if pups were greater than one week old. Pup age was determined from visual body size estimates and observations of births (Bryden et al. 1984). Cows were given an identification number (painted on the hair) with peroxide hair-dye (Bristol Myers Squibb, Rydalmere Australia) at the beginning of the season. This was conducted by one person who quietly approached the seal while at rest to avoid the seal responding to the person and possibly confounding the results.

Each experiment consisted of four drive-bys. For both vehicle types, one drive-by was made at the closest distance at a slow speed of 15 km/hr and another drive-by was made at the furthest distance, also at 15 km/hr. The remaining two drive-bys were both made at the middle distance, however one drive-by occurred at a slow speed (15 km/hr for both vehicles types) and the other was at a faster speed (45 km/hr for the quad and 25 km/hr for the Hagglund). Between each drive-by, vehicles were switched off for 10 minutes. The order in which seals were exposed to the different distances and speeds was randomised to avoid any bias associated with previous runs (distance/speed). Due to logistical constraints (i.e. access to vehicles), the five seals
exposed to both the quad and the Hagglund were always exposed to the quad treatment first.

The behaviour of the cows during each drive-by was recorded on Hi8 Digital video cameras mounted between 5-30 m out of sight of the seals behind rafted ice or rocks.

For each experiment, two positional co-variates were recorded; (i) the distance of the cow to the nearest conspecific and (ii) the distance of the cow to water (potential refuge); and one biological co-variate: the position of the pup in relation to its mother and the vehicle (i.e. whether the pup was directly exposed to the vehicle or not).

5.2.3 Analysis

5.2.3.1 General

The recorded behaviour was later quantified using The Observer (Version 5 Noldus Information Technology 2003), a software package specifically designed for integrated behavioural analyses.

Although eleven behavioural categories were identified (Table 5.2) only one behavioural category, ‘looking at vehicle’, was taken to indicate that the seal had perceived the stimulus and responded to it. This behaviour was recorded both as a binary variable, indicating whether or not the seal looked at the vehicle, and as the duration of time that the seal spent looking at the vehicle, expressed as the proportion of total drive-by time.

All analyses were conducted using R statistical software (version 1.8.1 2003). Binomial generalised linear models (GLMs) (McCullagh and Nelder 1989) were fitted to the binary data to test if the probability that an individual seal would react during a drive-by differed with the type of vehicle, the drive-by distance, travel speed or the positional and biological co-variates.

Exploratory analysis showed that the proportion of time that the seal spent looking at the vehicle was not normally distributed, so permutation tests (Good 2000) were used to test if the distribution of the duration data differed with vehicle type, drive-by distance, speed or the positional and biological co-variates.
Table 5.2 Categories and description of Weddell seal behaviour.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>To whom the behaviour is directed</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rest</td>
<td>N/A</td>
<td>Lying still, no sign of activity, eyes closed.</td>
</tr>
<tr>
<td>Comfort</td>
<td>N/A</td>
<td>Included scratching, yawning, grooming and stretching. These behaviours increase the physical comfort of the animal (Allaby 1999).</td>
</tr>
<tr>
<td>Look</td>
<td>Pup, conspecific, surroundings, bird or approachers.</td>
<td>Involved the seal looking. The seal's body position was not taken into account, that is, no distinction was made between lying still and raising the head.</td>
</tr>
<tr>
<td>Attack</td>
<td>Pup, conspecific, surroundings, bird or approachers.</td>
<td>Agonistic behaviour, which included lunging or charging, biting and snapping of jaws.</td>
</tr>
<tr>
<td>Ice sawing</td>
<td>N/A</td>
<td>Short duration behaviour consisting of incomplete and often slow swings of the head from side to side where the upper jaw makes contact with the ice or snow (Kaufman et al. 1975).</td>
</tr>
<tr>
<td>Eating ice</td>
<td>N/A</td>
<td>Ingesting snow or ice. Often seen after ice-sawing.</td>
</tr>
<tr>
<td>Vocal</td>
<td>Pup, conspecific, surroundings, bird or approachers.</td>
<td>The seal vocalised. Vocalisations were not differentiated.</td>
</tr>
<tr>
<td>Interact</td>
<td>Pup or conspecific.</td>
<td>Unlike ‘attack’, this category included behaviours such as the cow placing her fore flipper on the pup and the cow and pup nuzzling together.</td>
</tr>
<tr>
<td>Travel</td>
<td>N/A</td>
<td>Purposeful movement involving the seal moving from one location to another.</td>
</tr>
<tr>
<td>Pup bump</td>
<td>N/A</td>
<td>Cow responded to the pup touching her, usually when the pup was moving around her body. The cow shifted the affected part, for example, her head, out of the pup's way.</td>
</tr>
<tr>
<td>Shift position</td>
<td>N/A</td>
<td>Seal altered its posture by rolling or shifting part of its body. Did not include purposeful movement as described in ‘travel’.</td>
</tr>
</tbody>
</table>

5.2.3.2 Comparison of vehicles
Responses to the type of vehicle were tested by comparing seal behaviour in the presence of a quad and a Hagglund driven at 250 m at the slow speed. In both the binomial GLM and the permutation test, the seal was treated as a blocked factor to account for individual variation.

5.2.3.3 Drive-by distance
Binomial GLM and permutation tests were used to perform omnibus tests for a difference in response due to drive-by distance. These tests were performed separately for quad and Hagglund results. Where there was evidence of a difference in response, Holm adjusted pairwise comparisons were used to determine which treatments differed (Benjamini and Hochberg 1995).
5.2.3.4 Speed of travel
Binomial GLM and permutation tests were used to perform omnibus tests for a
difference in response due to travel speed. Where there was evidence of a difference
in response, Holm adjusted pairwise comparisons were used to determine which
treatments differed (Benjamini and Hochberg 1995).

5.2.3.5 Positional and biological co-variates
Binomial GLMs were fitted to the binary data to investigate the correlation between a
seal’s response and its distance from the nearest conspecific, its distance to water and
whether its pup was exposed to the vehicle.

As these co-variates were confounded with individual seals it was not possible to
treat seals as a blocked factor to control for individual variation. Each co-variate was
modelled separately because of the low power of the test when all three co-variates
were incorporated into the one model.

5.3 Results
5.3.1 Comparison of vehicle type
Of the five seals exposed to both types of vehicle examined in this study, only one
individual reacted to the quad, and a second individual to the Hagglund. The
binomial GLM showed no evidence that the probability of a seal reacting to the
drive-by of a quad at a distance of 250 m was different from the probability of the
seal reacting to the drive-by of the Hagglund at the same distance ($p = 0.87$, 6.7% of
individuals for the quad vs. 8.3% of individuals for the Hagglund, $n = 5$). Similarly,
the permutation test showed no evidence that the duration of response during the
drive-by of the two vehicles differed with vehicle type ($p = 1.00$, $X = 4.6 \pm 4.6\%$ of
time spent responding to the quad and $X = 1.7 \pm 1.7\%$ of time spent responding to the
Hagglund, $n = 5$).

5.3.2 Drive-by distance
5.3.2.1 Hagglund
For the Hagglund, the binomial GLM showed strong evidence that the probability of
a seal reacting differed with drive-by distance ($p = 0.0002$). Holm adjusted pairwise
comparisons showed significant differences between the 100 m and the 250 m
distance ($p = 0.0006$), and between the 100 m and the 400 m distance ($p = 0.0006$),
but no evidence for a difference between the 250 m and 400 m distance ($p = 1.00$).
Where there was a difference in seal response due to distance, the probability of a seal reacting was greater during the closer drive-bys (Figure 5.1a).

The permutation test of the three drive-by distances showed strong evidence that duration of response also differed with distance ($p = 0.0015$). However, the Holm adjusted pairwise comparisons showed only weak evidence of a difference in duration of response between the 100 m and 250 m distance ($p = 0.092$) and the 100 m and 400 m distance ($p = 0.092$) and no evidence of a difference between the 250 m and 400 m distance ($p = 1.00$) (Figure 5.1b).
Figure 5.1a) The percentage of lactating Weddell seals reacting to the drive-by of the Hagglund at the three experimental distances, b) the total duration of time (recorded as the % of time within each interval) ± 1 SE, that the seals (n = 12) spent looking at the Hagglund during the drive-bys at the three experimental distances. Statistically significance differences at the 0.05 level are indicated by letters, where ‘a’ signifies the difference between the 100 m and 250 m distance and ‘b’ signifies the difference between the 100 m and 400 m.
5.3.2.2 Quad
For the quad, the binomial GLM showed that the probability of a seal reacting differed significantly with drive-by distance ($p < 0.001$). Holm adjusted pairwise comparisons showed that this probability was significantly greater during the drive-by at 50 m than at either the 150 m or 250 m distances ($p = 0.0496$ and $p < 0.001$, respectively). The probability of a seal reacting to a quad was also greater at the 150 m distance than at the 250 m distance ($p = 0.0017$) (Figure 5.2a).

The permutation test of the three drive-by distances tested for a quad showed strong evidence that the duration of response to a quad also varied with distance ($p = 0.003$). The duration of response was longer when a quad travelled at 50 m compared to 250 m ($p = 0.014$). However, there was only no evidence of a difference in the duration of response between the 50 m and 150 m distances ($p = 0.106$), and between the 150m and 250 m distances ($p = 0.504$) (Figure 5.2b).
Figure 5.2a) The percentage of lactating Weddell seals reacting to the drive-by of the quad at the three experimental distances, b) the total duration of time (recorded as the % of time within each interval) ± 1 SE, that the seals (n = 15) spent looking at the quad during the drive-bys at the three experimental distances. Statistically significant differences at the 0.05 level are indicated by letters, where 'a' signifies the difference between the 50 m and 150 m distance, 'b' signifies the difference between the 50 m and 250 m and c signifies the difference between 150 m and 250 m.
5.3.3 Speed of travel

5.3.3.1 Hagglund
For the Hagglund, the binomial GLM showed no evidence of a difference in the probability of a seal reacting when the speed of travel changed ($p = 1.00$, 8.3% of individuals reacted during the slow drive-by and 8.3% reacted during the fast drive-by, $n = 11$). Similarly, the permutation test showed no evidence of a difference in duration of response due to speed of travel ($p = 1.00$, $\overline{X} = 0.8 \pm 0.8\%$ of time spent responding during the slow drive-by and $\overline{X} = 0.7 \pm 0.7\%$ of time spent responding during the fast drive-by, $n = 11$).

5.3.3.2 Quad
As with the Hagglund, the binomial GLM and permutation tests showed no evidence of an effect due to the speed of travel of a quad, either in the probability of a seal reacting or in the duration of response ($p = 0.41$, 33.3% of individuals reacted during the slow drive-by and 33.3% reacted to the fast drive-by, and $p = 0.44$, $\overline{X} = 2.9 \pm 1.4\%$ of time spent responding during the slow drive-by and $\overline{X} = 7.5 \pm 4.2\%$ of time spent responding during the fast drive-by, $n = 14$).

5.3.4 Positional and biological co-variates

5.3.4.1 Hagglund
There was a significant correlation between pup position (i.e. whether or not the pup was exposed) and seal response to the drive-by of a Hagglund ($p = 0.0003$). Cows were more likely to react to the vehicle when they were between the pup and the Hagglund (Figure 5.3).

There was no evidence of a correlation between the distance of the focal seal to a conspecific and the probability of that seal reacting to the Hagglund ($p = 0.306$), nor was there a correlation between the distance of the focal seal to water and the probability of the seal reacting to the Hagglund ($p = 0.228$).
5.3.4.2 Quad

As with responses to the Hagglund, there was a significant correlation ($p = 0.009$) between pup exposure and response of the cow to a quad, and seals were again more likely to react when their pups were not exposed (Figure 5.4).

There was no correlation between the probability of a seal reacting to the quad and the distance the seal was to the nearest conspecific ($p = 0.116$), however, there was a significant correlation between the distance a focal seal was to the water and the probability of it reacting to the quad ($p = 0.0003$). Seals further from the water were more likely to react than seals closer to the water (Figure 5.5).

Since both pup exposure and distance to water were correlated with the probability of a seal reacting to a quad, both variables were included into the one model and one-term deletions were considered. This showed that if distance to water is retained, pup exposure was only weakly significant ($p = 0.082$). By contrast, if pup exposure was retained in the model then there was strong evidence that distance to water significantly affected the response of the seal ($p = 0.002$).
Figure 5.4 The percentage of lactating seals (n = 15) reacting to the quad during each of the four drive-bys differentiating between pup position, i.e. pups exposed (black colouration) and pup not exposed (grey colouration).

Figure 5.5 The mean distance ± 1 SE of the seals (n = 15) from the water during the four passages of the quad, differentiating between the seals that did not react (black) and those that did react to the quad (grey).
5.4 Discussion

Most, but not all, lactating Weddell seals responded to the passage of both types of over-snow vehicle examined in this study. In particular, the distance at which the vehicles passed influenced the number of seals that reacted, and the duration of their response. The number of seals that reacted was also dependent upon whether their pup was directly exposed to the vehicle. For experiments examining responses to quads, the probability of a seal reacting was also influenced by the proximity of the seals to water.

5.4.1 Effects of vehicle type on seal response

For the one distance at which both types of vehicle were driven, the behavioural response of the seals did not differ with vehicle type, even though visually and acoustically the vehicles were considerably different. A Hagglund is approximately double the height and triple the length of a quad, and although the peak sound frequency produced in-air by the two vehicles travelling on sea-ice is the same (i.e. centred at 0.86 kHz), the noise level generated by the Hagglund is greater. The noise level generated by a quad travelling at 15 km/hr at a distance of 250 m is 19 dB re. 20 µPa, while the noise level generated by a Hagglund is 24 dB re. 20 µPa (see Chapter 6).

The lack of a difference in response of the seals towards the different vehicle types may, however, be related to the small sample size. Only five seals were exposed to both the quad and Hagglunds and only two individuals reacted to the vehicles (one to the quad and one to the Hagglund). Results must be interpreted cautiously. If however, the absence of a difference in response was 'real', then it contradicts some of the limited number of studies making controlled comparisons between the effects of vehicle type on wildlife response. Born et al. (1999) found that a greater number of ringed seals (Phoca hispida) reacted to a Bell 206B helicopter that than to a fixed-wing aircraft (Partenavia PN68 Observer), even though the helicopter was operating at a further distance. The difference in response was attributed to the different noise levels produced by each aircraft type. Although the results from another study on the variability in reactions of Pacific harbour seals (Phoca vitulina richardsi) to disturbance also suggest response can be influenced by vehicle type, Suryan and Harvey (1999) report that kayaks within 1 km of the harbour seals cause more harassment (55%) than did powerboats (9%) operating at the same distance. However, as an example of the differential effects of different vehicle types on
wildlife, the results of that study are ambiguous because the seals were thought to respond differently due to the different levels of previous experience they had had with kayaks and powerboats. The results of these two studies highlight the many different factors that can affect the response of wildlife to stimuli and the difficulty of isolating the effect of any one particular variable, such as vehicle type, in studies of human-wildlife interactions. Nevertheless, results from the current study suggest that a Hagglund and quad, operated under the same conditions, had a similar effect on lactating Weddell seals.

At the 250 m distance tested in this study, the noise levels generated by the two vehicles were within 5 dB of each other (Chapter 6), which could explain the similarity in the response to the two types of vehicles. Differences of this magnitude are unlikely to be differentiated by the seals given the low decibel level of the noise and background noise levels, making it probable that the vehicles were acoustically indistinguishable to the seals.

The similarity in the duration of the seals' response to the quad and Hagglund also suggests that the vehicles were perceived to be the same in terms of their potential interest or threat to the seals. This may be related to the fact that at 250 m, objects such as over-snow vehicles are outside the 'area of concern' for Weddell seals, that is, the objects are considered far enough away to not warrant expending time and energy responding.

5.4.2 The effect of drive-by distance on seal response
The distance between a focal animal and a stimulus is a key factor influencing wildlife responses to human activity (e.g. Salter 1979; Grubb and Bowerman 1997; Born et al. 1999). This study also provided evidence for effects of approach distance, as both the number of seals that reacted to the vehicles and the duration of their response increased with decreasing distances.

Increasing the distance between the Hagglund and the seals, from 100 m to 250 m, resulted in a significant decrease in the number of seals that reacted. There was no evidence that increasing this distance to 400 m further influenced the seals' response. For the quad, increasing in distance from 50 m to 150 m, and then to 250 m resulted in a significant decrease in the number of seals that reacted.

Auditory detection of the vehicles may explain the seals' variable response to the drive-by distances tested in this study. Received noise level decreases with distance.
due to transmission loss (6 dB decrease with a doubling of distance Albers 1965; Richardson et al. 1995; Carlin 1996). Therefore detection of the noise generated by the vehicles would become harder with the increase in distance, especially if the noise levels were already low, i.e. barely audible to the seals (see Chapter 6). However, the effect of distance on the received noise levels was at most 3 dB (Chapter 6). Such simple comparisons may be misleading though, as the noise recordings were made on different days and at different times. Differences in ambient air temperature and wind speed, which affect received noise levels, could explain the small difference in received noise level generated from the different distances (Richardson et al. 1995). For example, on sunny days the air temperature directly above the ice is cooler than the air temperature further up the air column. This results in refraction of the sound wave towards the cooler area, i.e. to where the seal is, which means that the received noise level is louder (Carlin 1996). Further, any differences in the ice surface could also influence received noise levels. A layer of snow has a dampening effect on noise (Richardson et al. 1995), thus a snow layer at the 100 m distance but not at the 250 m distance could result in the received noise levels being the same. Thus, variations in these and other ambient conditions may have confounded the effects of distance per se on noise levels.

The duration of response of the Weddell seals to the drive-bys was also affected by distance to the vehicle. For the experiments with the Hagglund, significant differences between two sets of distances, i.e. 100 m and 250 m or 250 m and 400 m, were not found even though an overall difference in response duration was observed. This is likely to be due to the low statistical power of the Holm adjusted pairwise comparison relative to the omnibus test. For the quad drive-bys, duration of the seals’ response was greatest at the closest distance (50 m) when compared to the furthest distance (250 m) suggesting that the drive-by of the quad at 50 m was perceived to be of greater interest to the seals than a quad operating at 250 m. The absence of a difference between the other distances suggests that duration of response decreased somewhere between 150-250 m. Many studies have identified critical distances at which wildlife respond to human stimuli. For example, in a study on the effects of tourist approaches to South American fur seals (Arctocephalus australis) Cassini (2001) found that approaches closer than 10 m elicited strong responses. Approaches at further distances, did not result in strong responses. In another study, ringed seal response to predators occurred at distances of 100 m or less, even though the seals could see predators at distances of ~200 m (Smith and Hamill 1981). The
results of these studies, along with the present study, indicate that distance of approach/drive-by affects the duration and intensity of wildlife response.

5.4.3 The effect of vehicle speed on seal response
Increases in speed of 20 km hr$^{-1}$ for the quad and 10 km hr$^{-1}$ for the Hagglund resulted in no measurable difference in Weddell seal response. Increases in boat speed have been shown to affect cetacean behaviour, for example beluga whales (*Delphinapterus leucas*) showed an increase in avoidance behaviour with an increase in boat speed (Blane and Jaakson 1994), although in this case the speed and distance effects could not be separated. The absence of an effect due to travel speed in the present study may be related to the small number of seals that reacted during the 150 m drive-by for the quad and the 250 m drive-by for the Hagglund, irrespective of speed. This suggests that drive-bys at these distances may not be perceived to be of interest to the seals. Alternatively, the increase in speed, which resulted in a 1-3 dB re. 20 µPa increase in noise levels (see Chapter 6) may not have been sufficient to cause a greater number of seals to react.

One caveat of the experimental design used here, that influences interpretation of results, is that experiments testing for differences in speed are confounded either by duration of exposure or distance from the animal. Differential duration of exposure occurs when the transect length at each distance tested is identical. The time taken to drive the length of the transect is obviously less for the fast vehicle than it is for the slow vehicle. When the duration of exposure to the stimulus is identical, the length of the transect for the ‘fast’ speed of travel must be increased. This results in the distance between the animal and the stimulus being greater for the ‘fast’ travelling vehicle. Therefore, no true comparison in speed can be made when comparing the duration of time spent responding, and caution should be used when interpreting results.

5.4.4 The effect of distance to water and conspecifics (positional factors)
Analogies can be drawn between disturbance caused by human activity and by predation risk (Frid and Dill 2002). Under both scenarios, animals divert time from other ‘fitness-enhancing activities’ such as feeding, parental care or mating displays (Frid and Dill 2002), in favour of responding to the perceived threat. Responses to disturbance, either human induced or as a result of natural predators, have been
shown to depend on factors such as proximity to shelter, group size and proximity to conspecifics (Robinson 1981; Dill and Houtman 1989; Blumstein et al. 2003).

Weddell seals spend the majority of their time in the water, however when hauled out, they lie near cracks in the ice, which provide predictable access to water (Stirling 1969). Although Weddell seals do not have land-based predators, the sea is likely to represent a refuge from any disturbing stimulus on the ice. Vigilant responses of lactating Weddell seals to approaches by a single person (see Chapter 2) suggested that the seals might consider the sea to be a refuge. In that case, the seals closer to the water were more tolerant of the person, enabling a closer approach before the seal responded. None of the seals exposed to the over-snow vehicle drive-bys fled to the water, which either suggests that the sea was not considered to be a refuge when exposed to this stimulus, or that the flight initiation distance, or more precisely the 'fleeing response', i.e. the approach distance at which the benefits of fleeing exceed the costs of remaining, was not breached (Hediger 1934; Ydenberg and Dill 1986; Blumstein et al. 2003). Given that seals positioned further from the water were more likely to react to a quad at all distances tested, it is likely that the seals did consider the sea to be a place to retreat to if necessary. The further the distance from water, the larger the seal's flight initiation distance and the less tolerant the seal is to the traverse of the quad. This also suggests that the quad was perceived to be a potential threat that warranted a vigilant response.

The lack of an effect of distance to water on the number of seals that reacted to the Hagglund may be attributable to the small range of distances to the water that were recorded from animals used in these experiments (i.e. all < 10 m). The range of distances of the seals to water during the quad drive-bys was greater (1-40 m). This may indicate that the effect of distance to water for over-snow vehicles is only influential when seals are > 10 m from the water.

The distance to the nearest neighbour can influence vigilant responses of animals (e.g. Robinson 1981; Roberts 1988). The vigilant responses of Weddell seals to pedestrian approaches indicate that they may consider people to be less threatening when another seal is near-by, as evident by seals becoming vigilant as people approached to a closer distance (see Chapter 2). In the current study, however, responses to over-snow vehicle operations were not influenced by the seal’s distance to her nearest neighbour. This suggests that the advantages of lying in close proximity to conspecifics i.e. reduced probability of being taken (dilution effect) and
increased vigilance levels to spot the predator (greater chances of escape) (Barnard 2004), were not present under the test conditions. Perhaps the distance of travel from the seals was too great for distance to a conspecific to be an influencing factor.

5.4.5 The effect of pup exposure (biological factor)
During pregnancy and in the presence of young, animals tend to be aggressive toward conspecifics, with increased vigilance levels associated with the protection of the young, as well as territory maintenance (Boness et al. 1982; Harcourt 1991; Maestripieri 1992). The position of the young in relation to the mother is a critical factor in the vigilance response of some species, such as rhesus monkeys (*Macaca mulatto*) (Leighton-Shaprio 1986). In this study, vigilance levels of mothers were significantly greater when their infant was further away, than when it was closer (Leighton-Shaprio 1986).

In the present study, Weddell seals that were lying between their pup and the vehicle were more likely to react to the drive-bys than seals whose pups were directly exposed to the vehicle. Weddell seals show aggressive behaviour towards conspecifics and people who venture too close to their pups (Cline et al. 1971; Kaufman et al. 1975), particularly if the ‘zone of interference’ (an area approximately 3 m around the cow-pup pair), is breached (Mansfield 1958; Stirling 1969; Smith and Burton 1970; Tedman and Bryden 1979). Kaufman et al. (1975) described adult female Weddell seals with pups to crawl between the pup and approaching people, which suggests that the seals shield their pup from a potential threat. Why Weddell seal cows, whose pups were already shielded from the approaching vehicle, were more responsive to the drive-bys is therefore unclear, and may be due to factors that were not measured during this study. One such factor may be related to the orientation of the cow to the stimulus. Seals facing the stimulus (as they would often be if the pup were between them and the vehicle) would only have to open their eyes to see the stimulus, while seals not facing the stimulus, would have to physically move in order to see the stimulus. Subtle changes in behaviour such as the opening of eyes, which signify an alert response, were impossible to detect from the behavioural video recordings made during this study, and so could not be distinguished.

Given the small sample size, I was unable to test for interactions between the co-variates (positional and biological factors) and seal response, although these factors could have direct effects on each other and alter the interpretation of the results. In
this study, distance to water and pup exposure were both influential in determining the probability of a seal reacting to a quad. Adjusting for the effect of distance to water for quad drive-bys, where sample sizes were the largest, resulted in pup exposure having no effect on the probability of the seals reacting, while adjusting for pup exposure still showed distance to water to have a strong effect. This suggests that the significant effect of pup position on the probability of reacting to the quad may be a consequence of the distance the seals were from the water. Further research, with larger samples sizes, could clarify this result and in doing so provide more detailed information for the management of vehicle activity around Weddell seals.

5.4.6 Implications for management

Most lactating Weddell seals responded to the passage of a quad and Hagglund at one or more of the tested distances (50, 150 and 250 m for the quad and 100, 250 and 400 m for the Hagglund). The operation of the vehicles at the current AAD guideline of 150 m for the quad and 250 m for the Hagglund did, therefore, elicit a short-term behavioural response from some individuals. The AAD acknowledges that these distances are a guide only and that greater distances should be adopted if signs of disturbance are detected (Australian Antarctic Division 2004a). If disturbance were defined as any change in behaviour, then the current AAD guidelines would need to be modified. If it were the goal of management to avoid all visible signs of Weddell seal response, then the distance of travel for a quad would need to be greater than 250 m and for a Hagglund, greater than 400 m.

However, the behavioural changes observed in this study were all of relatively short duration. Moreover, eliciting a vigilance response from Weddell seals is unlikely to have adverse consequences for the seals or their young. This means that changing existing guidelines and potentially increasing the complexity of travel near wildlife may be unnecessary. The results of this study do not generally allow interpretation of the seals' perception of the stimulus. However, no seals fled towards the water during the drive-bys, indicating that the stimuli were not considered to be overly threatening, although the response of seals to a quad was influenced by distance to water, suggesting that close approaches by this vehicle type may not be regarded as completely benign. Further research is needed to determine whether a) there are any adverse effects associated with the seals becoming vigilant, and b) whether there are any cumulative effects of repeated exposure to vehicle
activity. This information would then provide the necessary detail to allow managers to set guidelines that are effective for the protection of Weddell seals, that are also practical, and useable for over-snow vehicle users.
An Assessment of the Audibility of Weddell Seals to Sound Generated by Human Transport
6.1 Introduction

Human activity in the Antarctic has been steadily increasing since the continent was discovered in 1820 (Kimball 1999). Early human activities included harvesting of wildlife (primarily seals and whales), exploratory expeditions, and scientific research. In recent decades, activity has been largely limited to science and tourism. Many of these activities have had a range of effects on the wildlife (see for example Richardson et al. 1995; Giese and Riddle 1999; National Research Council 2003), but of particular interest here, is that these activities have associated sounds of varying frequencies and intensities. Anthropogenic sounds have no context-specific meaning and are therefore effectively 'noise' for the wildlife. However, many marine mammals in the Antarctic use sounds as an important sense of foraging and social facilitation, so alterations of the acoustic medium are potentially adverse for the wildlife.

Despite this, very little research has been conducted to establish whether Antarctic wildlife is affected by anthropogenic noise. Studies have investigated the effect of helicopter operations on the behavioural response of king penguins (*Aptenodytes patagonica*) (Cooper et al. 1994), emperor penguins (*Aptenodytes forsteri*) (Giese and Riddle 1999), Adélie penguins (*Pygoscelis adeliae*) (Culik et al. 1990; Wilson et al. 1991) and Southern elephant seals (*Mirounga leonina*) (Burton and van den Hoff 2002). However, these studies did not differentiate between the acoustic and visual components of the stimuli, so it is difficult to draw conclusions about the relative importance of acoustic effects. Studies on marine mammals elsewhere have found a range of effects due to anthropogenic noise, although it is difficult to establish cause and effect. For example, anthropogenic noise has been found to cause:

1) changes in behaviour, such as cessation of feeding and mating, increased alertness, vigilance and agonistic behaviour or increased avoidance and escape behaviour, for example harbor seals (*Phoca vitulina*) (Myrberg 1990) and ringed seals (*Phoca hispida*) (Born et al. 1999).

2) changes in vocal behaviour, such as cessation of calls, or change in call duration, repetition rate, frequency (kHz) and loudness, for example beluga whales (*Delphinapterus leucas*) in Canada (Lesage et al. 1999) bottlenose dolphins (*Tursiops truncatus*) (Scarpaci et al. 2000), Indo-Pacific humpbacked dolphins (*Sousa chinensis*) in Australia (Van Parijs and Corkeron 2001) and killer whales (*Orcinus orca*) in the USA (Foote et al. 2004),
3) changes in movement patterns such that animals temporarily or permanently leave an area, for example harbour seals in Canada (Henry and Hammill 2001) and killer whales in Canada (Morton and Symonds 2002),

4) masking of important sounds, affecting communication, navigation, and predator/prey interactions, for example killer whales in Canada (Morton and Symonds 2002),

5) temporary or permanent hearing loss and

6) physical injury or death, for example (Richardson et al. 1995; National Research Council 2003).

Measures and conventions controlling travel in the vicinity of wildlife exist under the Antarctic Treaty System (Kimball 1999). In addition to these, the International Association of Antarctic Tour Operators (IAATO), which is a member organisation founded to advocate, promote and practice safe and environmentally responsible private-sector travel to the Antarctic, has developed guidelines for vessel and aircraft operations in the vicinity of wildlife (IAATO 2004a). Many of the Antarctic Treaty Nations with research bases in the region, including Australia, have also developed guidelines (see Table 1.1). However, the majority of these guidelines are not based on scientific studies and have not been tested to determine whether they are actually sufficient to minimise or eliminate noise impacts to wildlife.

The Weddell seal (Leptonychotes weddellii) is the only Antarctic marine mammal that lives under and breeds on the same fast ice that people utilise for travel. As a consequence, seals near research bases or tourist operations are often exposed to anthropogenic noise. The vocal behaviour of Weddell seals is sophisticated, compared to other Antarctic phocids, and the species may therefore be especially vulnerable to acoustic interference (Ray and deCamp 1969; Evans et al. 2004).

Quantifying the effect of noise on the behaviour (and potentially the physical state) of Weddell seals requires knowledge of the auditory threshold of the Weddell seal, the factors affecting audibility of noises, the sound levels produced by various forms of transport (i.e. their sound/distance profile) and how the seals might respond to anthropogenic noise. The aims of this study were therefore to (i) provide sound/distance profiles for a number of commonly used Antarctic vehicles, (ii) establish the assumed detection threshold for Weddell seals, (iii) relate the sound/distance profiles to the Weddell seal detection threshold and (iv) determine,
from an experiment of vocal response, whether continuous vehicle noise affects the vocal behaviour of Weddell seals underwater.

6.2 Methods

6.2.1 Study sites, stimulus and experimental design

6.2.1.1 Sound/distance Profiles
Four recording locations in Princess Elizabeth Land, East Antarctica were used to record sound/distance profiles: Shirokaya Bay, at 68°31'30"S, 78°09'E (site A) Long Fjord, at 68°30'S, 78°20'E (site B) and Prydz Bay, 10 km from Davis station, at 68°33'24"S, 78°01'E and 68°35'S, 77°51'E (site C & D respectively) (Figure 6.1a). These locations were at least 1.75 km from Weddell seal pupping colonies. Although the sites differed in terms of bathymetry, ice thickness was similar at all sites (approximately 2 m). Recordings were made during November – January 2002/2003 between 08:45 and 14:45 hours (local time). All recordings were made with low wind and no precipitation.
**Figure 6.1a** Map of a section of the Vestfold Hills showing the four sites used to record the sound/distance profiles of the stimuli; the sites used in the vocal response experiment and the location of the seal colonies (data from Australian Antarctic Division 2004b).

**Figure 6.1b** Map of a section of the Windmill Islands showing the sites used in the vocal response experiment and the location of the seal colony (data from Australian Antarctic Division 2004b).
6.2.1.1 Stimulus
The modes of transport from which the sound profiles were recorded were those that are commonly used in the Australian Antarctic Territory. They included a pedestrian wearing crampons (metal spikes worn on the sole of the boot), a quad (4 wheeled all-terrain vehicle, Honda TRX350), a Hagglund (tracked, all-terrain vehicle, Mercedes Benz BV206D), a ‘Squirrel’ helicopter (Aerospatiale AS350B single engine), a Twin Otter aircraft (fixed wing, fitted with skis), and a Zodiac (5 m inflatable boat with a 35 hp outboard motor).

6.2.1.1.2 Sites
Site A was used to record sound/distance profiles for the pedestrian and over-snow vehicles. The ice was polished blue ice with little to no snow cover. The sound/distance profile for the helicopter was recorded at Site B. The ice at this site had a thin (approx. 1-2 cm) layer of snow in some areas and none in others. Sites C and D were used to record sound/distance profiles for the Twin Otter and site D was used to record the sound from the Zodiac. The ice over which the Twin Otter was flown was also covered in a thin layer of snow (approx. 1-2 cm). Sound/distance profiles for the Zodiac were completed later in the season when the ice had largely broken-out.

To guide vehicle movement during recordings, grids were marked on the ice with canes and marking paint, or on the water with buoys and the use of a GPS (Figure 6.2). Distances from the sound recording point (SRP) were based on \( \frac{1}{2}\log_{10} \) steps: 1, 31.6, 100, 316 m etc and distances specified by the AAD for travel in the vicinity of Weddell seals (Figure 6.2 & Table 6.1). The distance from the SRP, and therefore the number of transects, was dependent on the anticipated amplitude (audible in-air to humans) of the sound from a particular mode of transport (Table 6.1). Within the grid, markers were placed along transects at 10 m and 40 m intervals for the pedestrian and the over-snow vehicle grids respectively. To guide the helicopter activity, markers were placed at 0, 100, 250 and 750 m from the SRP (see 6.2.1.1.3), where 0 m was directly overhead. The Twin Otter flew directly above the SRP in straight lines. Speed of travel for the over-snow vehicles and watercraft was based on common speeds used in situ (quad, 15 and 40 km/hr, Hagglund, 15 and 25 km/hr, Zodiac, 15 and 25 km/hr) and aircraft speed was based on the cruising speed of the aircraft (helicopter, 100 km/hr, Twin Otter, 220 km/hr). Distance from the SRP for both the helicopter and the Twin Otter was measured in height (altitude) and horizontal distance.
Each stimulus traversed the grid five times while sound was recorded. Sounds were recorded irrespective of whether the vehicle was travelling towards or away from the SRP for the pedestrian, quad, Hagglund and helicopter. In order to establish the baseline against which the noise generated by vehicles could be compared, background noise levels were recorded three times for a period of 15 mins. Recordings were made prior to the beginning of the experiment, between the 3rd and 4th traverse (approximately half way through the experiment), and at the completion of the traverses.

Table 6.1 Dimensions of the grid used for each of the stimuli, including the number of transects, the speed of travel and the distance from the sound recording point.

<table>
<thead>
<tr>
<th>Stimulus</th>
<th>Transect length</th>
<th>No. of transects</th>
<th>Speed (km/hr)</th>
<th>Location of SRP</th>
<th>Distance from SRP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pedestrian</td>
<td>80 m</td>
<td>8</td>
<td>3-4</td>
<td>Underwater</td>
<td>1,5,10,15,20,30,40,50 m</td>
</tr>
<tr>
<td>Quad</td>
<td>240 m</td>
<td>3</td>
<td>15</td>
<td>In-air</td>
<td>50,150,250 m</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4</td>
<td></td>
<td>Underwater</td>
<td>1,31,6,100,316 m</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1</td>
<td>40</td>
<td>In-air</td>
<td>150 m</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td></td>
<td>Underwater</td>
<td>100,316 m</td>
</tr>
<tr>
<td>Hagglund</td>
<td>240 m</td>
<td>3</td>
<td>15</td>
<td>In-air</td>
<td>100,250,400 m</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5</td>
<td></td>
<td>Underwater</td>
<td>1,31,6,100,316,486 m</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1</td>
<td>25</td>
<td>In-air</td>
<td>250 m</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td></td>
<td>Underwater</td>
<td>316,486 m</td>
</tr>
<tr>
<td>Helicopter</td>
<td>1600 m</td>
<td>3</td>
<td>100</td>
<td>In-air &amp; Underwater</td>
<td>200,800,2500 ft (altitude)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>N/A</td>
<td>Idle/land/take off</td>
<td>In-air &amp; Underwater</td>
<td>0,100,250,750 m (horizontal)</td>
</tr>
<tr>
<td>Twin Otter</td>
<td>N/A</td>
<td>5</td>
<td>220</td>
<td>In-air &amp; Underwater</td>
<td>328,500,1500,3000,5000 ft</td>
</tr>
<tr>
<td></td>
<td></td>
<td>N/A</td>
<td>Idle/land/take off</td>
<td>In-air &amp; Underwater</td>
<td>20,100,500 m</td>
</tr>
<tr>
<td>Zodiac</td>
<td>No set length</td>
<td>11</td>
<td>15</td>
<td>In-air &amp; Underwater</td>
<td>0,10,31.6,100,316,500,1000,1500,2000,2500,3000 m</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10</td>
<td>35</td>
<td>In-air &amp; Underwater</td>
<td>0,31.6,100,316,500,1000,1500,2000,2500,3000 m</td>
</tr>
</tbody>
</table>
Figure 6.2 Grid pattern for the pedestrian (a), helicopter (b) and Zodiac (c) recordings (the over-snow vehicles grid is similar to the pedestrian grid). Direction of travel is indicated with the arrow. Distance is in metres.
6.2.1.3 Recordings

The sound recording point was a 15 cm diameter hole drilled through the ice. Two High Tech hydrophones, with built-in preamplifiers, were suspended in the water column, one at 0.5 m below the ice and the other 1 m from the bottom if the depth of water was < 30 m, or 29 m if the depth was > 30 m. Water depth ranged from 6.4 m to ~250 m. The frequency response of the hydrophones was ± 1 dB from 0.0 to 8 kHz and ± 3 dB from 0.0 to 20 kHz. In-air recordings were made with a Cesva SC-2 sound level meter, which was calibrated with a Cel-282 acoustic calibrator. The sound level meter was ‘A-weighted’ (microphone adjusted to the auditory sensitivity curve of humans). Stereo recordings (underwater) and mono recordings (in-air) were made using a Sony TCD-C100 digital audio tape (DAT) recorder (0.02 - 20 kHz ± 1 dB at standard recording speed or 0.01 - 16 kHz ± 1 dB in the long play mode).

The in-air ½-octave bands of interest were centred near 1 kHz and thus the A weighting effect of the sound level meter would not influence the sound measurements. We were therefore able to present sound levels in absolute units of dB re. 20 µPa; the standard in-air reference level. Underwater, the hydrophones had an essentially flat frequency response over the frequencies of interest and thus the underwater sound levels are presented in absolute units, dB re. 1 µPa; the standard underwater reference level.

6.2.1.2 Seal detection threshold

I created an assumed detection threshold (ADT) for Weddell seals, both underwater and in air (Figure 6.3), based on experimental studies on harbor seals (Mohl 1968; Terhune 1988, 1991; Kastak and Schusterman 1998; Wolski et al. 2003), harp seals (Pagophilus groenlandicus) (Terhune and Ronald 1971, 1972) and ringed seals (Terhune and Ronald 1975). Psychophysically and anatomically, all phocids are very similar and the detection thresholds among several species have been found to be very similar (Terhune and Turnbull 1995). I therefore took the lowest detection threshold reported for each frequency from the above phocid studies to generate a conservative estimate of in-air and underwater detection thresholds. Terhune and Turnbull (1995) also found that for a seal to correctly detect a signal 95% of the time, the sound source had to be 15-20 dB above the threshold. The signal detection criterion of the seal was found to affect audibility within the 1-20 dB range, where recognition increased exponentially from 50-95 percent correct response. Signal levels need to be about 20 dB above the threshold to permit recognisable speech in humans (Hirsch 1952).
The ADT in-air is also based on the results from behavioural observations of lactating Weddell seals to quad and Hagglund drive-by experiments (Chapter 5). The results of this study show that the seals react to quad and Hagglund drive-bys at 250 m. The lowest mean received noise level during the drive-by was 19 dB re. 20 µPa at 0.86 kHz frequency (Table 6.2). Although the stimulus that first alerted the seals to the drive-bys, i.e. sight, sound, smell or vibration, was not determined, sound was thought to be the most likely stimulus. Vision, olfaction and vibrations were thought to be unlikely triggers at this distance. The chance of the seals becoming alert due to sight is small as the seals spend a larger proportion of their time resting with their heads down (92.7%, Chapter 2) and would have to be looking in the exact direction of the vehicle to be alerted to it by sight alone. Weddell seals are also myopic and astigmatic in-air, which means that objects in the distance are blurred (Lavigne et al. 1977). Olfactory cues at these distances are unknown. In this study, vibrations generated by the vehicles driving on the ice were also unlikely to be felt by a seal because of the distance between the seals and the vehicles, and the thickness of the snow cover, which would have a dampening effect. Acoustic potential energy does not propagate well laterally as the energy is absorbed, spread and scattered as it travels through the ice (Richardson et al. 1995; Carlin 1996). The results therefore suggest that the seals can detect noise in the 0.86 kHz frequency range at noise levels of 19 dB re. 20 µPa.

It is important however, to point out that the noise levels recorded during the quad and Hagglund drive-bys at the tested distances are crude and may be erroneous. Noise levels decrease with an increase in distance due to transmission loss (Albers 1965; Richardson et al. 1995; Carlin 1996); however, the levels recorded showed little, if any, decrease with an increase in distance. This suggests that some of the received levels are erroneous. The most likely reason for the similarity in noise levels between the distances tested is equipment error and variability in abiotic conditions, which affect transmission loss (in the order of ± 3 decibels). For example, sound can be refracted towards the ice (height of the seal) on sunny days because the air temperature directly above the ice is cooler than the air temperature higher up, which means that the received noise levels are louder.

Despite this, a conservative approach was taken and the assumed in-air detection level was set at 0.86 kHz, as the lowest level recorded during the behavioural experiment was 19 dB re. 20 µPa.
Three distinct audibility levels were specified; inaudible, barely audible (noise levels between 0-20 dB above threshold), where the sound would only be audible under low levels of background noise or when the seal is actively listening, and clearly audible, where noise levels were > 20 dB above threshold.

<table>
<thead>
<tr>
<th>Assumed underwater audiogram</th>
<th>Assumed in-air audiogram</th>
</tr>
</thead>
<tbody>
<tr>
<td><img src="image" alt="Assumed underwater audiogram graph" /></td>
<td><img src="image" alt="Assumed in-air audiogram graph" /></td>
</tr>
</tbody>
</table>

Figure 6.3 Assumed Weddell seal audiogram, a) underwater and b) in-air. Points above the curve illustrate the scatter of the data. The curve represents the lowest threshold measurement at that frequency for any phocid (Mohl 1968; Terhune and Ronald 1971, 1972, 1975; Terhune 1988, 1991; Kastak and Schusterman 1998; Wolski et al. 2003).

6.2.1.3 Vocal response experiment

To determine the effect of continuous vehicle noise on the vocal behaviour of Weddell seals underwater, vocal behaviour was recorded with and without vehicle noise, at six Weddell seal breeding colonies in East Antarctica. Two sites were in Penny Bay, Windmill Islands (66°25'S, 110°40'E) and the remaining four were in Long Fjord, Vestfold Hills (68°35'S, 77°58'E) (Figure 6.1a & 6.1b). The recordings at the Vestfold Hills (sites 1-4) were made between the 3rd and the 20th November 2002. The recordings at the Windmill Islands (sites 5-6) were made between 31st October and 15th November 2001. Although the sites were different in terms of bathymetry, the ice conditions were similar (2 m thick ice and no surface snow).

Sites selected were 300 m from the centre of the nearest breeding colony to ensure that the closest distance from the edge of the 50 m radius circle, drawn around the SRP on which the Hagglund drove, was 250 m from the seals. This distance met the
AAD guideline limit for Hagglund travel near Weddell seals (Australian Antarctic Division 2004a). The distance was also thought to be far enough away to minimise the disturbance to hauled out seals but close enough to capture underwater vocalisations. The circumference of the circle was marked on the ice with spray paint. In the center of the circle a 15 cm diameter hole was drilled and two High Tech hydrophones were suspended in the water column, one at 0.5 m below the ice and the other at 27.5 m or less, but at a minimum of 0.5 m above the bottom. Stereo recordings were made as before, using the two hydrophones with built-in preamplifiers and a Sony TCD-C100 digital audio tape recorder (DAT).

The recordings were made at the peak calling times for the seals (6 – 8 pm local time for the Windmill Islands and 8 – 10 pm local time for the Vestfold Hills) (Green and Burton 1988). An initial recording, on Day 1 of experiments, was undertaken to establish an index of the ‘normal’ vocal behaviour of the seals in the absence of anthropogenic noise (the control). A second recording, on Day 2, was made during continuous anthropogenic noise generated by a Hagglund traveling at a constant speed of 15 km/hr along the marked circle.

6.2.2 Analysis
All acoustic signals were calibrated in the field with a Cel-282 acoustic calibrator. The hydrophones were calibrated in the lab by the comparison technique using a Brueel & Kjaer 8100 hydrophone, Brueel & Kjaer 2635 Charge Preamplifier and Brueel & Kjaer 4220 pistonphone (comparison technique Caruthers 1977). Recordings were played back with a Sony TCD 750 DAT recorder, a Krohn-Hite Bandpass filter (model 3364) and Digitor C4116 headphones.

6.2.2.1 Sound/distance profile
A one second sample of sound was taken as the vehicle passed each of the marked distances along the transect. From this sample, the frequency with the highest amplitude above the assumed detection threshold was selected (both in-air and underwater). The level (dB) of the ½-octave bandwidth that was centered near this frequency using Multispeech (Kay Elemetrics Corp, model 3700 version 2.2, 1999) was then measured. Using the ½-octave bandwidth distance is a conservative approach because the actual masking bandwidth may be smaller (Richardson et al. 1995). A sound/distance profile for each stimulus was then made for the distances tested under the abiotic conditions measured (Tables 6.2 & 6.3).
Because continuous recordings along transects were made, it was possible to determine sound levels at additional distances. However, because of the large number of distances obtained in this method and the close proximity of some of the distances to each other, only the distances of the transects, *i.e.* 1, 31.6, 100 m, and additional distances along the furthest transect are presented (Tables 6.2 & 6.3).
Table 6.2 Average sound level (dB re. 1µPa) recorded underwater at a shallow and deep depth of a) pedestrian, b) quad, c) Hagglund, d) helicopter, e) Twin Otter and f) zodiac, travelling at various speeds and distances from the sound recording point. The sounds are categorised as to their audibility to a theoretical Weddell seal, where inaudible sounds are below threshold, barely audible sounds are between 0-20 dB above threshold and clearly audible sounds are > 20 dB above threshold.

a) Pedestrian

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<th>Sound level (dB re. 1µPa)</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>(Hz)</td>
<td>(m)</td>
<td>(km/hr)</td>
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<td>Deep</td>
<td></td>
</tr>
<tr>
<td>1033†</td>
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<td>Inaudible</td>
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</tr>
<tr>
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<td>5</td>
<td>3-4</td>
<td>-</td>
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<td></td>
<td>10</td>
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<td>80</td>
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</tr>
<tr>
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<td>40</td>
<td>3-4</td>
<td>-</td>
<td>74</td>
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</tr>
<tr>
<td></td>
<td>50</td>
<td>3-4</td>
<td>-</td>
<td>75</td>
<td>-</td>
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* The speed of walking was not measured, however a "normal" walking pace of 3-4 km/hr was maintained.
Table 6.2 continued.

b) Quad

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<th>Deep</th>
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<td>87</td>
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Table 6.2 continued.

c) Hagglund

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<th>Speed (km/hr)</th>
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Table 6.2 continued.

d) Helicopter

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<tr>
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<th>Distance (m)</th>
<th>Altitude (feet)</th>
<th>Speed (km/hr)</th>
<th>Action</th>
<th>Sound level (dB re. 1µPa)</th>
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</tr>
<tr>
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</tr>
<tr>
<td></td>
<td>100</td>
<td>0</td>
<td>-</td>
<td>Idle</td>
<td>Inaudible 73 Barely audible 70 Clearly audible -</td>
</tr>
<tr>
<td></td>
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<td>-</td>
<td>Idle</td>
<td>Inaudible 68 Barely audible 65 Clearly audible -</td>
</tr>
<tr>
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<td>Take off</td>
<td>Inaudible 80 Barely audible 77 Clearly audible -</td>
</tr>
<tr>
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</tr>
<tr>
<td></td>
<td>750</td>
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<td>~100</td>
<td>Cruise</td>
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<td>200</td>
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<tr>
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<td>200</td>
<td>~100</td>
<td>Cruise</td>
<td>Inaudible 81 Barely audible 82 Clearly audible 82</td>
</tr>
</tbody>
</table>
Table 6.2 continued.

d) Helicopter

| Frequency (Hz) | Distance (m) | Altitude (feet) | Speed ~100 (km/hr) | Action    | Sound level (dB re. 1µPa) |
|               |              |                 |                    |           | Shallow       | Deep          |
|               |              |                 |                    |            | Inaudible     | Barely audible | Clearly audible | Inaudible | Barely audible | Clearly audible |
| 1033†         | 0            | 800             | ~100               | Cruise    | -             | 80            | -             | -         | 79           | -               |
|               | 100          | 800             | ~100               | Cruise    | -             | 75            | -             | -         | 80           | -               |
|               | 250          | 800             | ~100               | Cruise    | -             | 75            | -             | -         | 75           | -               |
|               | 750          | 800             | ~100               | Cruise    | -             | 73            | -             | -         | 74           | -               |
|               | 0            | 2500            | ~100               | Cruise    | -             | 76            | -             | -         | 73           | -               |
|               | 250          | 2500            | ~100               | Cruise    | -             | 74            | -             | -         | 73           | -               |
|               | 750          | 2500            | ~100               | Cruise    | -             | 74            | -             | -         | 72           | -               |
Table 6.2 continued.

e) Twin Otter

<table>
<thead>
<tr>
<th>Frequency (Hz)</th>
<th>Distance (m)</th>
<th>Altitude (feet)</th>
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<th>Action</th>
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Table 6.2 continued.

f) Zodiac

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<th>Speed (km/hr)</th>
<th>Action</th>
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<th>Clearly audible</th>
<th>Deep Inaudible</th>
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Table 6.2 continued.

f) Zodiac

<table>
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<tr>
<th>Frequency (Hz)</th>
<th>Distance (m)</th>
<th>Speed (km/hr)</th>
<th>Action</th>
<th>Sound level (dB re. 1µPa)</th>
<th>Shallow</th>
<th>Deep</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Inaudible</td>
<td>Barely audible</td>
<td>Clearly audible</td>
</tr>
<tr>
<td>2000</td>
<td>35</td>
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<td>-</td>
<td>-</td>
<td>90</td>
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<td>2500</td>
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† The reason that the centre frequencies of the ½-octave bandwidth with the highest amplitude is the same for the pedestrian, aircraft and zodiac, even though these modes of transport are highly different and sound different, is because the noise spectrum is relatively flat and the sensitivity of the seal drops as the frequency increases from above 0.8 kHz.
Table 6.3 Average sound level (dB re. 20µPa) recorded in-air for the a) quad, b) Hagglund, c) helicopter, d) Twin Otter, and e) Zodiac, travelling at various speeds and distances from the sound recording point. The sounds are categorised as to their audibility to a theoretical Weddell seal, where inaudible sounds are below threshold, barely audible sounds are between 0-20 dB above threshold and clearly audible sounds are > 20 dB above threshold.

<table>
<thead>
<tr>
<th>Frequency (Hz)</th>
<th>Distance (m)</th>
<th>Speed (km/hr)</th>
<th>Sound level (dB re. 20µPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td>861†</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>50</td>
<td>15</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>150</td>
<td>15</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>150</td>
<td>40</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>250</td>
<td>15</td>
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### Hagglund

<table>
<thead>
<tr>
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<th>Distance (m)</th>
<th>Speed (km/hr)</th>
<th>Sound level (dB re. 20µPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Inaudible</td>
</tr>
<tr>
<td>861†</td>
<td>100</td>
<td>15</td>
<td>-</td>
</tr>
<tr>
<td></td>
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<td>15</td>
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### Table 6.3 continued.

#### c) Helicopter

<table>
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<th>Frequency (Hz)</th>
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<th>Altitude (feet)</th>
<th>Speed (km/hr)</th>
<th>Action</th>
<th>Sound level (dB re. 1µPa)</th>
</tr>
</thead>
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<td>Barely audible</td>
</tr>
<tr>
<td></td>
<td>250</td>
<td>0</td>
<td>-</td>
<td>Idle</td>
<td>Clearly audible</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>0</td>
<td>-</td>
<td>Take off</td>
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<td>0</td>
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<td></td>
<td>750</td>
<td>0</td>
<td>-</td>
<td>Take off</td>
<td>Clearly audible</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>0</td>
<td>-</td>
<td>Land</td>
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</tr>
<tr>
<td></td>
<td>100</td>
<td>0</td>
<td>-</td>
<td>Land</td>
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<tr>
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<td>0</td>
<td>-</td>
<td>Land</td>
<td>Clearly audible</td>
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<td>750</td>
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<tr>
<td></td>
<td>0</td>
<td>200</td>
<td>~100</td>
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</tr>
<tr>
<td></td>
<td>10</td>
<td>200</td>
<td>~100</td>
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</tr>
<tr>
<td></td>
<td>100</td>
<td>200</td>
<td>~100</td>
<td>Cruise</td>
<td>Clearly audible</td>
</tr>
<tr>
<td></td>
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<td>200</td>
<td>~100</td>
<td>Cruise</td>
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</tr>
<tr>
<td></td>
<td>750</td>
<td>200</td>
<td>~100</td>
<td>Cruise</td>
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</table>
Table 6.3 continued.

c) Helicopter

<table>
<thead>
<tr>
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<th>Altitude (feet)</th>
<th>Speed (~100 km/hr)</th>
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<th>Sound Level (dB re. 1μPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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</tr>
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<tr>
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<td>~100</td>
<td>Cruise</td>
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<td>~100</td>
<td>Cruise</td>
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</tr>
<tr>
<td></td>
<td>750</td>
<td>2500</td>
<td>~100</td>
<td>Cruise</td>
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Table 6.3 continued.

d) Twin Otter

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<th>Action</th>
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</thead>
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<tr>
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<td>-</td>
</tr>
<tr>
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<td>0</td>
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<td></td>
<td>0</td>
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<td>~220</td>
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Table 6.3 continued.

<table>
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<td>Drive</td>
<td>24</td>
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</tbody>
</table>

† The reason that the centre frequencies of the &frac1;octave bandwidth with the highest amplitude is the same for all modes of transport, even though they are highly different and sound different, is because the noise spectrum is relatively flat and the sensitivity of the seal drops as the frequency increases from above 0.8 kHz.
6.2.2.2 Vocal response experiment

Seal vocalisations were analysed using Spectrogram (R.S Horne’s Spectrogram, version 6.0.9) at a sampling rate of 32 or 44 kHz with 16-bit resolution. Only calls between 0.010 – 16 kHz were analysed because of the upper frequency limit (16 kHz) of the DAT recorder in long-play mode. This frequency range is less than that recorded for Weddell seal vocalisations (up to 20 kHz) (Thomas and Kuechle 1982b), however it allowed capture of most calls.

Vocalisations were categorised as per Thomas and Kuechle (1982b) and Pahl et al. (1997) with the addition of one call type, the tongue click, which was included as a new category (Table 6.4). For each two hour recording, the first 100 clearly discernable calls were sampled (thus, the cumulative total of all individual seals). For each recording the following parameters were recorded:

1) Call type (for each of the first 100 calls)

2) Call duration

3) Number of elements within each call

4) Whether the focal call was overlapped, i.e. one call occurring at the same time as another from a different individual

5) The time taken to record 100 calls

6) The number of calls made in 10 minutes.
Table 6.4 Classification of Weddell seal calls based on (Thomas and Kuechle 1982b) and (Pahl et al. 1997).

<table>
<thead>
<tr>
<th>Type</th>
<th>Symbol</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tone</td>
<td>O</td>
<td>Constant frequency, predominantly sinusoidal</td>
</tr>
<tr>
<td>Growl</td>
<td>L</td>
<td>Constant frequency, broad bandwidth, long call</td>
</tr>
<tr>
<td>Whoop</td>
<td>W</td>
<td>Constant frequency call with a terminal upsweep</td>
</tr>
<tr>
<td>Squeak</td>
<td>S</td>
<td>Brief call with a constant frequency or rising frequency and an irregular waveform</td>
</tr>
<tr>
<td>Whistle Ascending</td>
<td>WA</td>
<td>Ascending frequency, sinusoidal waveform</td>
</tr>
<tr>
<td>Trill Constant Frequency</td>
<td>TC</td>
<td>Narrow bandwidth trill with a constant frequency beginning, sinusoidal or frequency modulated waveform (&gt; 2 seconds)</td>
</tr>
<tr>
<td>Trill</td>
<td>T</td>
<td>Narrow to broad bandwidth, beginning with a frequency downsweep (&gt; 2 seconds)</td>
</tr>
<tr>
<td>Whistle Descending</td>
<td>WD</td>
<td>Descending frequency, sinusoidal waveform (&lt; 2 seconds)</td>
</tr>
<tr>
<td>Mew</td>
<td>M</td>
<td>Abruptly descending frequency followed by a long constant frequency ending</td>
</tr>
<tr>
<td>Chug</td>
<td>C</td>
<td>Abruptly descending frequency followed by a brief constant frequency ending</td>
</tr>
<tr>
<td>Guttural Glug (Grunt)</td>
<td>G'</td>
<td>Descending frequency call that is lower than a chug and has a brief duration</td>
</tr>
<tr>
<td>Whistle Ascending Grunt</td>
<td>WAG</td>
<td>Brief ascending whistle followed by a guttural glug; the two types alternate in a regular pattern</td>
</tr>
<tr>
<td>Knock</td>
<td>K</td>
<td>Abrupt, brief duration broadband sound</td>
</tr>
<tr>
<td>Tongue Click</td>
<td>CL</td>
<td>Brief sharp call with slowly repeating elements, broadband and an irregular waveform</td>
</tr>
</tbody>
</table>

6.2.2.2.1 **Statistical procedure**

Regression analysis indicated a positive relationship between call duration and the number of elements within a call \( (R^2 = 0.539, p < 0.001) \) (Fig 6.4), so call duration alone was used for further analysis. Call duration allowed the inclusion of all call types in the analysis rather than splitting the call types into single and multiple element calls.

Weddell seals may increase the duration of their call in response to another seal calling simultaneously, thus overlapping the calls (Terhune et al. 1994b). The effect of overlap on call duration with treatment and site as independent variables was therefore examined using a 2-way analysis of variance (ANOVA). Overlap was found to increase in the presence of vehicle noise \( (F = 143.61, df = 1, p < 0.001) \), and therefore the data were separated into overlapped calls and non-overlapped calls. Paired t-tests were then used to compare mean duration of calls between the control and experimental recordings.
Figure 6.4 Quadratic relationship between the number of elements in a call and call duration. Calls made in the absence of Hagglund noise.

An analysis of similarity (ANOSIM) was used to compare the number of calls (within each call type) to the absence or presence of vehicle noise. Log (x+1) transformations were used and each site was regarded as a replicate, giving a total sample size of six.

Paired t-tests were also used to compare the mean length of time required to record 100 calls, as an index of calling rate, and to compare the frequency of occurrence of calls emitted during the 10 minute segments of the control and experimental recordings.

Site 1 was excluded from the analyses for comparisons of the time taken to record 100 calls, the number of calls emitted in 10 minutes and the duration of calls, because of the small number of measurable calls in both the control and experimental recording (9 and 21 respectively).

All data were tested for normality and homogeneity of variance, and log transformations were applied where necessary. The alpha level of all tests was set at 0.05 and stand error was unless otherwise stated. Statistical analyses were performed using SPSS (SPSS for Windows, version 11.5.1, 1989-2002) and Primer 5 (Plymouth Marine Laboratory, version 5.2, 2001).
6.3 Results

6.3.1 Sound/distance profiles in relation to the assumed detection threshold of the Weddell seal

Tables 6.2 and 6.3 list the sound level for each of the stimuli and the likely detectability of the sound for a Weddell seal in water and in-air.

The direction of travel, *i.e.* whether approaching the SRP or receding from the SRP, for the pedestrian, quad, Hagglund and helicopter, was found to result in slight differences in sound level (mean of 2.7 dB), however, this degree of difference was close to the error range of the equipment and was therefore disregarded.

6.3.1.1 Pedestrian

The peak frequency (centre of the ½-octave bandwidth) of underwater noise produced by a person wearing crampons walking on the ice was 1.03 kHz. Based on the assumed detection threshold, this frequency would be barely audible when decibels levels are > 66 dB re. 1µPa. The noise level generated by the pedestrian walking on the ice at all distances (up to 50 m) would be barely audible to a seal under the water (Table 6.2). The highest noise level recorded (16 dB above threshold) was 25 m from the SRP, recorded from the lower hydrophone (Figure 6.5). No in-air recordings were made.

6.3.1.2 Over-snow vehicles

6.3.1.2.1 Quad

The peak frequency produced underwater by a quad travelling on sea-ice was within the ½-octave bandwidth centred at 0.2 Hz. The noise would become audible to a theoretical seal at levels above 84 dB re. 1µPa. In-air, the peak frequency of the quad was 0.86 kHz, and from behavioural response experiments it appears that the seals react to noise levels above 19 dB re. 20 µPa.

The noise produced by a quad at the distances tested would be barely audible to the seal in-air and underwater (Tables 6.2 & 6.3). The only distance at which the noise would be clearly audible (34 dB above threshold) would be at 1 m, and then at the shallow depth only. Deeper in the water column, the noise would be barely audible. A quad travelling at a distance of 40 m from the SRP would only be barely audible. A further 10 meters away and the quad would be inaudible (Figure 6.5). The increases in speed tested resulted in an increase of 1-5 dB in the sound level recorded (Table 6.2 & Figure 6.5). At 128 m, the underwater sound level of the quad would be 4 dB above threshold at the shallow depth and 1 dB above threshold at 156 m for
the greater depth. Any distance past this point and the quad would be inaudible (Figure 6.5).

6.3.1.2.2 **Hagglund**
The peak 1/3-octave bandwidth of noise produced underwater by a Hagglund travelling on sea-ice was centred at 0.075 kHz. The noise would be detected by the seal when levels are >66 dB re. 1μPa. In-air, the peak frequency of the Hagglund was centred at 0.86 kHz and would be audible to seals at levels above 19 dB re. 20μPa.

The noise produced by a Hagglund at the distances tested would be barely audible to a seal on the ice (Table 6.3). Observations on the behavioural response of lactating Weddell seals hauled out on the ice to the drive-by of a Hagglund at 400 m (15 km/hr) suggest that the seals cannot hear the vehicle (Chapter 5). Only one of 12 seals looked up at the vehicle. It is highly possible that the seal that reacted to the Hagglund did so because she was already alert and sighted the vehicle rather than having detected the vehicle by sound. If this was indeed the case then the noise generated by a Hagglund at a distance of 400 m (15 km/hr) is most probably inaudible to seals hauled out on the ice.

Underwater, the loudest noise level recorded (42 dB above threshold) was at 1 m from the SRP (0.5 m below the ice) (Table 6.2 & Figure 6.5). This would be the only distance at which the Hagglund would be clearly audible at the shallow depth, while at the greater depth the Hagglund would be clearly audible at distances up to 31.6 m. The noise level at both depths decreased to within the 0-19 dB range at 156 m from the SRP, (barely audible), and then would be undetectable between 156 and 316 m (Figure 5). The increase in speed during the 316 m transect did not make the noise audible, however it did increase the dB level by 3-5 dB at the shallow depth and 0-2 dB at the greater depth (Table 6.2 & Figure 6.5). In comparison to the quad, the Hagglund noise level underwater was louder and would be audible at greater distances (Figure 6.5).
Figure 6.5 Underwater noise levels generated by over-snow vehicles (where Hag = Hagglund) and the pedestrian (Ped) relative to the assumed detection threshold of the Weddell seal (0 dB). Noises below 0 threshold are undetectable, noises between 0 and 20 dB are detectable by an actively listening seal in a quiet environment and noises above 20 dB (black line) are clearly detectable. The distance at which the noise first falls below the 20 dB threshold is an estimate based on the distances tested. Shallow and deep refer to the hydrophone depths (see text).

6.3.1.3 Aircraft

6.3.1.3.1 Aerospatiale AS350B helicopter

The peak 1/3-octave bandwidth of the helicopter was centred at 1.03 kHz underwater, and 0.86 kHz in-air. Both frequencies would be detected by a Weddell seal when noise levels are > 66 dB re. 1 µPa and 19 dB re. 20 µPa respectively.

At most of the distances tested, the noise of a helicopter idling, landing or during takeoff, would be barely audible. The only exception occurred during landings at a distance of 10 m from the SRP and during take off at 100 m from the SRP. At these distances, the noise would be clearly audible (Table 6.3 & Figure 6.6). The loudest noise level occurred during the landing at 10 m (33 dB above threshold, underwater at the deep hydrophone, and 60 dB above threshold in-air). Detectability would be similar in-air for the distances and activities tested with the exception of landing at a
distance of 100 m from the SRP, and takeoff at 250 m, which would be clearly audible (Figure 6.7).

During flight, the noise produced by the helicopter at all of the altitudes and distances, i.e. up to 800 ft and 750 m from the SRP, would be barely audible underwater (Table 6.2 & Figure 6.8). Noise level in-air would be clearly audible at altitudes of 2500 ft with distances up to 250 m from the SRP (Table 6.3 & Figure 6.9).

![Figure 6.6 Underwater noise levels generated by the aircraft (where TO = Twin Otter) relative to the assumed detection threshold of the Weddell seal (0 dB). Noises below 0 threshold are undetectable, noises between 0 and 20 dB are detectable by an actively listening seal in a quiet environment and noises above 20 dB (black line) are clearly detectable. The distance at which the noise first falls below the 20 dB threshold is an estimate based on the distances tested. 'Ice' refers to the hydrophone 0.5 m below the ice and 'deep' refers to the hydrophone at the deeper depth (29 m if the water depth was > 30 m and 1 m above bottom if < 30 m).]
Figure 6.7 In-air noise levels generated by aircraft (where TO = Twin Otter) relative to the assumed detection threshold of the Weddell seal (0 dB). Noises below 0 threshold are undetectable, noises between 0 and 20 dB are detectable by an actively listening seal in a quiet environment and noises above 20 dB (black line) are clearly detectable. The distance at which the noise first falls below the 20 dB threshold is an estimate based on the distances tested.
Figure 6.8 Underwater noise levels generated by aircraft (where TO = Twin Otter) during flight relative to the assumed detection threshold of the Weddell seal (0 dB). Noises below 0 threshold are undetectable, noises between 0 and 20 dB are detectable by an actively listening seal in a quiet environment and noises above 20 dB (black line) are clearly detectable. The distance at which the noise first falls below the 20 dB threshold is an estimate based on the distances tested. 'Ice' refers to the hydrophone 0.5 m below the ice and 'deep' refers to the hydrophone at the deeper depth (29 m if the water depth was > 30 m and 1 m above bottom if < 30 m).
Figure 6.9 In-air noise levels generated by aircraft (where TO = Twin Otter) during flight relative to the assumed detection threshold of the Weddell seal (0 dB). Noises below 0 threshold are undetectable, noises between 0 and 20 dB are detectable by an actively listening seal in a quiet environment and noises above 20 dB (black line) are clearly detectable. The distance at which the noise first falls below the 20 dB threshold is an estimate based on the distances tested.

6.3.1.3.2 Twin Otter
The peak 1/3-octave bandwidth of a Twin Otter was centred at 1.03 kHz underwater and 0.86 kHz in-air. Both frequencies would be audible to the seals at levels > 66 dB re. 1 µPa and 19 dB re. 20 µPa respectively.

The noise from the Twin Otter while idling on the ice would be clearly audible underwater at both depths at a distance of 1 m (Table 6.2). Landing at 100 m would be also clearly audible at both depths, and was the activity that produced the highest noise levels during the study (52 dB above threshold). The noise produced during take off at 500 m would be barely audible (Figure 6.6). The same pattern was observed for in-air recordings (Table 6.3 & Figure 7.6). The loudest in-air recording measured (62 dB above threshold) was during landing at a distance of 20 m from the SRP.

During flight, the noise level underwater at all altitudes (330-5000 ft) would be barely audible. The only distance at which the noise level would be clearly audible
was at 500 ft (Figure 6.8). Noise recorded in-air would be clearly audible at altitudes up to 3000 ft (Figure 6.9).

6.3.1.4 Zodiac
The peak 1/3-octave band of noise produced by a Zodiac was centred at 1.03 kHz underwater and 0.86 kHz in-air. Both frequencies would be audible to the seals at levels >66 dB re. 1 µPa and 19 dB re. 20 µPa respectively.

At the distances tested, the Zodiac idling would be clearly audible both underwater and in-air, with the exception of the in-air noise level during idle at 10 m from the SRP; in this case the noise would be barely audible (Tables 6.2 & 6.3 and Figures 6.10 & 6.11). During travel, underwater noise levels would be clearly audible with the exception of travel at 15 km/hr at 1000 m in which case the noise would be barely audible. The other exception would be during travel at 35 km/hr at 3000 m (both depths) (Table 6.2 & Figure 6.10). Noise levels in-air would be barely audible when distances exceed 100 m (up to 2000 m) for travel at 15 and 35 km/hr (Figure 6.11). The highest decibel level recorded was during travel at 35 km/hr directly above the hydrophones both underwater (61 dB above threshold) and in-air (35 dB above threshold). The increase in speed resulted in an average 7 dB increase in noise level underwater.
Figure 6.10 Underwater noise levels generated by a travelling Zodiac relative to the assumed detection threshold of the Weddell seal (0 dB). Noises below 0 threshold are undetectable, noises between 0 and 20 dB are detectable by an actively listening seal in a quiet environment and noises above 20 dB (black line) are clearly detectable. The distance at which the noise first falls below the 20 dB threshold is an estimate based on the distances tested. 'Ice' refers to the hydrophone 0.5 m below the ice and 'deep' refers to the hydrophone at the deeper depth (29 m if the water depth was > 30 m and 1 m above bottom if < 30 m).
Figure 6.11 In-air noise levels generated by a travelling Zodiac relative to the assumed detection threshold of the Weddell seal (0 dB). Noises below 0 threshold are undetectable, noises between 0 and 20 dB are detectable by an actively listening seal in a quiet environment and noises above 20 dB (black line) are clearly detectable. The distance at which the noise first falls below the 20 dB threshold is an estimate based on the distances tested.

6.3.2 Vocal response experiment

6.3.2.1 Call profiles
There was no significant difference in the pattern of call types used and the number of calls within each call type, between periods when the vehicle was absent and when it was present ($Global R = 0.048, p = 0.234$) (Figure 6.12).
Figure 6.12 Multidimensional scaling (MDS) plot showing that the call profile did not vary significantly between recordings (presence/absence of the vehicle). Site 1 (two points furthest right) is separate from the other sites due to the small sample size.

6.3.2.2 Time taken to record 100 calls and the number of calls in a 10 minute period

The time taken to measure 100 clearly discernable calls was higher during vehicle activity from $23 \pm 13\text{ min}$ to $60 \pm 13\text{ min}$ ($t = -3.463$, $df = 4$, $p = 0.026$). The frequency of occurrence of calls was lower during vehicle activity from $47 \pm 7$ in $10\text{ min}$ to $20 \pm 4$ in $10\text{ min}$ ($t = 3.476$, $df = 4$, $p = 0.025$).

6.3.2.3 Call attributes

Regression analysis indicated that call duration was still positively related to the number of elements in both circumstances, (overlap: $R^2 = 0.326$, $p < 0.001$, non-overlap: $R^2 = 0.419$, $p < 0.001$).

Paired t-tests investigating the difference in call duration between the control recording (absence of noise) and the experimental recording (Hagglund noise) found that continuous noise did not influence the duration of calls: overlap control recording $\bar{X} = 10.1 \pm 1.5\text{ sec}$ and experimental recording $\bar{X} = 10.2 \pm 0.6\text{ sec}$ ($t = -0.308$, $df = 4$, $p = 0.774$), non-overlap control recording $\bar{X} = 3.7 \pm 0.6\text{ sec}$ and experimental recording $\bar{X} = 5.0 \pm 1.2\text{ sec}$ ($t = -0.760$, $df = 4$, $p = 0.442$).
6.4 Discussion

6.4.1 Sound/distance profiles in relation to the assumed detection threshold of the Weddell seal

The sound/distance profiles from this study provide baseline propagation data for several common sources of anthropogenic noise in the Antarctic environment. The peak frequency range relative to the likely detection thresholds of the seals for these modes of transport, underwater and in-air fell between 0.075-1.03 kHz. Weddell seal vocalisations have been recorded at frequencies between 0.2-12.8 kHz by others, with some vocalisations at frequencies as high as 30 kHz (Schevill and Watkins 1971). Thus, in terms of frequency, all of the sources of anthropogenic noise tested, with the possible exception of the Hagglund, if generated at sufficient noise levels, would be audible to Weddell seals. Consequently, there is a real potential for anthropogenic noise to interfere with seal vocal behaviour and even to disturb them.

The majority of the noise levels recorded in this study, both in-air and underwater/under ice, were greater than background noise levels and were above the assumed detection threshold (ADT) of the Weddell seal at close ranges. In most cases, anthropogenic noise from nearby sources was between 0-20 dB above the ADT and therefore audibility was dependent on background noise levels and the behavioural state of an attentive seal. There were only a small number of instances where the noise level was in the clearly audible range (> 20 dB above threshold). However, these levels were well below the highest level recorded for Weddell seal vocalisations, i.e. 193 dB re. 1 µPa at 1 m (which in human hearing terms is an equivalent level in-air of 131 dB re. 20 µPa at 1 m) (Thomas and Kuechle 1982b). Consequently, even at the closest distances or altitudes tested, the noise levels generated from the anthropogenic sources were less than those of the loudest natural vocalisations. This means that the loudest noise levels generated by anthropogenic sources in this study would not be expected to cause physical damage to the seals beyond a few metres.

These data can be used to develop guidelines for distance and speed of travel for vehicles near Weddell seal colonies. However, there are a number of other factors that will further influence the nature of the sound and therefore the corresponding effect on the seals. Direct comparisons between in-air and underwater noise levels and auditory thresholds are difficult because of acoustic impedance differences between air and water (Richardson et al. 1995). When comparisons are made, underwater hearing is more sensitive than in-air hearing in pinnipeds, especially in
phocids (Mohl 1968; Terhune 1991). However, it is unclear in which medium anthropogenic noise has the greater potential to affect the seals. In many cases, particularly in-air, the visual element of the stimulus confounds the response of an animal. In most studies, no distinction is made between the two stimuli, so that a distance that is regarded as 'acoustically safe' may still result in an adverse behavioural response because of the visual component of the stimulus.

Direct comparisons between different types of anthropogenic noise are also difficult due to differences in engine type and vehicle structure, and frequency characteristics of the noise generated. For example, one of the differences between a Hagglund and a quad is that the tracks of a Hagglund do not isolate the engine noise from the ice as effectively as do the tyres of a quad. In addition, the contact between the tracks and the ice is also generating sound, unlike the rubber tyres of the quads. The result is that transmission loss is less for the Hagglund and therefore the decibel level (under the ice) is greater. The activity of the vehicle can also play an important role in determining the extent of noise effects. For instance, during flight, the noise from a helicopter or Twin Otter aeroplane is first transmitted through the air before transmission through the ice into the water. Sound transmission through the ice and then into the water is complex and variable. Not only does sound attenuate as it travels along its path, but transmission loss also occurs at the air/ice interface where most of the acoustic energy is reflected. Therefore, although sound pressure is greater directly under the ice (Richardson et al. 1995), the noise level recorded under the ice is much less than in-air. During landing and idling, the skids of both the helicopter and the Twin Otter transmit sound directly through the ice into the water.

Higher vehicle travel speeds are also a factor when relating detection thresholds and decibel levels for the purpose of investigating noise effects. For many small vessels, an increase in speed results in higher noise levels (McCauley and Cato 2003). In this study the increase in speed did not result in a significant increase in decibel levels. Rather, only a small number of shifts occurred between the audibility categories, i.e. from inaudible at the slowest speed to barely audible at the fastest speed. Although speeds were not specified, research on cetaceans suggests that a slow moving boat has less of an effect on behaviour than a fast moving one (e.g., Richardson and Würsig 1997; National Research Council 2003). Again, determining precisely what an animal is responding to in these situations is difficult because the acoustic and visual components of the stimuli are difficult to separate.
Received noise level will also vary according to abiotic conditions. For example, a thick layer of snow will dampen the transmission of airborne sounds heard underwater. Changes in temperature, salinity or humidity will also result in refraction of the sound. Thus, the convergence or divergence of the sound waves will either amplify or reduce the received noise (Richardson et al. 1995). Although in this study abiotic factors such as snow cover were controlled for when generating sound/distance profiles, Weddell seals under the ice would normally be exposed to varying noise levels because the ice surface on which over-snow vehicles travel and people walk is variable. It would be reasonable to assume that if the differences in received noise were in the order of a few decibels then the seals would be able to accommodate the change by shifting their position in the water column, i.e. swim/call at a deeper depth if the noise is louder. Wind speed will also affect the detectability of the vehicle, with increased wind speeds resulting in increased background noise levels which in turn increase the detection threshold. Further study would be necessary to determine the effect of such factors on Weddell seals.

The characteristic of the noise, in particular whether it is continuous or transient and constant or changing, is also an important factor influencing the effect of noise on wildlife. In rodents, exposure to continuous, intensive noise can result in health effects, while intermittent noise does not (Borg 1981), possibly because the animals recover between successive exposures (Bowles 1995). Humans have also been found to be more sensitive to continuous noise than to pulsed noise (at equivalent peak levels) (Fidell et al. 1970). In gray whales (Eschrichtius robustus), the threshold for distinct reactions to seismic pulses, with an average pulse level of 170 dB re. 1 µPa at 1 m, was reported as approximately 50 dB higher than that for continuous industrial noise (Malme et al. 1984; Richardson et al. 1995). Continuous noise can mask marine mammal vocalisations for long periods of time with a concomitant reduction in the effective range of communication (Bowles 1995). The distinction between transient and continuous sounds is not absolute, thereby making it difficult to specify which noise types Weddell seals are more often exposed to. For example, much of the anthropogenic noise that the seals are exposed to in the Australian Antarctic Territory is vehicular, which varies in duration, is not pulsed, does not necessarily have an obvious start and end (transient), but does not originate from a fixed point (continuous).

Changing noises, associated with rapid shifts in speed or direction for example, have also been found to have a greater behavioural effect than constant noises. Rapid
movements of vessels, with fast shifts in speed or direction, are especially disturbing to marine mammals (Richardson and Würsig 1997). Reactions of Californian sea lions (Zalophus californianus) to nearby boats were most common when motor noise levels varied (Richardson et al. 1995) (Peterson and Bartholomew 1967). In their study, hauled out pinnipeds were found to react most strongly if the aircraft made abrupt changes, affecting sound levels. Myrberg (1990) reports that a sudden change in sound level is considered a prime stimulus to avoid or to exhibit responses indicative of disturbance.

A number of factors determine whether anthropogenic noise is audible to Weddell seals. Thus, not only is it necessary to establish the noise levels generated by vehicles operating at various distances and altitudes, it is also necessary to establish both the characteristics and the context of the noise. Furthermore, it is important to recognise that noise levels in-air are louder for humans than they are for seals. The lowest detection threshold of a human is less than the assumed threshold for the Weddell seal (see Figure 1 in Terhune 2004). Therefore, noise levels that we consider loud and potentially damaging or disturbing to the Weddell seals may in fact be barely audible to the seals.

### 6.4.2 Vocal response experiment

The experiments to determine the effects of vehicle noise on Weddell seal vocal behaviour indicated that during continuous vehicle noise at 0.075 kHz, Weddell seals detected the noise and modified their behaviour as a result.

During this study, the location of the seals relative to the test stimulus was unknown. However, if vocal behaviour were only to change when noise levels were clearly audible (> 20 dB above threshold), then the seals would need to have been closer than 40 m. Although this is possible, it is more likely that the seals were closer to the pupping colony (300 m from the SRP), and therefore further away from the sound recording point (SRP). This is because males are actively holding territories under the pupping colony (Siniff et al. 1977; Kooyman 1981c). Even low levels of noise therefore appear to have the potential to affect vocal behaviour in Weddell seals. It is not surprising that the seals responded to the noise, considering that the SRP was close to the pupping colony (300 m) and male Weddell seals are actively listening and communicating both with other males and with receptive females during this time (Thomas and Kuechle 1982b).
Harp seals have been found to alter their vocal behaviour in a number of ways to compensate for increased noise in their environment. For example, they can adjust their call repertoire, so that fewer call types are used that fall within or close to the frequency bandwidth of the noise (Serrano and Terhune 2002). Shifts in frequency have also been recorded for beluga whales when exposed to boat noise (Lesage et al. 1999). It has been suggested that this response was made to increase signal detection by avoiding frequencies that were being masked (Lesage et al. 1999). In the current study no decrease in call types within or close to the 0.075 kHz frequency bandwidth were recorded, nor an increase in call types with frequencies > 0.075 kHz. The absence of a shift in frequency may be a result of the low noise levels the Weddell seals were exposed to (i.e. the Hagglund was simply not loud enough).

Another method observed among marine mammals of altering vocal behaviour to increase detection over noise, is to decrease the use of low amplitude calls and increase the use of high amplitude calls. The use of long and repetitive call types, which 'cut through' background noise, also enhances detection (Watkins and Schevill 1979; Serrano and Terhune 2001). Weddell seals have been reported to lengthen many underwater vocalisations in response to conspecific vocalisations, with calls that were overlapped being longer in duration than solitary calls (Terhune et al. 1994b). The increase in duration has been attributed to the addition of elements (for multi-element calls). Also, detectability should increase for calls of longer duration in the presence of sporadic noise. Changes to vocalisations would either reduce or eliminate masking effects of the vehicle noise, thereby increasing detectability. However, in this study, there was no evidence of the lengthening of calls, for either the overlapped or non-overlapped call types in the presence of Hagglund noise. The absence of an increase in call duration in response to Hagglund noise probably reflected the fact that the noise level was not sufficient to require the seals to alter individual vocalisations to enhance detection.

Although the amplitude of the noise generated by the Hagglund in this study was low, and did not seem to cause any masking, the increase in ambient noise during vehicle activity resulted in an increase in the time taken to record 100 definable calls and a decrease in the frequency of occurrence of calls. This suggests that either some seals left the immediate area during vehicle noise, or that the seals vocalised less. Similar results have been found in a study on the influence of vessel noise on underwater vocal activity of harp seals (Terhune et al. 1979). The authors found a significant reduction in the number of calls following a day of nearby vessel activity.
and suggested this was due to either a decrease in the number of seals in the area, or a change in the vocalisations emitted. Studies on whales have also recorded a decrease in calling rate during vessel approach/activity, for examples see Watkins (1986) for right whales (*Eubalaena glacialis*) and Blane and Jaakson (1994) for beluga whales. Belugas have also been recorded to swim 80 km from their original location in response to a ship and remain away for 1-2 days (Richardson and Würsig 1997). Without knowledge of the activity of the seals, it is impossible to determine which of the two theories best explains the response of Weddell seals in this study.

In conclusion, continuous Hagglund activity was found to have an effect on the vocal behaviour of the seals. However, the effect was only manifest in the frequency of occurrence of calls and the number of calls recorded in a specified time period. The absence of changes to the individual calls, such as the lengthening of calls, was attributed to the low received noise levels of the Hagglund. Experiments in which the location of the seals are known would greatly improve our knowledge of the distance at which the noise generated by a Hagglund would affect the actual calls of Weddell seals underwater and the received noise levels at which these changes would occur.
7 General Discussion and Implications for Management
The broad aim of this study was to measure the effects of various forms of human activity on Weddell seals in the Australian Antarctic Territory (AAT), with a view to verify existing guidelines for pedestrian approaches to seals and for over-snow vehicle operations around seals, and to make recommendations as appropriate. More specifically, this study follows up on recommendation XVIII-Ia in Rothwell and Davis (1997) by determining the critical distances for pedestrian approaches and over-snow vehicle operations that will minimise disturbance to seals. In order to achieve this, a series of experiments was conducted to measure, (i) the immediate behavioural responses of lactating Weddell seals and their pups to pedestrian approaches, and the factors affecting response; (ii) the nature of the seals' responses to repeated pedestrian activity; and (iii) the immediate behavioural responses of lactating cows to over-snow vehicle operations, and the factors affecting responses. The study also aimed to measure the immediate physiological response of Weddell seals to pedestrian approaches and to develop standardised sound/distance profiles for the types of vehicles commonly used in the AAT to determine the potential for vehicle activity to affect the seals.

Detailed discussions of these experiments have been presented through previous chapters (Chapters 2-6), of which key findings are repeated briefly here. This chapter then reviews human-wildlife interaction studies, before examining existing management guidelines for human activity around Weddell seals in the AAT and the implications of results from this study for those guidelines. Finally recommendations are made as to how guidelines could be improved to further minimise effects of human activity on Weddell seals.

7.1 Summary of findings

7.1.1 Responses to pedestrians
In chapters 2-4, I explored the short-term and longer-term behavioural and physiological responses of lactating Weddell seals and their pups to pedestrian approaches by a single person and a small group of people.

Generally, lactating Weddell seals and lone pups responded to pedestrians by becoming alert. Only one individual cow showed a more extreme response of attacking both her pup and the approachers. Cows with pups apparently considered humans to be of greater interest than did lone pups. Furthermore, groups of visitors elicited a greater level of interest from cows than did the approach of a single person. For cows with pups, the stage of approach a pedestrian could reach before the seal
responded was determined by the distance of the cow to the water, the distance she was from a conspecific and whether the pup was positioned between her and the approachers. The relative importance of these factors during the two approach types (i.e. single person and group) suggested that the cows adopted different strategies depending on the number of people approaching (Chapter 2). The responses of the cows, particularly in relation to distance to water, indicated that approaching people were at least perceived as a novel stimulus, and possibly as a threat. If the seals perceived approaching humans as a threat, then the level of threat was apparently not seen as particularly great because no seals fled to the water or exhibited responses stronger than looking up at the people. Nevertheless, factors such as distance to water, and position of pups can be incorporated into guidelines by the use of contour maps to help pedestrians determine which seals they can approach most closely while causing the least amount of disturbance.

The effects of pedestrian approaches on Weddell seals recorded during this study were of short duration, lasting no more than five minutes after pedestrians were out of sight. However, visitation to colonies occurs both over short-time periods (hours), and over longer-time periods (e.g. a breeding season). Regular and frequent approaches by a single person to lactating Weddell seals over a period of less than two hours produced evidence of rapid habituation among the seals (Chapter 3). Evidently, the stimulus was sufficiently predictable and regular for the seals to recognise the stimulus, but was weak enough to represent no harm, allowing seals to resume ‘normal’ behaviour within moments of assessing the approaching stimulus. By contrast, irregular approaches over a full breeding season, revealed no evidence of habituation. Rather, for the cows, their responses suggested that they might have become sensitised to human activity prior to the experiment. For the pups, the results suggested that repeated exposure to pedestrian activity resulted in sensitisation, suggesting that the pups regarded humans as a negative stimulus and that previous exposure can affect response and therefore that this factor needs to be considered in human-wildlife interaction studies.

Physiological responses can provide information about the autonomic responses of wildlife to their environment and therefore can provide a more complete understanding of the effects of human activity than behavioural observations alone (Withers 1992). The study described in Chapter 4 provides valuable background information on the heart rate of Weddell seals in various behavioural states, and highlighted the importance of understanding the degree and nature of individual
differences in physiology before apparent changes can be associated with external factors such as human approaches. The one animal from which heart rate responses to pedestrian approaches were successfully recorded during this study showed no indication of a response and further investigation of the physiological responses of Weddell seals to human activity remains an important area of future investigation (Chapter 4).

7.1.2 Responses to vehicles
Most lactating Weddell seals in this study responded to the operation of over-snow vehicles by becoming alert (Chapter 5). The distance from the seals at which the vehicles were driven had a significant effect on the probability and duration of seal response. As with responses to pedestrians, seals that were closer to the water were less likely to respond to vehicle activity, suggesting that the seals may have regarded water as a refuge and that vehicles were seen as a potential threat. Interestingly, the position of the pup (*i.e.* whether exposed to the vehicle or not) was also important during vehicle activity, with cows more likely to respond when pups were protected (*i.e.* the cow was between the pup and the vehicle). However, unlike pedestrian approaches, the distance of the cow to a conspecific did not influence her response to vehicles. During vehicle drive-bys, the cows did not appear to consider the speed of travel or vehicle type to be important.

Continuous Hagglund operations resulted in a decrease in the calling rate of seals underwater. This finding can be used to guide vehicles around known feeding areas and underwater territories of Weddell seals to minimise disturbance to seals under the ice.

7.1.3 Sound/distance profiles
Based on behavioural observations of Weddell seals, and the similarity in detection thresholds amongst phocids (Terhune and Turnbull 1995), I constructed an assumed detection threshold (ADT) for the Weddell seal (Chapter 6). Sound/distance profiles were generated for the vehicles commonly used at Australian Antarctic research stations. At the tested distances (1-500 m) and speeds (15-45 km/hr), the noise generate by a quad, Hagglund and pedestrian would be barely audible (0-20 dB above threshold) to Weddell seals occupying in-air and underwater environments.

Much of the noise generated by a Twin Otter fixed-wing aircraft, a helicopter and a Zodiac at the tested distances (1-3000 m) and speeds (idle-cruise), would also have been barely audible to seals. However, there were some instances where the noise
was sufficiently loud to have been clearly audible (> 20 dB above threshold). These higher noise levels were still below the noise levels generated by the animals themselves, and were therefore not expected to cause physical damage to the seals, although there is a possibility that the noise levels could cause disturbance.

The sound/distance profiles generated by this study provide baseline propagation data for several common sources of anthropogenic noise in the Antarctic environment. Not only can these data be used to develop guidelines for optimal distances and speeds of travel for vehicles near Weddell seal colonies, but they can also be used for any future assessments of the potential impacts of human activity on wildlife in Antarctica.

7.2 Review of human-wildlife interaction studies

The growing concern about the effects of human activity on wildlife and the environment in general, is reflected in an increasing number of studies on the effects of human activity on wildlife and the numerous attempts to manage human-wildlife interactions (e.g. Shackley 1996; Manfredo 2002; Kirkwood et al. 2003; Higginbottom 2004a). Notable are discussions on and reviews of the different types of effects that humans can have on wildlife (e.g. Hall 1992; Gutzwiller 1995; Richardson et al. 1995; Higginbottom 2004a) and studies of the effects of specific types of human activity on individual species (e.g. Burger and Gochfeld 1983; Ellis et al. 1991; Cooper et al. 1994; Delaney et al. 1999). Certainly, these studies provide greater understanding about the possible effects of human activity on wildlife and this enables the generation of more adequate guidelines. However, not all studies have been rigorously designed. The result is that the guidelines often reflect anecdotal field studies and observations of the response of wildlife to human activity, rather than empirical studies that identify the possible cause and effect relationships upon which guidelines are more appropriately based (Kirkwood et al. 2003; Higginbottom 2004a).

Previous knowledge of the effects of human activity on Weddell seals has been largely derived from opportunistic observations while conducting other research. For example, in a study on the behaviour of Weddell seals in a breeding colony at Hutton Cliffs in Antarctica (77°51'S, 166°45'E), Kaufman et al. (1975) also described the response of adult males, lactating females and pups to the approach of people. Such descriptions have contributed to Weddell seals having a reputation of being docile in response to humans. In the absence of other available information, such descriptions
may influence visitor guidelines. Where guidelines are based on false or misinterpreted information, they could result in unnecessary disturbance to the wildlife and an unsatisfactory wildlife viewing experience for visitors.

Manipulative experiments, as employed in the current study, that control for as many confounding variables as possible and test the response of the wildlife to just one stimulus at a time, are comparatively more likely to identify cause and effect relationships between human activity and wildlife response. It is the results of these experiments, conducted on a representative sample size, that enable validation of long standing opinions about individual species and their response to human activity and allow the development of adequate guidelines that minimise impact to wildlife and allow satisfying and safe human activity.

### 7.3 Management guidelines

Scientific studies investigating changes in wildlife behaviour, physiology, reproductive success or survival as a result of human activity can provide a valuable basis for recommendations for the management of those interactions. For example, Cassini (2004) investigated the behavioural response of South American fur seals to visitors and found that the use of a fence to restrict visitor movement could be a simple and affordable means of reducing stressful behaviours of the seals, such as threats, attacks and leaving the colony. In another study, Boren et al. (2002) quantified the response of New Zealand fur seals to approaches by people on foot, in kayaks and in boats, and on the basis of their results recommended new separation distances to minimise disturbance to breeding seals.

In cases such as these, managing human-wildlife interactions involves the development of guidelines to ensure, firstly, that human activity has minimal impact on the wildlife and the environment in general and, secondly, that the human activity can continue. However, the relative importance of these two factors depends on the perspective adopted by the management agency. One viewpoint is to manage human-wildlife interactions to ensure that there is no visible effect on the wildlife. The approach of the Australian Antarctic Division (AAD) could be interpreted in this way as their guidelines stipulate that if the activity is ‘disturbing’ the wildlife, then greater distances should be maintained (Australian Antarctic Division 2004a). Another viewpoint, and one that is likely to predominate in situations where wildlife viewing is the primary purpose of the action, is to manage interactions so that visitor satisfaction is guaranteed, but that any changes in animal behaviour do not have
adverse long-term effects. This viewpoint appears to be that held by commercial tour operators in Antarctica and is reflected in the guidelines recommended by organisations such as the International Association of Antarctic Tour Operators (IAATO). The difference between these two approaches lies in their respective definitions of disturbance and in the purpose of the management guidelines.

Defining disturbance and establishing an acceptable level of disturbance must involve consideration of a number of factors such as the goals of management, legal requirements, social expectations, safety and ethical considerations (e.g. Claridge 1997; Moscardo 2001; Kirkwood et al. 2003; Higginbottom 2004a, b). A manager wishing to ensure that no visible changes among wildlife occur is likely to interpret disturbance as being demonstrated by any visible change in behaviour, while the manager attempting to find a balance between visitor satisfaction and the welfare of the animals, is likely to interpret disturbance as only a significant change in behaviour, for example one that results in a disruption to reproductive and social behaviours (i.e. having a demonstrable biological impact). In the case of managing visitation around Weddell seals, the distances, speeds and group sizes reported here would be acceptable to the latter, but not to the former.

Determining what constitutes a biologically significant impact requires the measurement of a response that can be directly linked to parameters such as reproductive success or survival. A threefold increase in the frequency of alert behaviour of lactating Southern elephant seals at Macquarie Island during human activity, for example, may be considered to be acceptable because the changes in behaviour did not subsequently appear to influence the efficiency of lactation or the mass or condition of affected cows and pups (Engelhard et al. 2002a). A review of the literature, however, reveals that many studies are unable to, or do not attempt to, determine which changes in wildlife behaviour have a significant biological effect. Without empirical evidence of biologically significant effects, managers must often interpret available evidence themselves to determine the extent to which human activity affects the wildlife and, therefore, how to manage human activity around the wildlife.

There is evidence from this study that many seals become alert in the presence of both pedestrians and over-snow vehicles, but that these stimuli may nevertheless be perceived as a low level threat. This might suggest that an alert response does not
have a biologically significant impact on the seals, although one seal in this study responded aggressively, potentially limiting the growth of her pup.

In managing human-wildlife interactions ‘blanket’ guidelines are often used. One guideline is recommended per activity per species or in some cases multiple guidelines per activity per species are suggested. For example, to distinguish between breeding animals and presence of young, the AAD have set different guidelines for pedestrian approaches to cow-pup pairs, pups on their own and adult seals (Australian Antarctic Division 2004a). Blanket guidelines have the advantage of often being simple, providing visitors with just one or two management messages to remember. In this way, there may be an increased probability of people understanding, remembering and adhering to them.

However, blanket guidelines treat each interaction the same, despite individual differences in wildlife sensitivity and responses to human activity, and therefore may not minimise disturbance to all individuals or maximise visitor satisfaction. This is because for blanket guidelines to ensure that all individuals are protected, limits to human activity must be set conservatively, at a level that causes no visible behavioural response in any animal, and this has implications for visitor satisfaction and the practicality of implementing guidelines. For example, in the present study, increasing the separation distance for Hagglunds to 400 m may be problematic because it may not always be possible to maintain such separation distances, due to the terrain surrounding certain seal breeding sites. In a case such as this, the desire to minimise disturbance to wildlife would have to be traded off against maximising human safety and the practicality of travel on the ice. Augmenting blanket guidelines with the relevant species-specific information, can greatly improve the effectiveness of the guidelines in minimising disturbance and maximising visitor satisfaction.

### 7.4 Implications of this study for existing management guidelines

The specific guidelines examined during this study were those currently employed by the Australian Government through the AAD, and by the peak Antarctic tourist body, IAATO. Although the AAD recently increased their recommended distance for pedestrians approaching breeding Weddell seals and lone pups to 20 m (as part of their annual review process) (Australian Antarctic Division 2004a), at the time of this study the recommended distance was 15 m. The furthest distance statistically tested in this study for pedestrian approaches to seals was 20 m. However, a small number
of lone pups and cows were observed to respond when people were 30 m away. In line with recommendation XVIII-la of the Madrid Protocol, and assuming disturbance is taken as any change in the behaviour of an animal, the 20 m separation distance for pedestrian approaches to cow-pup pairs and lone pups can thereby be shown to be ineffective at preventing disturbance.

The current AAD guideline for over-snow vehicle operations in the vicinity of Weddell seals is 150 m for quads and 250 m for Hagglunds (Australian Antarctic Division 2004a). In the present study, some cows became alert when a quad was within 250 m and at least one cow responded to the Hagglund at 400 m. Thus, if these results are interpreted as for results from pedestrian approach experiments, the separation distances currently recommended by the AAD are shown to be ineffective at preventing disturbance.

A strict interpretation of the results of this study would suggest that the separation distances currently recommended by the AAD need to be modified if the goal of management is to avoid behavioural changes in Weddell seals. If management wishes to reduce behavioural responses then at a minimum, appropriate separation distances could be as follows: quads 250 m, Hagglunds 400 m and greater than 20 m for pedestrians.

If, on the other hand, an alert response was considered acceptable, then the results of this study indicate that a single person could approach the majority of cow-pups pairs to a distance of 15 m and to a distance of 5 m from lone pups, without causing significant disturbance. Equally, a group of people could approach cow-pup pairs to a distance of 20 m. Using this approach, a quad could maintain a separation distance of 50 m when travelling at 15 km/hr past cow-pups pairs, and a Hagglund could maintain a separation distance of 100 m when travelling at 15 km/hr.

The minimum distance stipulated by IAATO for pedestrian approaches to seals is 5-10 m (IAATO 2005). Based on the results of this study, approaches to this distance would also be causing an alert response among Weddell seals. This distance could also result in a stronger response, e.g. an attack, as observed in this study, and would therefore still be considered unacceptable even with the acceptance of an alert response.

7.4.1 Enhancing wildlife management guidelines
Blanket guidelines for managing human-Weddell seal interactions are likely to be only partly effective at minimising disturbance to the seals because of the individual
variation in the seals’ responses. For example, in this study, while the majority of animals responded to human activity with mild responses, one lactating cow responded in an extreme manner involving behaviours that could have been detrimental to the growth and survival of her pup. Guidelines can be greatly enhanced by incorporating species and site-specific details that should ensure guidelines can better cope with individual variation in responses. This study has demonstrated one way in which guidelines may be enhanced, particularly if the nature of response to human activity of a species is known. The proportional odds regression model (PORM) method of analysis can be used to generate contour maps that incorporate factors that influence an individual animal’s response, such as, the distance an animal is to a refuge. These maps may then be used in the field by visitors to determine which individual animal they could approach most closely while causing the least amount of disturbance. Using such an approach could effectively tailor blanket guidelines to local conditions, minimising disturbance to wildlife, while maximising visitor satisfaction.

Although the use of PORMs adds complexity to guidelines controlling human-wildlife interactions, the contour maps can be presented as an opportunity to achieve a more intimate encounter. Both close approaches and minimising impacts are considered by tourists to be important in wildlife-interactions (e.g. Finkler and Higham 2004; Valentine et al. 2004). Species-specific contour maps may therefore enrich the overall wildlife experience of visitors, and could become a successful management tool applicable to managing visits to a range of wildlife species.

7.5 Final conclusion
Observations of the response of Weddell seals to the various forms of human activity presented in this study suggest that Weddell seals in the Vestfold Hills and in the Windmill Islands are not particularly responsive to the human activities investigated. Specifically, the seals appear not to show threat, displacement or escape behaviours during pedestrian approaches and over-snow vehicle drive-bys, which have been shown to occur in other pinniped species when exposed to similar stimuli (e.g. Kovacs and Innes 1990; Cassini 2001; Boren et al. 2002). Results from this study with respect to physiological responses of the species to the stimuli tested are ambiguous because of the small sample sizes achieved.

It is, however, important to recognise that the populations examined in this study may not be representative of the species throughout its range, as seals in the Vestfold
Hills and Windmill Islands have been exposed to some human activity prior to the experimental approaches and may therefore have formed an association with human activity that influences their response to the stimuli tested. Guidelines therefore need to be tested on Weddell seals in other areas before they can be considered appropriate for use at other colonies. Nevertheless, this study has demonstrated an approach to objectively investigating the responses of a pinniped species to human activity and has identified at least some of the factors that may affect their response.

In measuring the effects of human activity on Weddell seals, it was apparent that a number of factors influence the seals’ behavioural response. As a result, behavioural responses can show high individual variation, and so blanket guidelines may not necessarily be effective at minimising disturbance to all individuals whilst maximising visitor satisfaction or vehicle operational efficiency. The particular factors that influence response can only be determined through carefully designed studies that establish cause and effect relationships between human activity and wildlife response. Identification of these factors can then be incorporated into guidelines to generate species-specific and context-specific controls. Within this study I have shown that it is possible to tailor blanket guidelines to generate maximally effective and sensitive guidelines for Weddell seals. This approach can be applied to other, more responsive species, in an effort to manage human-wildlife interactions for the protection of the species and more sustainable human-wildlife interactions.
Appendix 1

Table 1 Comparison of the total duration (% of interval) of the most commonly occurring behaviours between lactating Weddell seals during a group approach and the lone pups during a single person approach in Colony A and in Colony B. Differences in behaviour were tested using a Mann-Whitney U test. Significance difference occurred at <0.013 because of the Sequential Bonferroni Correction.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Group Approach</th>
<th>Lone pup Approach</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean ± St. deviation</td>
<td>Significance level</td>
</tr>
<tr>
<td>Rest</td>
<td>92.45 ± 5.56</td>
<td>0.756</td>
</tr>
<tr>
<td>Comfort</td>
<td>5.63 ± 4.69</td>
<td>0.782</td>
</tr>
<tr>
<td>Look</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Approacher</td>
<td>0.00 ± 0.00</td>
<td>1.000</td>
</tr>
<tr>
<td>Surrounding</td>
<td>0.24 ± 0.35</td>
<td>0.101</td>
</tr>
<tr>
<td>Shift position</td>
<td>0.10 ± 0.13</td>
<td>0.026</td>
</tr>
</tbody>
</table>
## Appendix 2

**Table 1** The percentage of seals that performed each measured behaviour during the approach for each of the three experimental treatments. The five most common behaviours are in bold.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Single % of seals</th>
<th>Group % of seals</th>
<th>Pup % of seals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rest</td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Comfort</td>
<td>96.55</td>
<td>89.13</td>
<td>87.80</td>
</tr>
<tr>
<td>Look</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pup</td>
<td>34.48</td>
<td>41.30</td>
<td>N/A</td>
</tr>
<tr>
<td>Conspecific</td>
<td>3.45</td>
<td>0</td>
<td>4.88</td>
</tr>
<tr>
<td>Approacher</td>
<td>62.07</td>
<td>76.09</td>
<td>39.02</td>
</tr>
<tr>
<td>Surrounding</td>
<td>41.38</td>
<td>65.22</td>
<td>34.15</td>
</tr>
<tr>
<td>Bird</td>
<td>0</td>
<td>0</td>
<td>2.44</td>
</tr>
<tr>
<td>Attack</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pup</td>
<td>3.45</td>
<td>2.17</td>
<td>N/A</td>
</tr>
<tr>
<td>Conspecific</td>
<td>3.45</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Approacher</td>
<td>3.45</td>
<td>2.17</td>
<td>0</td>
</tr>
<tr>
<td>Ice sawing</td>
<td>0</td>
<td>15.22</td>
<td>7.32</td>
</tr>
<tr>
<td>Eating ice</td>
<td>0</td>
<td>13.04</td>
<td>7.32</td>
</tr>
<tr>
<td>Vocal</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Pup</td>
<td>26.90</td>
<td>4.35</td>
<td>N/A</td>
</tr>
<tr>
<td>Conspecific</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Approacher</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Unknown</td>
<td>13.79</td>
<td>6.52</td>
<td>14.63</td>
</tr>
<tr>
<td>Interact</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pup</td>
<td>10.34</td>
<td>15.22</td>
<td>N/A</td>
</tr>
<tr>
<td>Conspecific</td>
<td>3.45</td>
<td>0</td>
<td>4.88</td>
</tr>
<tr>
<td>Travel</td>
<td>3.45</td>
<td>6.52</td>
<td>7.32</td>
</tr>
<tr>
<td>Pup bump</td>
<td>20.69</td>
<td>8.70</td>
<td>N/A</td>
</tr>
<tr>
<td>Shift position</td>
<td>55.17</td>
<td>45.65</td>
<td>19.51</td>
</tr>
</tbody>
</table>
### Appendix 3

**Table 3** Post-hoc comparisons of the Wilcoxon signed rank test comparing the most commonly occurring behaviours observed during the single, group and lone pup approach experiments across the three stages of approach (pre-approach recording, the approach and the post-approach recording). Significant results at the 0.05 alpha level are in bold.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Pre vs. approach</th>
<th>Approach vs. post</th>
<th>Pre vs. post</th>
<th>Z</th>
<th>p</th>
<th>Z</th>
<th>p</th>
<th>Z</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Single n=29</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Looking-at-Approacher</td>
<td>-3.724</td>
<td>&lt;0.001</td>
<td>-3.724</td>
<td>&lt;0.001</td>
<td>0.000</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Group n=46</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rest</td>
<td>-3.305</td>
<td>0.001</td>
<td>-3.110</td>
<td>0.002</td>
<td>-1.180</td>
<td>0.238</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Looking-at-Approacher</td>
<td>-5.159</td>
<td>&lt;0.001</td>
<td>-5.159</td>
<td>&lt;0.001</td>
<td>0.000</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Looking-at-Surroundings</td>
<td>-4.095</td>
<td>&lt;0.001</td>
<td>-2.247</td>
<td>0.025</td>
<td>-1.718</td>
<td>0.086</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Pup n=39</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Comfort</td>
<td>-1.005</td>
<td>0.315</td>
<td>-3.307</td>
<td>0.001</td>
<td>-1.898</td>
<td>0.058</td>
<td></td>
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<tr>
<td>Looking-at-Approacher</td>
<td>-3.296</td>
<td>0.001</td>
<td>-3.296</td>
<td>0.001</td>
<td>0.000</td>
<td>1.000</td>
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</table>
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