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Impacts of Human Disturbance Stimuli on the Behaviour and Breeding Biology of Subantarctic Yellow-eyed Penguins (*Megadyptes antipodes*)

A thesis presented

in partial fulfilment of the requirements

for the degree of:

Master of Science

In

Conservation Biology

at Massey University, Palmerston North, New Zealand

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2018

Abstract

Eco-tourism is increasing in popularity worldwide, particularly in previously isolated areas such as Antarctica and the subantarctic. This may be increasing the levels of human disturbance stimuli (human-related presence, objects or sounds), which can have impacts on wildlife at an individual level (behaviourally and physiologically) and at a population level. Human disturbance (the response of an animal to a disturbance stimulus) has been studied in most penguin species, showing both inter- and intra-specific differences in responses to disturbance stimuli at similar distances. The Yellow-eyed Penguin (*Megadyptes antipodes*) is negatively impacted by human disturbance stimuli, but very little research of any kind has been conducted on the subantarctic population. This is despite some areas within the subantarctic being regularly exposed to tourism, and the subantarctic population making up an estimated 60% of the entire species. I used an experimental approach to investigate the behavioural impacts of human disturbance stimuli on subantarctic Yellow-eyed Penguins, on Enderby Island. Human presence significantly changed their behaviour, resulting in an increased time spent vigilant and a decrease in the frequency of maintenance behaviours. By modelling the probability of disturbance at varying distances from the penguin to the human, I showed the current minimum approach distance of 5 m (with a 99% chance of disturbance) was not effective. I also quantified the breeding biology of subantarctic Yellow-eyed Penguins, and investigated the impact of human disturbance stimuli on their breeding success. There was no difference in nesting success (expressed as number of eggs, chicks and fledglings surviving per pair) between the disturbed and undisturbed site and no significant difference in the average weight and body size of fledglings at the disturbed site compared to fledglings at the undisturbed site. My results indicate that at current levels human disturbance stimuli has a behavioural impact on subantarctic Yellow-eyed Penguins, but a population-level impact was not detectable. This may be due to the low level of tourism and high degree of tourism management in the New Zealand

subantarctic, and the resulting low number of interactions between penguins and humans. Enderby Island tourism may therefore be an example of sustainable eco-tourism and successful management, although more research including multi-year studies would be needed to confirm this.

Acknowledgements

I would firstly like to say a huge thank you to my primary supervisor Phil Battley. I feel very lucky to have had such a knowledgeable, supportive and approachable mentor! Thank you for all the advice, guidance and support. I would also like to say a big thank you to my co-supervisor Louise Chilvers, for her very helpful feedback throughout the process.

This thesis would not have been possible without Chris Muller – thank you for your unwavering support, your confidence in me and all the help you gave me from beginning to end. Thank you for keeping me sane during those long months on Enderby. I am also particularly grateful for all the freezing cold evenings you spent out in the rain and wind being my ‘human disturbance’, after long days in the field!

I am grateful to Mel Young, Trudi Webster, Jim Fyfe, Simon Childerhouse, Tony Preston and Jo Hiscock for your assistance and advice. Thank you to Sharon Trainer and Rory Hanan for all your help at the Quarantine store. Thank you to Steve Kafka and the crew of *Evohe*, and the HMNZS Otago for safely transporting us through the Furious Fifties. Thank you to Shannon Taylor for your support, and for helping with field work. Thank you to the New Zealand Department of Conservation for logistical, funding and practical support including transport to the island, and providing essentials including food and the loan of equipment. Thanks also to the following for supplying equipment: Ecology Group Massey University, Yellow-eyed Penguin Trust and Blue Planet Marine. I am also grateful for the funding provided by a Massey University MSc Scholarship, Birds New Zealand Research Fund, and Massey University Ecology Group Scholarship.

Finally, I am very grateful to my family. A big thank you to my parents – you have been, and always will be a huge source of inspiration to me, and I am so proud to be your daughter.

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Chapter 1:

General Introduction



Nature-, wildlife- and eco-tourism

Nature-, wildlife- and eco-tourism are all forms of tourism focused on nature and wildlife, often aiming to be sustainable and to assist in conservation of species or habitats (Bjork 2000; Trave et al. 2017). Wildlife tourism has been increasing in popularity and economic importance, with wildlife-based tourist attractions accounting for 20 – 40% of global tourism (Moorhouse et al. 2015; Trave et al. 2017). They can have many benefits for both participants and wildlife, including education, increased ecological awareness and motivation to protect an area, and revenue for conservation programmes (Chiu et al. 2014; Das & Chatterjee 2015). Where revenue for conservation is generated, tourism can increase some species' expected survival, as the conservation benefits outweigh the negative ecological impacts (Buckley et al. 2016). Some endangered and threatened species rely on tourism for funding; for some species almost two thirds of the population are supported by tourism (Buckley et al. 2012). For example, over 25% of the African Elephant (*Loxodonta spp.*) population and over 60% of the Tana River Crested Mangabey (*Cercocebus galeritus*) population is reliant on funds from tourism (Buckley et al. 2012). Successful tourism can also increase the perceived value of the visited area, which in turn increases environmentally responsible behaviour (Chiu et al. 2014). To be sustainable the industry itself relies on the areas they visit to remain relatively 'unspoiled', so that they remain attractive places for tourism. Tourism may therefore result in the halting of industries that cause the destruction of habitat, such as logging (Buckley et al. 2016). As a result, they indirectly generate revenue from biodiversity, unlike many other industries that directly or indirectly generate revenue from the reduction of biodiversity and destruction of the environment (Nyaupane & Poudel 2011).

However, many of the benefits detailed above may be of limited use in practice. One of the key problems with wildlife tourism is that even if the involved parties aim to be sustainable, there is often little knowledge of the ecology, population biology and behaviour of the species, meaning it can be hard to determine whether the operation is genuinely sustainable (Trave et al. 2017).

Furthermore, 'ecological sustainability' does not have a commonly agreed definition, which can lead to difficulties when attempting to determine sustainability (Hardy et al. 2002; Harding 2006; Trave et al. 2017). In my thesis, I define sustainable tourism in the same way as Trave et al. (2017) – activity that does not result in chronic or irreversible detrimental changes. Studies that have attempted to determine if there is a net benefit or cost have found mixed results; while some tourism appeared to provide a net benefit many did not, and had negative impacts on the welfare and conservation of the subject species (Moorhouse et al. 2015; Buckley et al. 2016). Furthermore, competition between tourism companies and high demand can result in less focus on sustainability and responsible practises, resulting in degradation of the environment (Das & Chatterjee 2015). For example, a boom in tourism in Doubtful Sound, New Zealand, resulted in a large increase in the number of boats active on the water (Lusseau & Higham 2004). This in turn increased the pressure on the Bottlenose Dolphins (*Tursiops spp.*) resident in the area, who frequently interact with tourist boats and are one of the key tourism attractions (Lusseau 2005). In addition, eco-tourism does not always result in the predicted attitude and behavioural changes – a study of visitors in Antarctica found no evidence for increased environmental awareness or environmentally responsible behaviour following a visit (Eijgelaar et al. 2010). Any perceived benefits also come at a cost. For example, many tourists visit Polar Bear (*Ursus maritimus*) habitats because they believe it may be their last chance to see them before extinction. In doing so, they greatly increase their greenhouse gas emissions per person, thereby increasing their contribution to global warming and indirectly to Polar Bear decline (Eijgelaar et al. 2010). Increased human traffic can also cause indirect disturbance through, for example, habitat degradation through damage to vegetation, increased pollution (including oil spill disasters), waste generation and increase risk of the spread of disease (Eijgelaar et al. 2010; Aronson et al. 2011; Su & Swanson 2017). However, arguably the greatest cost to individual species is the direct impact of human disturbance stimuli.

Tourism management

Recent growth in eco-tourism has led to a growing interest and research in the effects of human disturbance stimuli on wildlife, and ways to manage that disturbance (Muller-Schwarze 1985; Tin et al. 2008; Weston et al. 2012). These include excluding visitors from sensitive areas through either management zoning or infrastructure (Ikuta & Blumstein 2003; Beale & Monaghan 2004b), or managing tourist behaviour through either self-regulation (facilitated by guidelines) or supervision (Rodgers & Smith 1995; Giese 1998; Acevedo-Gutiérrez et al. 2011a).

While many measures are already in place to reduce disturbance in sensitive areas, the reasoning and scientific basis for them is often lacking, which can result in sub-optimal outcomes (Sutherland et al. 2004; Trave et al. 2017). These measures are also rarely tested for efficacy after they have been put in place, meaning the outcomes and long-term impacts are unknown. Studies have shown sensitivity to human disturbance stimuli is species-specific, yet many guidelines do not cater for the most sensitive species in the area (Burger & Gochfeld 1993; Blumstein et al. 2005; Holmes 2007; Tin et al. 2008; Coetzee & Chown 2016; Pertierra et al. 2017). In some areas there are sufficient data already to allow for more informed management decisions; in Australia the flight initiation distance of birds can be estimated using the interactive tool 'avianbuffer' (Guay et al. 2016). However, in other areas issues often arise due to a lack of data preventing the creation of regulations with a scientific grounding (Trave et al. 2017). For example, management guidelines for Humboldt Penguins (*Spheniscus humboldti*) in The Humboldt Penguin National Reserve were originally based on research on Magellanic Penguins (*S. magellanicus*) (Ellenberg et al. 2006). However, Humboldt Penguins have since been shown to be much more sensitive to human disturbance stimuli and less capable of habituation than Magellanic Penguins (Ellenberg et al. 2006). The disturbance responses are often also site-specific, as they depend on frequency of visitation and history of disturbance, yet many guidelines apply to entire regions instead of specific sites (Pfeiffer & Peter 2004). There is also likely

to be a trade-off between specificity and ease of implementation; the more general the measures are, the easier they are to implement (Pfeiffer & Peter 2004).

Providing a sound basis for these guidelines requires a quantification of the effects of human disturbance, and documenting how changes in the nature of the disturbance stimuli may impact on the animal (Coetzee & Chown 2016; Bateman & Fleming 2017). It is recognised that the best approaches to study these effects are evidence-based assessments to determine the behavioural, physiological or population-level impacts of human disturbance (Holmes et al. 2005). These can be used to evaluate the effectiveness of current management, and whether the level of tourism is sustainable.

Minimum approach distances and buffer zones

Managers can set conservative thresholds beyond which people should not continue to approach wildlife (Blumstein 2003; Fernández-Juricic et al. 2005). These are known as minimum approach distances, and are often set either arbitrarily, or based on behavioural or physiological studies (Blumstein 2003; Fernández-Juricic et al. 2005). Minimum approach distances vary hugely between areas and species, from 5 m for Royal Penguins (*Eudyptes schlegeli*) to over 100 m for Northern Giant Petrels (*Macronectes halli*) (Holmes et al. 2005; de Villiers et al. 2006). Areas can be created where human activities are restricted to avoid displacing wildlife activities, known as buffer zones (Blumstein 2003; Fernández-Juricic et al. 2005). The use of buffer zones can be enforced using infrastructure such as fences or hides, which also make the disturbance stimuli more predictable, possibly facilitating habituation (Weston et al. 2012). After implementation, sustainability can be determined by monitoring population-level impacts through measuring demographic parameters (including population size and breeding success).

Visitor density

In particularly vulnerable areas or areas with high tourist numbers, closing off parts completely to tourist activity is a common management strategy. For example, in the Galápagos Islands, only certain parts are designated as tourist areas to reduce impact on seabirds (Burger & Gochfeld 1993). In areas where visitors are given access, hides and trenches can also be used to minimise impact (Ratz & Thompson 1999). In areas where tourism is highly regulated, managers can control the number and behaviour of tourists, as well as restricting visitor timings. Restricting access times can be particularly useful for reducing impact on nocturnal or crepuscular species. For example, Wilson et al. (1989b) showed that Adélie Penguins (*Pygoscelis adeliae*) have a diurnal rhythm, leaving to forage early in the morning and returning to the colony late at night (Wilson et al. 1989b). This led to recommendations that human activities be conducted close to midday when the colony was smallest (Wilson et al. 1991).

Antarctic/subantarctic tourist management

Between 2000 and 2007, the number of ecotourists in Antarctica tripled, and is expected to continue to increase (Eijgelaar et al. 2010; Stewart et al. 2017). In the 2017 – 18 season, 46,385 tourists visited Antarctica by sea or air, with 39,378 tourists landing (IAATO 2017a). High endemism and pressures from threats such as climate change and fluctuating prey availability mean these locations are particularly vulnerable to the additional negative effects of human disturbance stimuli (Pertierra et al., 2017). In addition, all Antarctic and subantarctic tourism and most research activities occur in summer, the period where most Antarctic wildlife are breeding and moulting, and are therefore most sensitive to disturbance stimuli (Pfeiffer & Peter 2004). As Antarctic and subantarctic wildlife is often situated in exposed and isolated places, most tourist activity is sporadic and high-intensity, which may reduce the likelihood of habituation (although habituation is not always positive, as discussed in Chapter 2) (Green et al. 2001).

In Antarctica, the large number of countries overseeing activities and the lack of undisputed sovereignty makes regulation of tourism complex (Stewart et al. 2017). Tourism is broadly regulated through the various Antarctic Treaty Consultative Parties (ATCPs), but is also self-regulated through the International Association of Antarctica Tour Operators (IAATO) (Stewart et al. 2017). The IAATO imposes a number "rigorous" codes of conduct, guiding tourists and general pedestrians, which also includes a minimum approach guideline of 5 m (IAATO 2017b). The organisation also regulate the tour guide to passenger ratios (1:20), the size of boats visiting the region (a maximum of 500 passengers) and the number passengers allowed to land at one time (100) (IAATO 2017a). The IAATO (2017a) claim these measures have ensured that "to date almost no discernible impact on the environment has been observed". This is despite a meta-analysis of 62 studies two years previously, which found significant negative physiological and population-level effects from human disturbance stimuli in the Antarctic region (Coetzee & Chown 2016). This shows the importance of independent and rigorous scientific studies on the impact of disturbance stimuli.

From a policy perspective, management is relatively simple in the subantarctic islands, as most are under the sovereignty of a single country (including Australia, New Zealand, France, the United Kingdom and South Africa). As many subantarctic islands are 'stop-over locations' for cruises travelling down to Antarctica, the size of boats visiting the subantarctic is often constrained by regulations specified by the IAATO (Hall & Wouters 1994; Tracey 2007). In general, subantarctic islands are managed conservatively, with emphasis on a precautionary and protective approach (Hall 1993; Tracey 2007). On most islands access is restricted to areas where tourism is considered to have minimal impact, and areas are closed where risks to wildlife are deemed too high (Tracey 2007). The number of tourists allowed at one time and the size of boats are generally low (100 or fewer passengers at a time, 500 passengers per boat or less), with the exception of South Georgia which allows 300 passengers ashore at one time and boats with up to 850 passengers (Tracey 2007). Minimum approach guidelines and other guidelines regulating tourist behaviour vary between islands. Some, such as the New Zealand subantarctic islands, have a 5 m minimum approach

guideline, which applies to all species (Department of Conservation 2013). Others such as Heard Island (managed by Australia) have a set of species-specific and life-stage specific minimum approach guidelines (for example, 30 m for breeding and moulting penguins, 5 m for all non-breeding seabirds) (Australian Government 2005; Holmes et al. 2008). Marion Island (managed by South Africa) also has species-specific guidelines that reflect the sensitivity of different species to disturbance stimuli; the minimum approach guidelines for King (*Aptenodytes patagonicus*), Macaroni (*E. chrysolophus*) and Rockhopper Penguins (*E. chrysocome*) are 15 m, but 100 m for the more sensitive Gentoo Penguin colonies (*P. papua*) (Holmes 2007).

Study species: the Yellow-Eyed Penguin

The Yellow-eyed Penguin (*Megadyptes antipodes*, hōiho) is endemic to New Zealand, occurring only on the south-east coast of the South Island/Te Wai Pounamu, Stewart Island/Rakiura, Codfish Island/Whenua Hou and in the subantarctic on the Auckland Island archipelago/Motu Maha and Campbell Island/Motu Ihupuku (**Figure 1.1**). The Yellow-eyed Penguin was originally restricted to the subantarctic until AD1500, when they colonised the mainland after a similar species (*M. waitaha*) that originally inhabited the mainland became extinct. Recent research has shown that Yellow-eyed Penguins in the subantarctic are genetically distinct from the mainland population, with a very low migration rate (Boessenkool et al. 2009a). They are therefore considered as two different management units, with the total population estimated at 2000 breeding pairs and 60% of the population thought to occur in the subantarctic (McKinlay 2001).

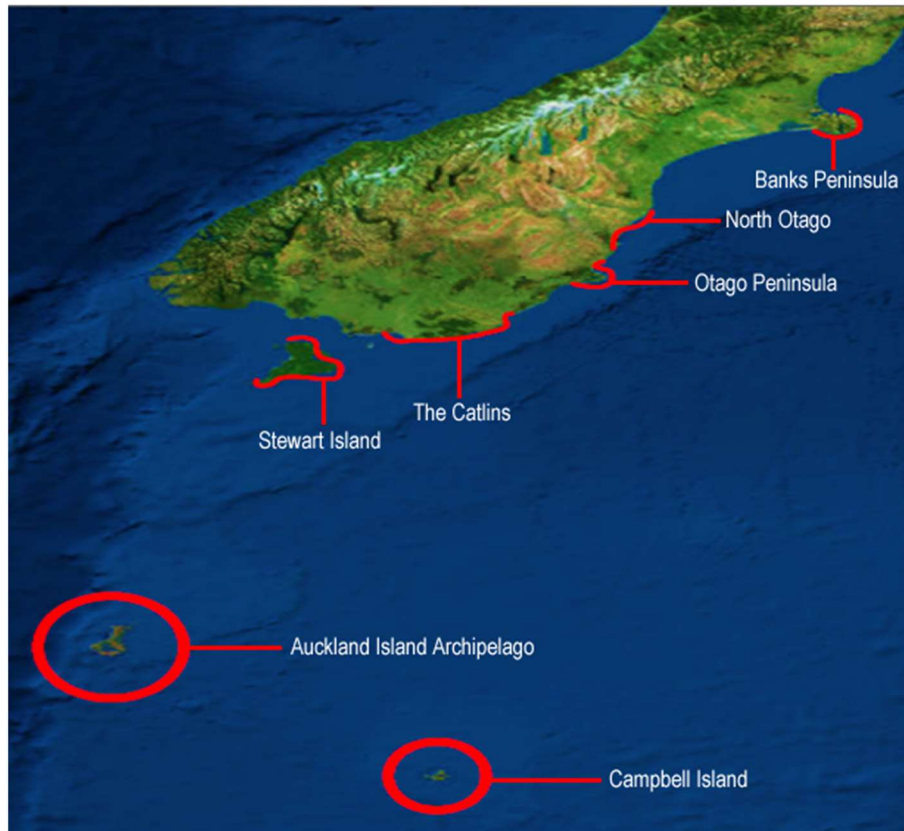


Figure 1.1. The distribution of the Yellow-eyed Penguin.

Classed as endangered by the IUCN and the New Zealand Department of Conservation (Birdlife International 2017; Robertson et al. 2017), the Yellow-eyed Penguin faces multiple threats, including introduced mammalian predators, habitat loss, disease, fishing activities and tourist disturbance (Darby & Seddon 1990; Moore 1992b; Alley et al. 2004; McClung et al. 2004; Ellenberg et al. 2007; King et al. 2012). The introduction of mammalian predators and habitat loss in the 20th century caused the population on the South Island to decline from an estimated 2000–3000 breeding pairs to fewer than 1000 (Darby & Seddon 1990; Ellenberg & Mattern 2012). During the last 30 years, the population has fluctuated greatly and population trends differ considerably between areas (Ellenberg & Mattern 2012). Periodic mass mortality has been the main contributor to the huge fluctuations in population size, with some events causing a loss as high as 60% of breeding adults in some areas (Darby & Seddon 1990). The exact cause of these mortality events has never been conclusively determined, but they have been attributed to avian malaria, food shortage, marine

biotoxins or combinations of these factors (Darby & Seddon 1990; Moore et al. 1990; van Heezik & Davis 1990; Gartrell et al. 2017).

A number of studies on Yellow-eyed Penguins in mainland New Zealand also indicate unregulated tourism is having considerable negative behavioural, physiological and population-level impacts. The presence of tourists decreases the likelihood an adult will come ashore to their nest, and increases transit times to and from the nest (Wright 1998). This may increase the amount of food digested before regurgitation, resulting in less food available for the chicks (Wright 1998; McClung et al. 2004; Ellenberg et al. 2007). Tourist presence also has a direct effect on adult penguins; adults in areas of high unregulated tourism have a greater stress reaction (expressed as higher stress-induced corticosterone concentrations) than penguins from undisturbed sites, suggesting they have been sensitised to humans (Ellenberg et al. 2007). Over the lifetime of the bird this may cause decreased fitness (Ellenberg et al. 2007). When on a nest, heart rate greatly increases when approached by a human, and Yellow-eyed Penguins take longer to recover compared to responses to natural stimuli (Ellenberg et al. 2013). An increase in heart rate is known to correlate with increases in energy expenditure; one 20 minute disturbance of a Yellow-eyed Penguin by a human (less than 2% of their day) accounts for approximately two thirds of their daily energy budget (Ellenberg et al. 2013). Penguins nesting in sites exposed to high levels of unregulated tourism also have significantly lower nesting success, with higher chick mortality and nest abandonment rates (Roberts & Roberts 1973; McClung et al. 2004; Ellenberg et al. 2007). Chicks from these sites also fledge at a lower weight, which decreases juvenile survival in their first year, affecting future population recruitment (McClung et al. 2004; Ellenberg et al. 2007). Yellow-eyed Penguins are highly philopatric; Richdale (1957) showed that 81% of birds returned to their place of hatching or a nearby area to breed. This means that reduced recruitment could have long-term population consequences (Ellenberg et al. 2007). One example of this is Sandfly Bay, a beach on the Otago Peninsula with extremely high levels of unregulated tourism (2400–800 people per month) (Ellenberg et al. 2007). Numbers of nests in the Sandfly Bay area have dropped from 12 in 2005/06 to two in 2017/18 (J. Fyfe Department of

Conservation Ranger pers. comm; Ellenberg et al. 2007). An average of 0.75 chicks fledged per nest in 2005/06, whereas in 2017/18 both nests failed and no chicks successfully fledged (J. Fyfe Department of Conservation Ranger pers. comm; Ellenberg et al. 2007).

Overall the number of Yellow-eyed Penguin breeding pairs on the Otago peninsula and Stewart Island have decreased in the last 30 years, and colonies in the Catlins on the south-east coast of the South Island are estimated to have remained stable (Ellenberg & Mattern 2012). In contrast, two colonies in North Otago have increased in the last 30 years (Ellenberg & Mattern 2012). However, this is probably due to the intensive management at these two colonies (Katiki Point and Barracouta Bay) including a penguin hospital conducting rehabilitation, habitat restoration, and intensive predator trapping which is not practical in all breeding areas (Ellenberg & Mattern 2012).

Managing tourism impact on mainland New Zealand Yellow-eyed Penguins

Yellow-eyed Penguins are a popular wildlife attraction in southern New Zealand. They are considered an 'iconic' coastal Otago species, and a flagship species for many governmental, iwi and community conservation efforts (McClung et al. 2004). On mainland New Zealand, many Yellow-eyed Penguin breeding sites can be easily accessed by car, and many of these sites are often also frequented by people living locally (without necessarily going with the intention of seeing Yellow-eyed Penguins) (pers. obs.). Managed by the Department of Conservation, the key tourism management strategies for the mainland Yellow-Eyed Penguin include identifying suitable locations for tourist activity to take place, and minimising impacts at these sites (McKinlay 2001). There is little emphasis on regulation of visitor timings or numbers (McKinlay 2001). At unregulated sites there are often guidelines including minimum approach distances, but there is no consistent set of guidelines applied. At most unregulated breeding sites there is little enforcement of these guidelines, however some have volunteer rangers during peak periods to regulate visitor behaviour (Department of Conservation 2018).

There is a mixture of commercial and unregulated access to breeding sites which are often highly promoted, particularly on the Otago Peninsula near Dunedin where visitor numbers are high. In this area there are a number of beaches with unregulated access, and there are also commercial operators who conduct tours to private beaches (McClung et al. 2004). Although commercial operators generally have smaller groups and are supervised, they may also cause considerable disturbance – at Penguin Place (a commercial operator with a private Yellow-eyed Penguin colony), the penguins can be observed to within 4 m (although hides and trenches are used to minimise disturbance) (Schänzel & McIntosh 2000). Unlike unregulated tourism, group size and visitor numbers can be restricted by commercial operators, but as the companies rely on revenue from tourism they require high numbers of visitors to remain viable. For example, Penguin Place restricts each group size to 15, yet in one year they received 39,500 visitors (Schänzel & McIntosh 2000). However, results from Ratz and Thompson (1999) indicate that activities at Penguin Place are not having a negative impact on the penguin colony.

Study area: the New Zealand subantarctic islands

The New Zealand subantarctic consists of five island groups: Snares Islands/Tini Heke, Bounty Islands, Antipodes Islands, Auckland Islands/Motu Maha and Campbell Island/Motu Ihupuku (Department of Conservation 2016). All lie between the latitudes 47° and 53° South, and have a combined land area of 76,458 ha (Department of Conservation 2016). The weather in these islands has been characterised as "cool, cloudy, wet and windy" (Peat 2006). The Auckland Islands are an archipelago situated 310 km south of Stewart Island (**Figure 1.2**) (Challies 1975). The main Auckland Island is the largest island of the group, being 50 km long and up to 25 km wide (62,560 Ha) (Challies 1975; Peat 2006). The islands have a mean temperature of 8°C, and rainfall occurs on over 300 days per year (Peat 2006). This rugged island is currently infested with feral pigs, feral cats, and mice, but there are plans to eradicate pigs in the near future (Department of Conservation 2016). The next largest islands, Adams Island and Enderby Island are both pest-free (Department of Conservation

2016). Adams Island has never had mammalian pests, while Enderby Island has had feral cattle, rabbits and mice removed (Department of Conservation 2016). Yellow-eyed Penguins nest in much higher densities on these pest-free islands than on the main Auckland Island, which is likely due to their pest-free status and perhaps also their better-quality habitat (Beer 2010). There are no airstrips in the New Zealand subantarctic, meaning the islands can only be reached via boat or helicopter, and there is no permanent human occupation. A very small number of researchers (usually fewer than 20) occupy some of the islands over the summer period (November to March), and the islands are completely uninhabited in winter. This makes them (in that sense at least) more isolated than Antarctica.

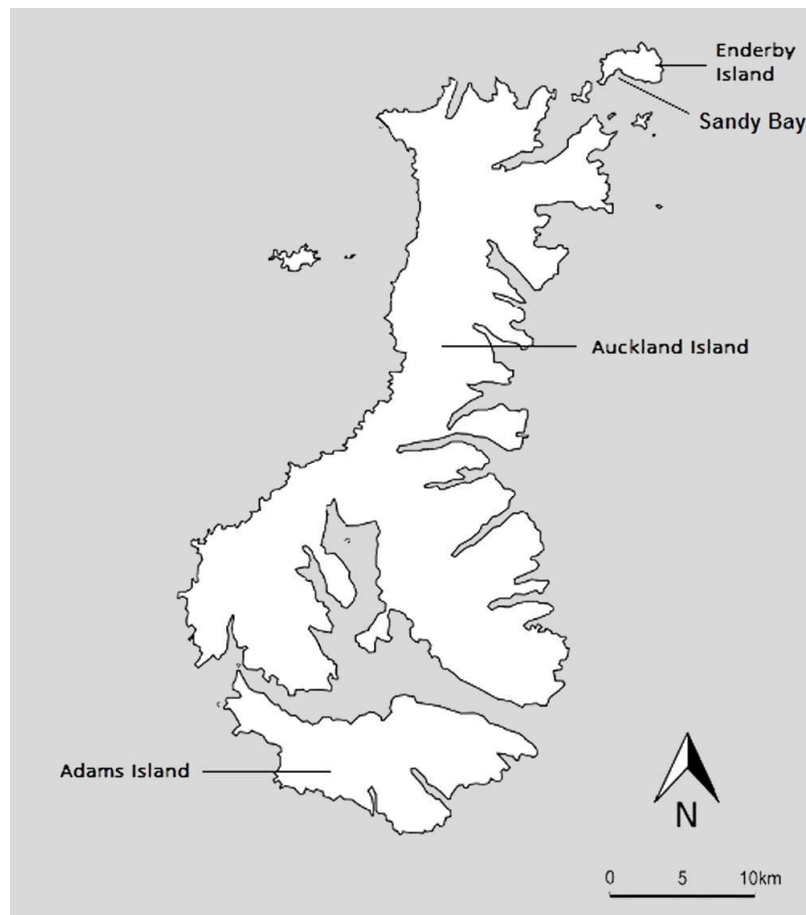


Figure 1.2. The Auckland Island archipelago.

Since many of the threats facing Yellow-eyed Penguins on mainland New Zealand are at lower levels in the subantarctic (i.e. tourism, mammalian predators and habitat loss), the subantarctic population

is considered to be a 'population stronghold' and an 'insurance population' in the face of the declining mainland populations (Ellenberg & Mattern 2012). However, due to the isolation and practical difficulties of carrying out research in these areas there is comparatively little known about the population trends, breeding success and impact of threats on these colonies, and therefore the 'stronghold' status is an assumption based on very limited knowledge (Ellenberg & Mattern 2012). In a review of population information of Yellow-eyed Penguins, Ellenberg and Mattern (2012) state that research in the subantarctic is urgently needed. Campbell Island has been surveyed using beach counts and mark recapture in 1988 and 1992, providing estimates of 490–600 breeding pairs in 1998 and 350–460 in 1992 (Moore 1992b; Moore et al. 2001). The breeding biology was also studied, providing the only estimates of breeding success and fledging weight in the subantarctic (Moore 1992a). The Auckland Islands were surveyed in 1989, producing an estimate of 420–580 pairs (Moore 1990). The Auckland Islands have been surveyed regularly from 2012/13 to 2017/18 using single beach counts. However, these are an index only and therefore provide limited information on population size and no information on breeding success or impact of threats. At time of writing, a population estimate is currently being generated using a mark-recapture study (Chris Muller pers. comm).

Managing tourism impact on subantarctic Yellow-eyed Penguins

All New Zealand subantarctic islands are part of a protected world heritage area and given the highest protection under New Zealand legislation (Department of Conservation 2016). This means that unlike the New Zealand mainland, tourism in the subantarctic is highly regulated by the Department of Conservation (Department of Conservation 2016). This includes the number of visitors per season, the number of boats per season, number of landings at each site per season, number of visitors at each site per day and the timings of landings (Department of Conservation 2016). Visitors (excluding permitted scientific researchers) are only allowed to land on Campbell Island, the main Auckland Island and Enderby Island, and are not allowed to stay overnight

(Department of Conservation 2016). The isolated nature of these islands means that the main source of tourism is from commercial operators in the form of cruise boats (Department of Conservation 2016). All tourists must get permission before landing on any New Zealand subantarctic island, meaning that unregulated tourism does not exist in the New Zealand subantarctic in any form (Department of Conservation 2016). Visitors are generally not allowed to land without supervision, and must adhere to minimum impact guidelines (Department of Conservation 2013, 2016). This includes a minimum approach guideline of 5 m, which applies to all species and all islands (Department of Conservation 2013). New Zealand subantarctic tourism has been increasing since the 1980s, reaching over 1200 passengers per year in 2007/08 (Hall & Wouters 1994; Stewart et al. 2017). Since this peak, numbers have dropped slightly to between 800 and 1000 visitors per year (Stewart et al. 2017).

Study site: Enderby Island

Enderby Island is part of the Auckland Island archipelago, situated to the north-east of the main Auckland Island. It is relatively small (688 hectares) and has a fairly flat topography, rising 45 m above sea level (Taylor 1971). The south and eastern sides of the island are covered in Southern rātā forest (*Metrosideros umbellata*), while the interior consists of areas of tussock (*Poa litorosa*), and extremely thick scrub primarily consisting of *Hebe spp.*, *Dracophyllum spp.* and *Myrsine divaricata*. This scrub in many places forms an almost impenetrable barrier. The northern and western side of the island is much more exposed to weather and ocean spray, and only hardier plants such as *Bulbinella rossii* and *Anisotome latifolia* appear to be able to grow there. To the south there is a large bay with a sandy beach (Sandy Bay), which is the site of a New Zealand Sea Lion colony (*Phocarctos hookeri*) (**Figure 1.2**). Above the beach is a sward area with short lawn-like vegetation (**Figure 1.3**). This is thought to be the result of human-induced fire and the introduction of grazing mammals (which have now been removed) (Taylor 1971).



Figure 1.3. The sward area above the beach of Sandy Bay, where many Yellow-eyed Penguins transit from the sea to their nest and vice versa, and where tourists are allowed to land and walk. The buildings are Department of Conservation research facilities, and a historic boat shed.

Yellow-eyed Penguins are known to nest in high densities around most of the island in both the rātā forest and scrub. Compared to mainland Yellow-eyed Penguins, there has been comparatively little research conducted on Yellow-eyed Penguins on Enderby Island. Beach counts have been conducted each year from 2001 to 2017 on Enderby Island, providing some indication of trends in population size (Chilvers 2014). However, these beach counts occur only once or twice each breeding season and therefore provide limited information. A more in-depth study in 2008 on Enderby Island monitored transiting Yellow-eyed Penguin behaviour over 2 weeks, showing no difference in the number or pattern of penguin landings and departures on days where humans were present, compared to days when no humans were present (Young 2009). However, the same study found an increase in alert behaviour when humans were present (Young 2009). As this was an observational study only it was unable to experimentally test the effect of different types of disturbance stimuli (such as comparing moving approaches and stationary human presence) on behaviour. It was also unable to examine the effect of distance, and therefore evaluate the effectiveness of the minimum approach guideline. In addition to behavioural studies, there has been some research on chick mortality and disease on Enderby Island, finding a high incidence of chick mortality (over 50%) in

2008/09 and a corresponding high prevalence of *Leucocytozoon spp.* on Enderby Island (Argilla et al. 2013). The cause of death was starvation, and it was hypothesised that human disturbance may have contributed to this (Young 2009; Argilla et al. 2013). This high mortality may be cause for concern, however as breeding success has not been monitored since 2008 it is not known if this high mortality was just the result of one unusually bad breeding season, or a common trend among years (Young 2009; Argilla et al. 2013).

Management of Enderby Island

The Department of Conservation allows a maximum of 1100 tourists to visit Enderby Island per year, more visitors than any other Auckland Island site (Department of Conservation 2016). This quota has been increased from an initial 500 set in 1991, to 600 the following year and finally increased to 1100 in 2016 (Hall & Wouters 1994; Department of Conservation 1998, 2016; Stewart et al. 2017). The actual number of visitors per season varies, with a high of almost 900 and a low of 300 between 2008 and 2015 (Stewart et al. 2017). Cruise boats visit Enderby Island at a rate of approximately 1 per week during the breeding season of the Yellow-eyed Penguin (**Table 1.1**). These boats hold between 50 and 200 tourists, who visit Enderby Island for 1 day per trip. A maximum of 200 people are allowed to visit per day.

Table 1.1. Details of each tour boat expedition that landed on Enderby Island in the 2016 – 2017 season: Date, Company, Maximum number of tourists on each boat (Max Pax).

Date	Company	Max Pax
19-Nov 2016	Heritage Expeditions	50
7-Dec 2016	Heritage Expeditions	50
18-Dec 2016	Heritage Expeditions	50
26-Dec 2016	Heritage Expeditions	50
6-Jan 2017	Heritage Expeditions	50
10-Jan 2017	Compagnie du Ponant	200
14-Jan 2017	Heritage Expeditions	50
19-Jan 2017	Heritage Expeditions	50
30-Jan 2017	Zegrahm Expeditions	100
12-Feb 2017	Heritage Expeditions	50
14-Feb 2017	Heritage Expeditions	50
27-Feb 2017	Hapag-Lloyd	150

Guidelines are in place to reduce tourism impact, including restrictions on landing and departing times, no-stopping areas and a minimum approach guideline of 5 m. The restrictions on times and the no-stopping area was instigated based on research by Young (2009) but the minimum approach guideline of 5 m has never been scientifically validated. The increasing popularity of the New Zealand subantarctic to tourism, the increasing quotas set by the Department of Conservation, and the demonstrated vulnerability of Yellow-eyed Penguins to disturbance stimuli emphasise the importance of investigating the impacts of disturbance stimuli on subantarctic Yellow-eyed Penguins.

Thesis aims

The aim of this research was to investigate the behavioural and population-level impacts of human disturbance stimuli on subantarctic Yellow-Eyed Penguins. Although physiological responses are

described and discussed in the literature review for completeness, for practical reasons physiology was not included in the study.

It was hypothesised that human disturbance stimuli would have a similar behavioural and population-level response as that observed in mainland Yellow-eyed Penguins. The data for this study were collected on Enderby Island from November 2016 to February 2017, including data presented in **Table 1.1**.

In Chapter 2 I review the current disturbance literature and describe the different research techniques used to measure and quantify disturbance, with an emphasis on seabird and penguin species.

In Chapter 3 I investigate the behavioural impact of human disturbance stimuli on subantarctic Yellow-eyed Penguins, and scientifically evaluate the current minimum approach guideline. This is compared to natural disturbance stimuli caused by the New Zealand Sea Lion.

In Chapter 4 I quantify the breeding biology of subantarctic Yellow-eyed Penguins, and investigate the impact of human disturbance stimuli on their breeding success. Additional environmental impacts on breeding success are reported, and implications for Yellow-eyed Penguin management.

In Chapter 5 I summarise my results, and compare subantarctic Yellow-eyed Penguin behaviour, population dynamics, exposure to tourism and management with mainland Yellow-eyed Penguins.

I conducted my research under a New Zealand Department of Conservation Wildlife Act permit 39214-FAU, Massey University animal ethics permit no. 14/67, and with the approval of local iwi (Māori tribe).

Chapter 2:

Literature Review

A review of the techniques for measuring human disturbance, with an emphasis on seabird and penguin research



Introduction

The term 'disturbance' is used widely, and can have different meanings depending on the subject and context (Rykiel 1985; Nisbet 2000). For example, 'disturbance' at an eco-system scale can refer to natural or unnatural perturbations (such as a mining operation), whereas at an individual animal level it can refer to a change in an animal's behaviour (Rykiel 1985; Frid & Dill 2002). Disturbance may also be referred to as either a cause or effect, which can create ambiguity and inconsistencies (Rykiel 1985; Nisbet 2000). As such, there are many different definitions, but in my thesis I define human disturbance as a response of an animal to a human-related stimulus (Frid & Dill 2002; Weston et al. 2012). I define a disturbance stimulus as a human-related presence, object or sound, as defined by Frid and Dill (2002). The 'impact of disturbance' I define as the consequences of the presence of human disturbance stimuli.

There are many different possible responses that an animal may have to human disturbance stimuli. At an individual level, responses can be either behavioural or physiological changes (Coetzee & Chown 2016). This can also lead to a response at a population-level, through changes in demographic parameters such as breeding success and survival (Coetzee & Chown 2016). Although at a different level to behavioural and physiological responses (population wide instead of at an individual level), I refer to population-level changes as a response, along with behavioural and physiological responses.

Behavioural responses can include changes in feeding behaviours, interactions with conspecifics, or changes in the animal's apparent perception of the threat (for example, increased aggression or fleeing in response to human presence) (Holmes 2007; Coetzee & Chown 2016). These responses create trade-offs, where responding to the perceived threat (such as humans) causes a reduction in other behaviours beneficial to survival, such as feeding and breeding (Frid & Dill 2002; Blumstein et al. 2005; Coetzee & Chown 2016). This is the same reaction as that caused by the presence of a 'real'

predator, meaning that humans should be considered 'non-lethal predators' in terms of the impact they have on animals (Frid & Dill 2002; Cooper & Blumstein 2015).

Responding to a disturbance stimulus can also be energetically costly, such as being aggressive or fleeing the area (Weston et al. 2012). Physiological responses include changes in heart rate, hormone levels and body temperature changes (Coetzee & Chown 2016). A prolonged and frequent increase in stress is thought to result in decreased adult fitness (Ellenberg et al. 2007). Thus, behavioural and physiological responses are costly to the individual animal, possibly resulting in, for example, decreased fitness and reduced offspring survival due to diminished parental care (Weston et al. 2012). These effects can also have a negative impact on the entire population by reducing reproductive output through lowered reproductive success, such as a decrease in hatching success and fledgling survival. A decrease in adult and juvenile fitness can also cause population decline, through increased adult mortality and decreased population recruitment (Coetzee & Chown 2016).

Although it is commonly accepted that any disturbance will have some form of negative impact, there is no consensus on what level of impact is acceptable (Trave et al. 2017). Disturbance can be thought of as having a 'dose-response' relationship, where the response varies depending on the degree of disturbance (Anderson 1988; Burger & Gochfeld 2007). How much disturbance is considered acceptable will depend on the vulnerability of the population to decline, the degree of stress the population is under from both human disturbance stimuli and other sources, and the practicality of measures that would need to be undertaken to prevent the impact. The most obvious impacts include mortality or failed breeding attempts, which in most cases is an unacceptable level of impact. Therefore, the more subtle, less severe impacts such as short-term behavioural or physiological changes need to be used to set the acceptable level of impact (Holmes et al. 2005).

In this chapter, I review the common methods of measuring disturbance at the three response levels (behavioural, physiological and population-level), and describe the benefits and drawbacks of each

method. I also review the current research on the impact of human disturbance stimuli on animals, with an emphasis on seabird and penguin research.

Behavioural responses to disturbance stimuli

The behavioural response to human disturbance stimuli is perhaps the most easily observable and obvious change in the species of interest (Tarlow & Blumstein 2007). It is also the basis for most evidence-based management decisions aiming to reduce human impact (Blumstein et al. 2003; Weston et al. 2012). The behavioural impact of disturbance stimuli is commonly studied by measuring flight initiation distances, changes in the frequency of vigilance behaviours, maintenance behaviours or changes in habitat use. Changes in behaviour are measured by quantifying the behaviour (using an ethogram) and measuring either the frequency of the behaviour (as a single event) or the time spent undertaking each behaviour (Altmann 1974). Flight initiation distances are often measured using controlled approaches, where the human(s), object(s) or vehicle(s) approach the animal until it begins to flee (Blumstein 2003). Other changes in behaviour (such as vigilance) or physiological changes (such as heart rate) could also be measured during these controlled approaches (e.g. Holmes et al. 2005).

The risk-disturbance hypothesis

The risk-disturbance hypothesis is based on the idea that humans can be non-lethal predators, and hypothesises that human disturbance stimuli are perceived by the animal as a form of predation risk. Originating in the 1960s, this theory is still being used and expanded upon today (Walther 1969; Frid & Dill 2002). Disturbance stimuli can affect the behaviour of an animal by causing an increase in behaviours associated with predator-avoidance, such as vigilance, fleeing and aggression (Frid & Dill 2002; Cooper & Blumstein 2015). These behaviours divert time and energy from other beneficial behaviours (Frid & Dill 2002; Cooper & Blumstein 2015). Disturbance can also indirectly affect habitat selection, for example causing animals to avoid certain areas when foraging (Gill &

Sutherland 2000; Frid & Dill 2002). This can reduce the carrying capacity of the area and cause greater mortality if density dependence is high (Gill & Sutherland 2000).

The trade-off to the animal is optimised when the investment in predator-avoidance behaviour matches the predation risk (Frid & Dill 2002). This ensures that unnecessary and costly reactions are avoided when the predation risk is low, but that the response is greater when predation risk is high so that predation is successfully avoided (Frid & Dill 2002). It is hypothesised that the variables that affect how the animal will react (age and sex of the animal, speed and direction of the approach etc.) will be similar between a human and predator approach (Frid & Dill 2002).

The non-lethality of the disturbance stimuli may invalidate the risk-disturbance hypothesis, particularly when habituation is considered (Frid & Dill 2002). Animals can become habituated to human disturbance stimuli when repeatedly exposed, as they learn that humans are not a predation risk and therefore the cost of predator avoidance is not offset by any benefit (Frid & Dill 2002). However, as the cost of predator avoidance is low compared to the cost of not avoiding the predator (for example reduced feeding compared to immediate death by predator), habituation is often a slow process and may only result in partial habituation (Bouskila & Blumstein 1992; Frid & Dill 2002; Blumstein 2016).

Measuring behaviour

Flight initiation distances using controlled approaches

The flight initiation distance (FID) of an animal is the distance at which an animal begins to flee from a disturbance stimulus (Ydenberg & Dill 1986; Stankowich & Blumstein 2005). It is often used to determine the degree of fear an animal experiences to a moving object at various distances, speeds, or approach angles, and can be adapted by wildlife managers to set minimum approach distances or buffer zones to minimise disturbance (Blumstein 2003; Stankowich & Blumstein 2005; Weston et al. 2012). This variation in FID can be predicted using optimal escape theory. This is an economic model

that predicts that an animal will begin to flee when the risk of predation is equal to the cost of escaping (Ydenberg & Dill 1986). Therefore, the FID will be greater if the threat from the predator increases, and vice versa (Ydenberg & Dill 1986; Cooper & Blumstein 2015).

The FID is a relatively easy metric to measure as the behaviour is in most cases clear and objective, unlike many other behaviours that can be difficult to classify and be subject to observer bias (Guay et al. 2013). It is measured using controlled approaches, where the disturbance stimulus (usually a human pedestrian) approaches the animal until the animal flees. The distance at which the fleeing first occurs is recorded, which is the FID.

One drawback of using FIDs is that by the time the animal flees it is obviously highly disturbed. It has been argued that the minimum approach distances and buffer zones should therefore be set based on the distance at which an animal can continue to undertake normal activity, instead of the distance at which it flees (Holmes et al. 2005). This can be achieved by measuring changes in the frequency of behaviours such as vigilance, foraging and parental care during the controlled approach, although these behaviours can be more susceptible to observer bias (Guay et al. 2013).

There are a number of variables that affect FIDs, which further illustrate the trade-offs between predator-avoidance and other beneficial behaviours, as predicted in the risk-disturbance hypothesis (Frid & Dill 2002; Stankowich & Blumstein 2005). Non-mammalian animals are particularly sensitive to the speed of the approaching disturbance stimulus; the perceived risk increases by 60% in non-mammalian animals when a 'predator' increases its speed (Martín et al. 2004; Stankowich & Blumstein 2005; Lethlean et al. 2017). However, there are some exceptions, such as in the New Zealand Dotterel (*Charadrius obscurus aquilonius*) where speed was not found to affect FIDs (Lord et al. 2001). The directness of the approach also has an effect; the perceived risk has been found to decrease by 31% across all studied taxa when a 'predator' appears to be bypassing the target animal (Frid & Dill 2002; Martín et al. 2004; Stankowich & Blumstein 2005). This is probably due to both speed and direction indicating the likelihood the 'predator' has detected the animal and intends to

capture it (Burger & Gochfeld 1981, 1990; Frid & Dill 2002; Stankowich & Blumstein 2005). Alpine grassland birds appear to be an exception to this rule however, with FIDs greater in four out of five birds studied when the approach was tangential compared to a direct approach (Fernández-Juricic et al. 2005). There was also no effect of approach type found in approaches towards juvenile Chinstrap Penguins (*Pygoscelis antarctica*) (Martín et al. 2004). In birds the FID increases with the starting distance of the predator (Blumstein 2003; Cooper & William 2005; Weston et al. 2012). This is thought to be because the total time spent displaying vigilance behaviours (which carry a cost) is greater if the approach begins from further away, so the benefits of remaining are lower than the costs of fleeing (Cooper & William 2005). In addition, with a longer approach there is a greater chance of perceiving predator persistence (and whether the predator has detected the prey), which may lead to earlier flight (Cooper & William 2005). However, it has also been suggested that in some cases the relationship between FID, alert distance and starting distance is merely a mathematical artefact, because starting distance (SD) must be greater than or equal to alert distance (AD), which must be greater than or equal to the flight initiation distance ($SD \geq AD \geq FID$) (Dumont et al. 2012; Cooper et al. 2015).

However, there are a number of other factors unrelated to the disturbance stimulus itself that need to be controlled or accounted for. Blumstein et al. (2003) showed FIDs are a species-specific trait. Across taxa, general life history characteristics (such as age and sex) are also likely to affect FID (Weston et al. 2012). Body mass is positively correlated with FIDs and explains most of the variation across taxa (Blumstein 2006). There are a number of possible reasons for this, including increased detectability, reduced agility and lower energy requirements in larger species compared to smaller ones (Weston et al. 2012). In addition, eye size (relative to body size) affects FID as it increases the animal's ability to detect approaching predators (Møller & Erritzøe 2010). Group size also affects FIDs across bird taxa (Weston et al. 2012). The effect of animal group size appears to differ widely between species; some tolerate closer approaches when in larger groups as they gain an increased perception of safety, whilst others are better able to detect threats when in larger groups and so flee

earlier (Stankowich & Blumstein 2005). The reverse applies for the group size of the 'predators', which cause a longer FID as they represent a greater threat (Burger & Gochfeld 1991a, b; Frid & Dill 2002). This also appears to be species-specific: Crimson Rosellas (*Platycerus elegans*) were found to increase their FID when approached by two people compared to an approach by one person, unlike Pied Currawongs (*Strepera graculina*) (Geist et al. 2005).

Environmental factors such as the distance to the refuge also play an important role (Stankowich & Blumstein 2005). When further from the refuge, the target animal is at a greater risk of 'predation' and therefore likely to flee at a greater distance from the disturbance stimuli (Frid & Dill 2002; Stankowich & Blumstein 2005). This appears to be consistent across taxa (Stankowich & Blumstein 2005). Juvenile Chinstrap Penguins were found to allow closer approaches when close to a sub-colony, although this is thought to be because of their reluctance to enter the colony (due to aggressive responses from adults) rather than an increased perception of safety (Martín et al. 2004). Other factors that influence the FID include the physical condition of the animal, the degree of density-dependence, the level of investment in the area (for example, territorial males are less likely to flee), and the amount of food available, which would increase the cost of predator-avoidance behaviour (such as leaving the area) (Gill & Sutherland 2000; Frid & Dill 2002; Stankowich & Blumstein 2005; Weston et al. 2012).

Vigilance behaviours

The degree to which an animal is disturbed can also be measured by changes in vigilance behaviours, such as increased time spent scanning the area (Frid & Dill 2002; Holmes 2007). An increase in vigilance increases the chance the animal will avoid capture by the 'predator' (Frid & Dill 2002). This comes at the cost of other beneficial behaviours such as foraging or offspring care, as discussed below. This alert distance is highly correlated with the FID, and the same factors that affect FIDs (such as starting distance, group size etc.) are thought to apply to vigilance behaviours (Frid & Dill 2002).

Using controlled approaches, the distance at which an animal becomes alert can be used as a proxy for the distance at which the animal first detects the disturbance stimulus (Blumstein et al. 2005). Across bird species, the size of the animal appears to positively influence alert distance (Blumstein et al. 2005; Fernández-Juricic et al. 2005; Blumstein 2006; Weston et al. 2012). As mentioned above, eye size (relative to body size) affects FID (Møller & Erritzøe 2010). However, eye size was in some cases not found to affect alert distance in birds, suggesting visual acuity is not always the defining factor determining alert distance (Blumstein et al. 2004). It may instead be because smaller bird species rely on crypsis and may be more agile and able to quickly escape predators, unlike larger bird species which need to rely on early detection (Blumstein et al. 2005).

Activity shifts

The behavioural impact of disturbance stimuli can be measured by the shift in activity as a result of increased vigilance, aggression, or flight (Frid & Dill 2002). Assuming animals normally behave optimally, any deviation results in sub-optimal behaviour. An increase in these behaviours can lead to a decrease in foraging, defence of territory, preening, nest building/maintenance, mating displays and parental care (Frid & Dill 2002). A reduction in any of these behaviours generally carries a cost, which may ultimately result in a decline in fitness (Frid & Dill 2002). For example, Gutzwiller et al. (1994) found that some passerine birds reduce singing when humans walked through their territories, which may reduce their ability to find a mate. However the disturbance response is not always a decrease in these behaviours; Gentoo Penguins (*P. papua*) increase the frequency of maintenance behaviours following a disturbance stimulus, presumably as a response to increased stress (Holmes 2007). This increase in maintenance behaviours is referred to as 'displacement activities', where the animal reacts to the disturbance stimulus by performing 'irrelevant' behaviours (Kortmulder 1998).

Disturbance stimuli can also result in reduced parental care, where the animal temporarily abandons their young (Frid & Dill 2002). This can result in reduced breeding success through exposure to cold

and predation, which is further discussed in the breeding success section. Species with cryptic eggs such as the New Zealand Dotterel may flush from the nest to reduce the vulnerability of the eggs and themselves to the predator (Lord et al. 2001). If the adult chooses to guard the nest instead of abandoning it (albeit temporarily), it can also result in reduced foraging and maintenance behaviours in the adult (Frid & Dill 2002).

Habitat use

The impact of disturbance stimuli can also be measured through changes in habitat use (Gill & Sutherland 2000; Frid & Dill 2002). For example, New Zealand Dotterel chicks reduce foraging in the more optimal littoral zone when humans are present, and spend more time foraging in the sub-optimal supralittoral zone (Lord et al. 1997). There is thought to be more prey in the littoral zone than in the supralittoral zone, which suggests that if people were frequently present the chicks may not be able to consume enough food to meet their energy requirements (Pienkowski 1983; Lord et al. 1997). This may lead to decreased growth and lower fledging rates (Lord et al. 1997). Bottlenose Dolphins (*Tursiops spp.*) reduce foraging in areas of high boat activity (Allen & Read 2000). Conversely, Gill et al. (2001) argues that species which display greater avoidance of disturbance stimuli may in fact be less vulnerable than species which remain, as it indicates they have more suitable habitat elsewhere.

Drawbacks of measuring behavioural responses

The behavioural response to a disturbance stimulus can depend on many experimental and environmental factors, as discussed above. This can be problematic if these factors are not accounted for, as is often the case (Coetzee & Chown 2016). This may be why there is large variation in findings between studies, as found in a review of Antarctic disturbance studies (Coetzee & Chown 2016). There may also be large variation due to observer bias. Behaviour can be difficult to study objectively, and bias can arise if using multiple observers. Guay et al. (2013) found that alert

distances (the distance at which vigilance behaviour first occurs) were particularly susceptible to observer bias, unlike FIDs.

While changes in behaviour can be an effective indicator of disturbance impacts, they can also present issues when determining the importance of this impact (Gill et al. 2001; Trave et al. 2017). Changes in behaviour do not always indicate a negative long-term impact, such as a decrease in the health of the animal, physiological changes or population-level effects (Gill et al. 2001; Tarlow & Blumstein 2007). Conversely, when no behavioural changes are observed, negative impacts such as physiological changes or poor health can still occur as a result of human disturbance stimuli (Beale & Monaghan 2004a; Bejder et al. 2009; Ellenberg et al. 2012). For example, Magellanic Penguin chicks (*Spheniscus magellanicus*) exposed to humans showed evidence of lower behavioural responses to humans but higher physiological stress responses, compared to chicks not exposed to humans (Walker et al. 2005). As most guidelines to prevent disturbance are based on behavioural cues, underlying physiological impacts may not be accounted for (Coetzee & Chown 2016).

Physiological responses to disturbance stimuli

Physiological data can be some of the most challenging data to collect, and are one of the biggest gaps in our understanding of disturbance worldwide (Trave et al. 2017). In a review of marine wildlife tourism, Trave et al. (2017) found that of the 396 studies they reviewed, only 10 focused on physiology. However, there has been considerable focus on physiological impacts in penguins (**Table 2.1**). Although comparatively rare, studies on physiological responses to disturbance stimuli clearly play an important role in understanding the more subtle impacts of disturbance stimuli on individual animals. Walker et al. (2006) argues that unlike behavioural and breeding success responses, physiological responses have the potential to have long-term effects on individual animals. Unlike some behavioural and population-level data, physiological responses can sometimes allow a direct objective comparison between different stressful scenarios, such as comparing corticosterone levels during a human approach and during capture by researchers (Walker et al. 2006).

The physiological stress response

When an animal becomes disturbed, it mounts a stress response, which (along with behavioural cues) causes physiological and hormonal changes in the body (Johnson et al. 1992; Romero 2004; Dantzer et al. 2014). This response includes the activation of the neurogenic system, which causes the release of adrenaline and leads to an increase in the heart rate (Perry 1973; Siegel 1980). This is the initial reaction to the stimulus (Perry 1973; Siegel 1980; Dickens & Romero 2013). It also includes activation of the hypothalamic-pituitary-adrenal axis (HPA, in birds and mammals, or hypothalamic-pituitary-inter-renal axis in amphibians, fish and reptiles), which causes secretion of glucocorticoid steroid hormones (cortisol and corticosterone) from the adrenal cortex (Dantzer et al. 2014; Vera et al. 2017). This can be measured and used as an indicator of stress (Fowler 1999; Romero 2004). Glucocorticoid steroid hormones are thought to play several roles in stress management: a stimulatory role to aid the animal in coping with the disturbance stimuli, a permissive role to improve the stress response of other systems (such as the cardiovascular system), a suppressive role to turn off aspects of the stress response once the disturbance stimulus has ceased, and a recovery role to enable future successful responses to stress (Sapolsky et al. 2000; Romero 2004). The permissive role appears to occur at the baseline level (i.e. the level of glucocorticoid steroid hormones prior to the disturbance), whereas the stimulatory, suppressive and recovery roles are thought to occur as a response to the stress (Sapolsky et al. 2000; Romero 2004). Thus, changes in baseline and stress-induced hormone levels have different physiological consequences (Romero 2004). An increase in the internal body temperature occurs as a result of disturbance stimuli, and can be used to measure increases in energy expenditure due to stress (Regel & Pütz 1997). An increase in energy expenditure is likely to either increase the need to forage, or cause a loss of body condition (Regel & Pütz 1997).

In physiological studies, as well as acute stress (the initial response to the disturbance stimuli) there is considerable interest in the impact of chronic stress, which is long-term physiological change as a

result of high intensity and/or persistent disturbance stimuli (Dickens & Romero 2013). This has been shown in Yellow-eyed Penguins (*Megadyptes antipodes*), where elevated base-line corticosterone levels (used as an indicator of chronic stress) were recorded at sites with high levels of unregulated tourism (Ellenberg et al. 2007). Chronic stress occurs when the stress-response system is no longer functioning at normal capacity, and the effect of these stress responses begins to have negative effects on the organism (Dickens & Romero 2013). For example, long-term release of glucocorticoid steroid hormones could disrupt the reproductive and immune systems, causing reduced reproduction and increased vulnerability to disease (Dhabhar & McEwen 1997; Berga 2008; Dickens & Romero 2013).

Measuring physiological responses

Heart rate

In some studies, heart rate is considered a more sensitive measure than behavioural observations, showing increased heart rate when no detectable behavioural response occurs (Culik et al. 1990; Wilson et al. 1991; Giese 1998; Pfeiffer & Peter 2004; Ellenberg et al. 2012). It can be measured using artificial eggs with microphones or infrared sensors inside, implants or external devices (electrocardiogram units) attached to the animal (Nimon et al. 1996; Giese et al. 1999; Weimerskirch et al. 2002; de Villiers et al. 2006; Ellenberg et al. 2012; Viblanc et al. 2012; Ellenberg et al. 2013). Artificial eggs are much less invasive than implants or attaching external devices (both of which require capture and prolonged handling). By waiting for the adults incubating the eggs to swap, artificial eggs also allow responses from naive birds to be measured, removing the confounding effect of disturbance by researchers. However, they rely on contact with the brood patch so can only be used to study incubating birds (Nimon et al. 1996; Giese et al. 1999; Ellenberg et al. 2013). There is also a risk that the real eggs will be negatively impacted resulting in reduced reproductive output (Ellenberg et al. 2013). Temporary nest abandonment was occasionally observed when

placing artificial eggs in Humboldt (*S. humboldti*) and Yellow-eyed Penguin nests (Ellenberg et al. 2006; Ellenberg et al. 2013).

Heart rate varies across species (de Villiers et al. 2006), and across individuals within a species according to sex, body condition and breeding stage (Froget et al. 2001; Green et al. 2001; Cockrem 2007). Heart rate can be used to objectively compare the response of different species to the same disturbance stimuli. For example, Humboldt Penguins have a greater response to a human approach than many other penguin species (Culik et al. 1990; Wilson et al. 1991; Nimon et al. 1995; Ellenberg et al. 2006). Their response to a human approach was similar to Adélie Penguins' response to capture and handling (which is more invasive), indicating Humboldt Penguins are more vulnerable to disturbance stimuli than Adélie Penguins (Culik et al. 1990; Ellenberg et al. 2006). Heart rate increases as a response to disturbance stimuli can also be compared to natural stimuli (such as predator overflights), which allows a direct comparison with 'natural' and 'unnatural' disturbance stimuli (Ellenberg et al. 2006).

An increase in heart rate linearly correlates with oxygen consumption and metabolic rate in some penguins, and can be used to estimate energy expenditure (Bevan et al. 1995; Froget et al. 2001; Green et al. 2001). Therefore, an increase in heart rate due to disturbance stimuli is assumed to increase the amount of energy used (Weimerskirch et al. 2002; Seddon & Ellenberg 2008; Ellenberg et al. 2013).

Stress hormones

The physiological response to disturbance stimuli can be measured by studying the adrenocortical stress response. Unlike the release of adrenaline which occurs immediately, it takes 3–5 minutes in mammals and birds for the hormonal cascade from the brain to the adrenal cortex to produce measurable increases in glucocorticoid steroid hormones (Wingfield & Romero 2001; Romero 2004). This means that samples collected immediately after the disturbance stimuli should reflect pre-stress hormone levels, and samples collected minutes later reflect the change from the base level in

response to the disturbance stimuli (Romero 2004). Samples are commonly collected using plasma, but hormone levels can also be detected in faeces, urine, hair/feathers and body tissues (Bortolotti et al. 2008; Dantzer et al. 2014; Vera et al. 2017).

However, in the same way as behavioural responses discussed above, the level of stress hormones can be affected by a number of factors such as species, brain size, temperament, time of day, body condition, chemical pollutants, season and breeding stage (Romero et al. 1997; Hood et al. 1998; Wikelski et al. 2001; Breuner & Orchinik 2002; Engelhard et al. 2002; Breuner & Hahn 2003; Pottinger 2003; Romero 2004; Cockrem 2007; Cyr et al. 2008; Martin & Réale 2008; Cockrem et al. 2009; Cockrem 2013; Lendvai et al. 2013; Dantzer et al. 2014; Newman et al. 2017; Small et al. 2017). For example, European starlings' (*Sturnus vulgaris*) stress responsiveness (expressed as both heart rate and glucocorticoid hormone level) decreases during the moulting period (Cyr et al. 2008). Stress responses vary considerably between individuals; it has been proposed that individuals with low glucocorticoid hormone responses to disturbance stimuli have greater fitness in an environment with constant and predictable conditions, whereas those with high glucocorticoid hormone responses have higher fitness in changeable and unpredictable conditions (Cockrem 2007; Cockrem et al. 2009; Cockrem 2013). Stress response can also be influenced by neonatal experiences, meaning that young exposed to long-term stress may have different stress responses as adults, which may lead to reduced fitness. This has been shown in Kittiwakes (*Rissa tridactyla*), where chicks exposed to high levels of corticosterone early in life became less successful at finding food as adults (implying reduced fitness), although the actual stress response as an adult was not tested (Kitaysky et al. 2003).

Researchers are interested in baseline levels as they provide an indication of chronic stress (long-term stress), which is thought to have a greater impact than short-term acute stress (Dantzer et al. 2014). A common method of comparing the impact of disturbance stimuli between populations (such as a disturbed and undisturbed population) is to compare baseline levels of glucocorticoid

steroid hormones (Romero 2004). However, this assumes that the difference in baseline levels is not natural variation (due to factors discussed above). It also assumes that the levels recorded are baseline, not the result of an unobserved stress response (such as the presence of predators not observed by the researchers) (Romero 2004). Other indications of chronic stress include increased responses to acute stressors (i.e. single disturbance events), and increased time to return to baseline levels following a disturbance (Sapolsky et al. 2000; Dantzer et al. 2014).

Body temperature

The physiological impact of disturbance stimuli can also be measured by increases in internal body temperature during disturbance. This is measured using rectal thermometers, surgically implanted telemeters or internal stomach temperature monitors, which the birds are induced to swallow (Boyd & Sladen 1971; Regel & Pütz 1997). Despite successful results on penguins by Boyd and Sladen (1971), and Regel and Pütz (1997) there appears to be little focus on this method, with more emphasis placed on heart rate and stress hormones as physiological indicators of disturbance.

Drawbacks of measuring physiological responses

Physiological data can be extremely difficult and expensive to collect in the wild, particularly in isolated and rugged areas, or with large species where handling is more challenging and dangerous (Trave et al. 2017). The nature of sampling can also mean physiological data are more invasive and have a higher impact than other forms of data (Trave et al. 2017). Aside from ethical considerations, this also presents issues with experimental design. If measuring physiological data requires an invasive procedure before the experiment can begin, it may predispose the animals to a more extreme response during the experiment, due to both a general increase in stress and a negative association with humans (Wilson et al. 1991; Nimon et al. 1995). For example, Culik and Wilson (1991) monitored the response of Adélie Penguins (*Pygoscelis adeliae*) to human presence by removing ten penguins from their nest and either attaching external ECG devices or surgically

implanting heart-rate transmitters (Culik et al. 1990). The degree of response to human presence reported was later questioned given the highly invasive nature of the surgical implants (Culik & Wilson 1995; Nimon et al. 1995).

Recently, some of the basic assumptions of physiological stress responses have also been challenged (Dantzer et al. 2014). For example, Dickens and Romero (2013) showed in a review that the effect of chronic stress on plasma baseline or stress induced levels of glucocorticoid stress hormones is not consistent – sometimes levels increased, decreased or did not change in response to chronic stress. This throws doubt on the validity of the assumption that glucocorticoid stress hormones will increase in response to chronic stress (Dickens & Romero 2013). The 'three minute rule' (the idea that baseline levels of stress hormones can be measured as long as the animal is sampled less than 3 minutes after capture) has also been questioned, with research showing that in some species a detectable hormonal stress response can begin at 2 minutes following disturbance (Newman et al. 2017; Small et al. 2017). This casts doubt on conclusions drawn from the measurement of plasma glucocorticoid levels (Dantzer et al. 2014).

The long-term impacts of physiological changes are commonly predicted in studies that find physiological responses to disturbance stimuli, such as reduced population viability over generations or decreased adult fitness (known as the cort-fitness hypothesis) (e.g. Walker et al. 2006; Bonier et al. 2009a; Villanueva et al. 2012). These claims mostly arise from biomedical research, which show increased stress can have long-term effects, such as exacerbating diseases through suppressing the immune system, and inhibiting reproduction (Wikelski et al. 2001; Romero 2004; Kirby et al. 2009). However, there is no consensus that physiological stress affects fitness (Breuner et al. 2008; Bonier et al. 2009a; Bonier et al. 2009b; Crespi et al. 2013). Romero and Wikelski (2001) showed corticosterone levels in marine iguanas (*Amblyrhynchus cristatus*) appear to predict survival probabilities during a naturally stressful time period (an El Niño-induced famine), and Ellenberg et al. (2007) showed that high baseline corticosterone in adult Yellow-eyed Penguins was correlated with

low fledging weight. However, there have been no studies showing physiological changes as a result disturbance stimuli affect fitness. The limited number of studies on long-term effects in wild populations means there is currently little evidence supporting predictions of reduced population viability, particularly as wild animals may display more adaptive phenotypic plasticity than laboratory animals (Breuner et al. 2008; Dantzer et al. 2014). This makes the study of physiological responses somewhat problematic, as when a change in physiological responses is reported it is not known what the long-term impacts of that will be, if indeed there are any at all (Villanueva et al. 2012).

Population-level responses to disturbance stimuli

Gill et al. (2001) argue that human disturbance is only important (providing welfare is a lower priority) if it results in a population-level decline by affecting survival or fecundity, and therefore animals that display behavioural responses without population-level consequences should not be high priorities for management. Clearly, population-level impacts such as survival and fecundity are important to study, as they are the inferred result of behavioural and physiological responses (i.e. changes in behaviour or physiology are considered important because they are thought to result in reduced survival or fecundity) (Hill et al. 1997; Gill et al. 2001; Seddon & Ellenberg 2008). Population-level effects are the only way to measure whether the current levels of human disturbance are sustainable, and are therefore an important measure for conservation managers trying to ensure long-term population health and persistence (Watson et al. 2014).

Population dynamics

An individual's immediate behavioural and physiological responses to disturbance stimuli may also result in a population-level response. The nature of this response may depend on the vulnerability of each life cycle stage, and thus may manifest as increased offspring mortality/breeding failure, juvenile mortality/recruitment failure, or adult mortality. All of these responses could lead to reduced population size.

Disturbance could lead to reduced incubation in birds resulting in a reduced hatching rate (e.g. Verhulst et al. 2001), reduced brooding or feeding of young (resulting in reduced offspring condition/increased mortality (e.g. Burger 1981; Fernández & Azkona 1993) or permanent nest abandonment resulting in breeding failure (e.g. Bolduc & Guillemette 2003). Defence of young can decrease the likelihood of offspring mortality, but also increases the vulnerability of the adult (Andersson et al. 1980; Greig-Smith 1980; Forbes et al. 1994). In birds, remaining on the nest as a predator approaches is often a form of risk taking, as it protects the young but increases the chances of predation (with the exception of cryptic nesters that protect the nest by leaving it) (Andersson et al. 1980). Long-term, frequent disturbances may redirect an individual's behaviour from reproduction to survival, increasing the likelihood of nest abandonment (Breuner et al. 2008; Bonier et al. 2009a). According to the risk-disturbance hypothesis, the same should apply to a human approach as a form of non-lethal disturbance.

Life history theory predicts that the amount of resources allocated towards reproduction should predict the level of parental risk taking at both an individual and species level (Andersson et al. 1980; Martin 1992; Ghalambor & Martin 2000). Therefore, it is hypothesised that species with long reproductive lifespans that produce few young per year are more likely to abandon their young to increase their own survival, because the probability of future breeding opportunities is high (Magnhagen 1991; Ghalambor & Martin 2000; Frid & Dill 2002). Likewise, species with short reproductive lifespans that produce many young are thought to protect their young at the expense of their own likelihood of survival. However, the r/K continuum theory predicts that species that produce few young also put more investment into each offspring, and thus may be more likely to defend their young (MacArthur & Wilson 1967). The likelihood of nest abandonment is thus highly species-specific and dependent on life history, as has been shown in passerines and ducks (Forbes et al. 1994; Ghalambor & Martin 2000). Within species, the offspring age can also affect the likelihood of abandonment as parents have invested more and more reproductive effort as the offspring grow, as has been shown in Fieldfares (*Turdus pilaris*) (Andersson et al. 1980). The effect of offspring age

has also been shown in female ducks of various species, who allow closer approaches by humans to the nest (before fleeing) the further incubation progresses (Forbes et al. 1994). Alternatively, in other species vulnerability to predators is likely to decrease as offspring age increases, reducing the risk to the offspring of temporary abandonment (Anderson & Keith 1980; Wilson et al. 1991).

The abandonment of young (either temporary or permanent) due to disturbance stimuli can increase offspring mortality, due to exposure to cold or predation (Anderson & Keith 1980; Frid & Dill 2002). This has been documented in a number of bird species when disturbed (Anderson & Keith 1980; Anderson 1988; Lord et al. 2001; Frid & Dill 2002). For example, a study of Adélie Penguins estimated that a human approaching an incubating penguin to within 5 m caused the penguin to stand up for on average 49 seconds, which was estimated to have reduced the temperature of the eggs by almost 4°C (Giese 1998). This has been linked to reductions in breeding success (Giese 1996). In addition, decreased time spent foraging as a result of disturbance stimuli can result in less food being provided to the young, reducing breeding success (Frid & Dill 2002). An increase in human disturbance stimuli may also result in an increase in offspring predation, such as an increase in gull predation on African Penguin (*Spheniscus demersus*), Double-crested Cormorant (*Phalacrocorax auritus*), Common Eider (*Somateria mollissima*) and Brown Pelican (*Pelecanus occidentalis*) colonies following human disturbance stimuli (Kury & Gochfeld 1975; Anderson & Keith 1980; Hockey & Hallinan 1981; Bolduc & Guillemette 2003). However, this was not the case in Gentoo Penguins with Skua (*Catharacta sp.*) predation (Crosbie 1999). In addition, nest desertion by the partner waiting on the nest is a possible result of delayed foraging trips. This is thought to be a factor in Humboldt Penguin disturbance, where the delayed return of partners as a result of human disturbance stimuli was considered to have at least partially contributed to nest desertion in areas of high tourist activity (Ellenberg et al. 2006).

Even if no offspring mortality occurs, the effect of disturbance may manifest as increased juvenile mortality as a result of a suboptimal early life, or reduced offspring quality (McClung et al. 2004).

Reduced food provided to the offspring could result in reduced condition as a juvenile (McClung et al. 2004). Juvenile condition is vital in many species as they need fat reserves when first learning how to survive in their environment, allowing for initial disadvantages such as inefficient foraging and lack of a territory (Martín et al. 2004). Juveniles may also have to disperse further and take more risks than adults, resulting in greater exposure to disturbance stimuli (Martín et al. 2004; McClung et al. 2004).

Substantial changes in behaviour as a result of disturbance stimuli may increase adult mortality (Frid & Dill 2002). A meta-analysis found that body weight in wild animals consistently declines in response to chronic stress, indicating reduced condition (Dickens & Romero 2013). This is due to reduced foraging, increased energy expenditure or increased corticosterone levels leading to metabolism of fat and protein reserves (Remage-Healey & Romero 2001; Dickens & Romero 2013). It is also possible that the adult reduces its own food intake to provide enough food to the offspring (Salihoglu et al. 2001). This could directly contribute to predation rates, increasing adult mortality. A disturbance stimulus could also directly contribute to predation rates by causing the animal to flee away from the disturbance stimuli and towards the predator. For example in Antarctica, penguins may flee from land or air disturbance stimuli (such as helicopter flights) into the sea, increasing their vulnerability to marine predators such as Leopard Seals (*Hydrurga leptonyx*) (Southwell 2005).

Measuring population-level responses to disturbance stimuli

Breeding success

The impact of human disturbance stimuli can be measured by monitoring breeding success. This can be achieved either by comparing between areas of disturbance stimuli and areas without, or monitoring breeding over multiple breeding seasons and comparing this to changes in exposure to disturbance stimuli (e.g. Anderson 1988; McClung et al. 2004; Carlini et al. 2007; Ellenberg et al. 2007; Watson et al. 2014). This is commonly expressed in birds either as nesting success (the

probability of a nest producing at least one fledgling over the nesting period) or reproductive output (number of fledglings produced per female/pair) (Armstrong et al. 2002; Jehle et al. 2004).

Apparent nesting success (the number of successful nests divided by the total number of nests found) is an over-estimate due to under-representation of nests that fail early; the longer it takes to find nests the greater this bias (Mayfield 1961; Armstrong et al. 2002). Thus multiple models have been created to reduce this bias by calculating daily survival probabilities, and taking into account delays in nest discovery (Mayfield 1961; Stanley 2000; Jehle et al. 2004; Stanley 2004; Devineau et al. 2014; Miller et al. 2017). These models also allow nesting success to be modelled with covariates (such as habitat and time), making the results more biologically meaningful (Jehle et al. 2004; Miller et al. 2017). However they often have assumptions that can be difficult to meet for species not being intensively studied or managed. For example, a key assumption of one of the models (the nest-survival model in MARK) (Dinsmore & Dinsmore 2007) is that nests are correctly aged when they are discovered, which requires either monitoring nests during laying or ageing eggs by candling. However, these models are being continuously improved – Stanley (2004) created a model that does not require nests to be aged, and Miller et al. (2017) made further improvements by creating a model that doesn't require hatch date or stage of failure to be known. Despite these improvements, reproductive output (i.e. number of offspring produced per breeding pair) may in some cases be a better measure than nesting success depending on the species and management questions, as nesting success does not differentiate between full success (all offspring survive) and partial success (some offspring survive, some die) (Thompson et al. 2001). It also doesn't account for re-nesting or multiple brooding during a breeding season (Thompson et al. 2001).

However, in many animals disturbance would not cause breeding failure but instead reduce condition of the offspring. Thus, when examining breeding success other metrics such as clutch/litter size, offspring/fledgling weight and size are also important (Tarlow & Blumstein 2007). These are important metrics of food intake either due to disturbance stimuli or reduced food availability

(Williams & Croxall 1990; Salihoglu et al. 2001). For animals that regurgitate food to their young, an increase in the time taken to reach their young due to disturbance stimuli can result in a reduction of food provided (Wright 1998; McClung et al. 2004; Ellenberg et al. 2007). An increase in required adult energy expenditure could also result in less food being available to chicks (Ellenberg et al. 2007). However, reduced food may not always result in reduced chick condition. In some species such as the Adélie Penguin, the adults are capable of modifying their feeding frequency according to the quantity and quality of food available, resulting in stable fledging weights across years of low and high food availability (Salihoglu et al. 2001). In some cases a reduction in food intake can also actually increase the average weight and size of chicks in a population; in years of low food intake higher mortality causes smaller and lighter chicks to die (that may in other years have survived), increasing the mean weight and size of live chicks in that year (Williams & Croxall 1990).

Juvenile mortality/recruitment

A loss of juvenile recruitment either through mortality or dispersal could result in long-term population-level consequences. In many species juvenile mortality is difficult to measure, as they often disperse widely and therefore are less observable than breeding adults and young (Wolff 1994). However, some species such as Hoatzin (*Opisthocomus hoazin*) juveniles remain in the breeding area, and thus can be monitored. Juveniles in sites exposed to tourism had higher mortality, lower mass and had a higher stress response than juveniles at unexposed sites (Müllner et al. 2004). This was in contrast to adults (who appeared to have habituated to human presence) and young chicks, showing the importance of monitoring the effect of disturbance stimuli on juveniles as well as on adults and chicks (Müllner et al. 2004). In addition, McClung et al. (2004) showed fledging weight was positively correlated to juvenile survival in Yellow-eyed Penguins, suggesting that reduced fledging weight at sites with high levels of tourism leads to increased juvenile mortality and low population recruitment.

A source-sink effect (dispersal from a highly productive population to a poorly productive population) could prevent (or at least obscure) overall changes in population size as a result of disturbance stimuli (Sauvajot et al. 1998). It may also create an 'ecological trap' where animals settle in a sub-optimal habitat due to factors such as human disturbance in their preferred habitat (Kolbe & Janzen 2002). However, this will not occur in species with high reproductive philopatry, as increased breeding failure and juvenile mortality will not result in dispersal into the site from elsewhere, and therefore is likely to result in a decreased population size at the exposed sites. For example, Yellow-eyed Penguins are highly reproductively philopatric, and decreased breeding success and juvenile recruitment is believed to have led to sharp population declines in some breeding areas (Roberts & Roberts 1973; McClung et al. 2004; Ellenberg et al. 2007).

Population size

Population size can also be studied to measure the impact of disturbance stimuli, but this also requires multi-year studies. In particular, species with high inter-annual variability require long-term monitoring, as a one-off census could lead to misleading results (Croxall et al. 1988). Long term colony counts (over 10 years) of Antarctic penguins have been used to study the effect of disturbance stimuli, but often environmental effects such as sea ice extent, snowfall and food availability are found to have greater effects than disturbance stimuli on population size (e.g. Patterson & Fraser 1998; Copley & Shears 1999; Copley et al. 2000; Micol & Jouventin 2001; Carlini et al. 2007; Trathan et al. 2008; Lynch et al. 2010). However, it is thought that human disturbance stimuli on the edge of the colonies prevents 'prospecting' new breeders from establishing, which may prevent colonies from growing (Woehler et al. 1994; Trathan et al. 2008). In breeding adults, their breeding success in the previous breeding season may also affect their choice of breeding site the following year (Carlini et al. 2007). In addition, population models could be used to determine the effects of different management strategies, such as the SODA (simulation of disturbance activities) model, which has been used to predict the effect of different park designs and visitor frequency on population sizes and breeding success of animals vulnerable to disturbance (Bennett et

al. 2009). Liley and Sutherland (2007) also used a population model to predict the population-level consequences of changes in human numbers on the Ringed Plover *Charadrius hiaticula*.

Drawbacks of measuring population-level responses

Population level effects may be considered more important than behavioural or physiological measures, as they are the result of mortality (offspring, juvenile or adult). These effects may be less likely to be detected than changes in behaviour or physiology, as levels of disturbance stimuli would need to be high to cause measurable population-level effects (Gill et al. 1996; Gill et al. 2001). While behavioural and physiological changes in response to disturbance stimuli may be common (such as increased heart rate and vigilance behaviour), this may not necessarily result in a reduction in breeding success, increased mortality or changes in population size (Gill et al. 1996; Gill et al. 2001). Researchers that do find significant effects in wild populations often struggle to show conclusively that disturbance is the cause, as other factors such as nesting habitat, food availability, predator density and disease are impossible to control for (Cobley & Shears 1999; Ellenberg et al. 2006; Clutton-Brock & Sheldon 2010). For example, a decrease in fledging weight may be due to disturbance stimuli, but could also be the result of reduced food availability (Williams & Croxall 1990). In addition, poorer quality individuals may be forced to breed in suboptimal habitats (areas of human disturbance stimuli), thereby confounding the effect of disturbance stimuli on breeding success (Dantzer et al. 2014).

Population level responses may not occur immediately after disturbance stimuli, meaning long-term datasets are often required to find any effect, which are difficult to fund and may be less attractive to managers who need to make decisions quickly (Trathan et al. 2008; Barbosa et al. 2013). Breeding success can be studied within a shorter time frame, but as not all populations are sensitive to changes in breeding success the long-term impact can be difficult to predict (Lebreton & Clobert

1991). Long-lived species are particularly vulnerable to changes in adult survival, and less susceptible to short-term changes in breeding success (Lebreton & Clobert 1991).

While population-level effects are useful for showing the long-term consequences of disturbance stimuli, they cannot generally be used to test small changes in disturbance factors (although Bolduc and Guillemette (2003) were able to experimentally test different densities and timings of human disturbance stimuli on nesting success of gull colonies). The effect of management could be studied by comparing populations and monitoring the effects of different management solutions on population trends, although again this requires long-term monitoring. In contrast, behavioural and physiological effects can examine disturbance on a much more short-term and dynamic timescale. Therefore, population-level effects are not as useful for developing management guidelines or comparing types of disturbance stimuli. For example, a minimum approach distance cannot be developed from studies solely measuring population-level effects.

Habituation and sensitisation

Habituation is when an animal no longer perceives a stimulus as threatening or rewarding, resulting in reduction in responses to the stimulus (Bejder et al. 2009; Blumstein 2016). Sensitisation is the opposite effect, where through learning an animal increasingly responds to a stimulus (Bejder et al. 2009). In theory, animals that are exposed to the disturbance stimulus regularly in a non-threatening way will become habituated; animals exposed to a disturbance stimulus that is always or occasionally negative will become sensitised (Frid & Dill 2002; Stankowich & Blumstein 2005; Weston et al. 2012). This can be a difficult factor to control or quantify, as often the previous experience of the animal to the disturbance stimulus is unknown (Weston et al. 2012).

There is evidence that some species can become habituated to human disturbance stimuli (Keller 1989; van Heezik & Seddon 1990; Lord et al. 2001; Blumstein 2003; Pfeiffer & Peter 2004; Walker et al. 2006; Baudains & Lloyd 2007; Hughes et al. 2008; Viblanc et al. 2012). For habituation to occur, the disturbance stimulus needs to be frequent, benign, slow and predictable (Weston et al. 2012).

This causes a reduction in the impact of human presence over time by reducing stress levels and the frequency of negative changes in behaviour (Walker et al. 2006; Baudains & Lloyd 2007; Cyr & Romero 2009). Habituation can occur as a learned response, where specific disturbance stimuli no longer produce a response, or as a physiological change resulting in a consistently lowered response to all disturbance stimuli. For example, King Penguins (*Aptenodytes patagonicus*) habituate to benign human presence, but not to capture and handling by researchers, indicating a learned habituation response (Viblanco et al. 2012). However, in Magellanic Penguins differences in responses to stress were the result of differences in the capacity of the adrenal gland to secrete corticosterone, and lowered stress responses were observed for multiple disturbance stimuli including capture and handling (Walker et al. 2006).

As well as within individuals, habituation can also have an effect over generations by displacing shy genotypes, and reducing genetic variation in personalities (Van Dongen et al. 2001; Dingemanse et al. 2004). Habituation ability appears to be highly species-specific, and also depends on the type, frequency and level of disturbance stimuli the animals are subjected to (Ellenberg et al. 2006; Walker et al. 2006; Villanueva et al. 2012). On a population level, it can also be difficult to determine whether habituation has actually occurred, as reduced responses within a population to disturbance stimuli may be due to stressed animals leaving the area, rather than habituation (Fowler 1999; Ellenberg et al. 2006). This may create an 'ecological trap' where animals leave a high-quality area (due to human disturbance or other factors) and instead disperse to a sub-optimal area (Kolbe & Janzen 2002). Within species there is also large variation in the habituation potential of individuals, which can depend on factors such as previous experience with humans, sex and character (Ellenberg et al. 2006). It is therefore difficult to predict which species will habituate. In addition, habituation is sometimes inferred when comparing across habitats (such as comparing between rural and urban areas) (Weston et al. 2012). This can create confounding effects of dispersal, site fidelity and habitat type, which are likely to affect behavioural responses such as FIDs (Weston et al. 2012).

Habituation in itself can also have negative effects by preventing normal stress responses, which may cause a decrease in fitness (for example a lowered response to genuine danger from real predators) (Baudains & Lloyd 2007; Bejder et al. 2009; Cyr & Romero 2009; Villanueva et al. 2012; Geffroy et al. 2015). For example, habituation to humans by White-fronted Plovers (*Charadrius marginatus*) may have contributed to the high levels of predation by dogs that accompany the humans (Baudains & Lloyd 2007). It can also have the opposite effect, causing increased responses to stresses (other than the one they have habituated to) (Bhatnagar & Vining 2003; Romero 2004; Bejder et al. 2009). Therefore, given the great cost of human disturbance on affected species and the difficulty of predicting the likelihood and consequences of habituation, it is imperative tourism is managed to reduce human impact as much possible.

In contrast, animals hunted by humans (or dogs) often become sensitised and have greater FIDs and other disturbance responses (Forbes et al. 1994; Frid & Dill 2002; Stankowich & Blumstein 2005; Weston et al. 2012). For sensitisation to occur, the disturbance stimulus is generally infrequent, dangerous, irregular, rapid and unpredictable (Weston et al. 2012). New Zealand Dotterels have greater FIDs when a human is walking with a dog compared to an approach by a lone person (Lord et al. 2001). Dogs can catch and kill dotterels and their eggs, so pose a greater threat than humans. This altered behaviour therefore indicates sensitisation to dog disturbance stimuli (Burger 1981; Lord et al. 2001; Weston & Stankowich 2013). Snares Penguins (*Eudyptes robustus*) that had been exposed to invasive research and filming have an increased response to a human approach the following year, compared to naive penguins (Ellenberg et al. 2012). This infrequent (once per year or less), invasive and unpredictable disturbance stimuli appears to have caused sensitisation to human presence (Ellenberg et al. 2012). Yellow-eyed Penguins have higher baseline corticosterone levels, lower breeding success and lower fledging weights in tourist areas compared to undisturbed areas, indicating the populations have become highly sensitised to human disturbance stimuli (McClung et al. 2004; Ellenberg et al. 2007). In some cases, both habituation and sensitisation can occur in the same species in different areas; the Pacific Black Duck (*Anas superciliosa*) became habituated to

humans in urban areas where humans gave out food, and sensitised in rural areas where it was hunted (Weston et al. 2012).

Disturbance by researchers

It has been argued that researchers have less of an impact than tourists, because they behave in a less threatening way (for example, walking slowly and quietly) and are more able to read behavioural cues than tourists (Burger & Gochfeld 1993; Watson et al. 2014). The disturbance stimulus is also often more brief and involves smaller groups than tourism (Watson et al. 2014). However, a review of disturbance in Antarctica found that disturbance by researchers has negative physiological and population-level consequences on wildlife (Coetzee & Chown 2016). One key concern of disturbance by researchers is that this may invalidate the interpretation of results and the conclusions from studies (Coetzee & Chown 2016). For example, Culik et al. (1990) concluded that low breeding success observed in Adélie Penguins was caused by research activities and associated logistical support, rather than tourism.

Research often involves direct interventions such as tagging, fitting devices, weighing, taking samples, and can be much more invasive than tourism (Wilson et al. 1989a; Wilson et al. 1990; Engelhard et al. 2002; Coetzee & Chown 2016). This can cause considerable disturbance, and the impact of these activities needs to be considered with the same weight as all other forms of human disturbance stimuli (Wilson et al. 1989a; Giese 1996; Carney & Sydeman 1999). In Adélie Penguins, merely clipping 1 cm off their tail feathers caused penguins to stay at sea 50% longer than controls (Wilson et al. 1989a). Researcher disturbance has been shown in a number of bird species to reduce reproductive success, nest-site fidelity and increase pair divorce rates (e.g. Götmark 1992; Blackmer et al. 2004; Carey 2009, 2011). In isolated areas such as Antarctica and subantarctic islands, the logistical support associated with research can also cause considerable disturbance (Rounsevell & Binns 1991; Wilson et al. 1991; Giese & Riddle 1999; Hughes et al. 2008; Coetzee & Chown 2016). Helicopter disturbance stimuli on penguin colonies in particular has received attention in the

literature (**Table A.1**). For example, King Penguins in South Georgia reduce vocalisations and increase displacement behaviours and aggression during helicopter flights overhead (Hughes et al. 2008).

Are seabirds particularly vulnerable to disturbance?

Compared to mammals, birds in general appear to be at greater risk of disturbance impacts (Coetzee & Chown 2016). An animal is also arguably most vulnerable to disturbance stimuli when breeding, so visiting densely packed seabird colonies is likely to have a higher impact (in terms of both the number of individuals affected and the impact per individual) than other forms of disturbance stimuli. Seabird colonies are also easy to find, making them popular visitor attractions, and pedestrian visitation is common (Burger & Gochfeld 1993, 2007; Holmes 2007). Colonial seabirds nesting in open areas are therefore often subjected to disturbance from human activities, and are thought to be particularly vulnerable due to the exposed nature of their colonies (Carney & Sydeman 1999; Giese 1999; Holmes 2007). Small colonies may also be particularly vulnerable due to edge effects (Jackson et al. 2005). However, even burrowing seabird colonies (which are much less exposed) respond negatively to human disturbance stimuli (Ellenberg et al. 2006; Watson et al. 2014). Studies on seabirds and other waterbirds have shown responses to human activity vary between species, and also vary according to other factors such as the frequency of disturbance stimuli (Holmes et al. 2005; Walker et al. 2005; Walker et al. 2006), the disturbance type (Lord et al. 2001), breeding density (Hockey & Hallinan 1981), stage of breeding (Burger & Gochfeld 1993; Forbes et al. 1994; Yorio & Quintana 1996; Bolduc & Guillemette 2003), individual variability (de Villiers et al. 2005; Ellenberg et al. 2009) and food availability (Beale & Monaghan 2004b).

Table 2.1. Current published literature on behavioural, physiological and population-level impacts on wild penguins. Number of publications for each species is listed by the result - as either habituation (defined as a reduced response to disturbance stimuli following previous exposure), negative, or 'none detected' (where no statistically significant impact was detected). Literature is counted more than once where multiple responses or species are studied within one paper.

Response measured	Penguin Species	Number of publications		
		Habituation	Negative	None detected
Behavioural	Adelie	0	5	2
	African	2	1	0
	Chinstrap	0	2	0
	Emperor	0	2	1
	Fiordland Crested	0	1	0
	Gentoo	1	3	0
	King	0	3	0
	Little	0	1	0
	Macaroni	0	1	0
	Magellanic	6	0	0
	Rockhopper	0	0	1
	Royal	2	0	0
	Yellow-eyed	1	1	1
Physiological	Adelie	0	7	0
	Emperor	0	3	0
	Gentoo	1	0	1
	Humbolt	0	2	0
	King	1	5	0
	Little	0	2	0
	Magellanic	3	2	1
	Rockhopper	0	0	2
	Royal	0	1	0
	Snares	0	1	0
	Yellow-eyed	0	2	0
Breeding/population size	Adelie	0	10	7
	African	0	1	0
	Chinstrap	0	1	0
	Gentoo	0	3	3

Response measured	Penguin Species	Number of publications		
		Habituation	Negative	None detected
	King	0	3	0
	Humbolt	0	4	0
	Little	0	2	1
	Magellanic	1	2	1
	Rockhopper	0	0	1
	Royal	0	0	1
	Yellow-eyed	0	1	1

Penguin disturbance

Due to their charismatic nature and extensive presence in media (such as the film *Happy Feet*), penguin breeding colonies are popular tourist attractions (Aronson et al. 2011; Villanueva et al. 2012). The open, exposed nature of most penguin colonies also means they are particularly susceptible to human disturbance stimuli (Holmes 2007; Seddon & Ellenberg 2008). In addition, they have evolved with predators such as Skuas and Giant Petrels (*Macronectes giganteus*) and are therefore very defensive of their nests (De Villiers, 2008; Tin et al., 2008). They are also potentially vulnerable to disturbance stimuli outside the colony, when travelling from their nest to the sea (van Heezik & Seddon 1990; Burger & Gochfeld 2007; Seddon & Ellenberg 2008). Unlike other seabirds, they cannot simply fly away when disturbed, and must travel on the ground from their nest to the sea and vice versa, sometimes past tourists (Burger & Gochfeld 2007). The high level of philopatry in some species also makes them more vulnerable to population-level effects of disturbance, as they are less able to disperse to avoid the threat. However, their comparatively large body size and (for some species) few interactions with humans may mean they are generally less threatened by disturbance than other animal groups (Blumstein 2006).

The impact of disturbance on penguins has been intensively studied (72 publications to date), with tourism shown to have impacts on behaviour, physiology, breeding success and reproduction (**Table**

2.1). Penguin species have not been studied equally, with almost one third of all publications on Adélie Penguins (**Table 2.1**). Some penguin species have received very little attention, such as the Rockhopper Penguin (*E. chrysocome*) (four publications), African Penguin (three publications), Chinstrap Penguin (three publications), Fiordland Crested Penguin (*E. pachyrhynchus*) (one publication), Snares Crested Penguin (one publication) and the Macaroni Penguin (*E. chrysolophus*) (one publication) (**Table 2.1**). To my knowledge the Galápagos Penguin (*S. mendiculus*) and Erect-crested Penguin (*E. sclateri*) have had no research on disturbance effects at all. For some species such as the Fiordland and Snares Crested Penguin this lack of attention may simply reflect the lack of human disturbance stimuli the species are subjected to. However it is surprising that no research has been conducted on the Galápagos Penguin given tourists are likely to come into contact with them fairly regularly (they are advertised as an attraction on many tourism sites), and negative impacts of tourism have been observed in other Galápagos species (Burger & Gochfeld 1993; French et al. 2010).

There is also little consistency in results, both across and within species (**Table 2.1**). This indicates that disturbance in penguins is not only species-specific, but also site-specific and dependent on the type of disturbance stimulus (**Table 2.1**) (Trathan et al. 2008). Evidence of habituation has been found, but only in some penguins (**Table 2.1**). African Penguins and Magellanic Penguins seem particularly predisposed to habituation, whereas habituation has not been found in Adélie Penguins despite the large amount of research (**Table 2.1**). Evidence of sensitisation has also been found in Humboldt, Little Blue (*E. minor*) and Yellow-eyed Penguins (Ellenberg et al. 2006; Ellenberg et al. 2007). Even when subjected to the same type of disturbance stimuli, studies have found considerable interspecific variation in responses to human disturbance in penguins. For example, Holmes (2007) found Gentoo Penguins displayed significantly increased levels of vigilance in response to a human approach, which was not found in King or Royal Penguins (*E. schlegeli*) when they were exposed to the same disturbance stimuli.

Conclusions

Disturbance can be measured by studying behavioural, physiological and population-level responses. Behavioural responses are the most studied disturbance response (**Table 2.1**), and therefore the basis for most evidence-based management decisions aiming to reduce human impact, through managing human behaviour, restricting human access or other measures. However, the importance of behavioural responses can be hard to define. Physiological responses are more difficult and invasive to study, but may show responses that would not be apparent in behavioural studies, and vice versa. Like behavioural studies, the importance of short-term physiological changes can be hard to define. Population level responses provide an indication of the long-term impact of disturbance (or lack thereof), which is important for determining sustainability. However, these effects can be more difficult to detect than changes in behaviour or physiology, and often require expensive long-term studies. If data already exist, modelling can be used to predict outcomes of management scenarios. However, as discussed in Chapter 1 a key barrier to tourism management is a lack of available data on ecology, population biology and behaviour of the species, which would prevent effective modelling (Trave et al. 2017). As all responses provide a different perspective and all have strengths and weaknesses, ideally when determining the impact of disturbance on a species all three levels of response would be studied. However, this is rare (**Table 2.1**, see Villanueva et al. (2012) for an exception). As the response to disturbance stimuli can also be affected by a multitude of external factors, the experimental design of these studies is important. The results of disturbance studies should therefore be interpreted carefully, and not over-generalised to include species, areas, or disturbance types not included in the original experiment. Ideally, management decisions should be based on scientific studies specific to the management problem (i.e. the same species, disturbance type and area as the management problem).

Chapter 3:

**The Behavioural Consequences of
Human Disturbance on Subantarctic
Yellow-eyed Penguins (*Megadyptes
antipodes*)**



For formatting consistency throughout this thesis Chapter 3 appears as a modification of the original manuscript published in the journal Bird Conservation International.

Publication: French RK, Muller CM, Chilvers BL, Battley PF. 2018. Behavioural consequences of human disturbance on subantarctic Yellow-eyed Penguins (*Megadyptes antipodes*). Bird Conservation International (**in press**). <https://doi.org/10.1017/S0959270918000096>

Abstract

Human disturbance can have behavioural, physiological and population-level consequences on wildlife. Unregulated tourism is having a negative effect on the endangered Yellow-eyed Penguin *Megadyptes antipodes* on mainland New Zealand. Subantarctic Yellow-eyed Penguins are exposed to tourism on Enderby Island in the Auckland Islands group, 450 km south of New Zealand. Restrictions and guidelines for tourism are in place on Enderby Island, but there has been little study on the efficacy of these. We quantified behavioural responses of the Yellow-eyed Penguin on Enderby Island to human presence by documenting movement patterns and behaviour of penguins in the presence and absence of humans, through both controlled approaches and monitoring penguin behaviour in the presence of tourists. We used these data to model the effective approach distances for reducing disturbance. Human presence caused a significant drop in the probability of a successful transit to or from their nest, and significantly increased the time penguins spent alert and decreased the time spent preening. Modelling showed the distance from a human to a penguin is a significant predictor of the likelihood of a bird displaying disturbance behaviour, with the current minimum approach guideline of 5 m not sufficient for preventing disturbance. Our results indicate that the minimum approach guideline needs to be revised if the probability of disturbance is to be reduced. Modelling the appropriateness of minimum approach guidelines by predicting the probability of disturbance is a useful technique that could be applied to other species and systems. Worldwide, management guidelines need to be scientifically evaluated to ensure efficacy and cater for the more sensitive species affected.

Introduction

There is growing awareness that the physiology and behaviour of animals can be altered by seemingly innocuous human activities such as wildlife tourism (Bateman & Fleming 2017). Increasing popularity and economic importance of wildlife tourism has led to a growth in research on the effects of human disturbance on wildlife, and ways to manage disturbance (Tin et al. 2008). In particular, previously isolated areas such as Antarctica and the subantarctic are becoming more popular for wildlife tourism (Perterra et al. 2017). High endemism and pressures from threats such as climate change and fluctuating prey availability mean these locations are particularly vulnerable to negative effects of human disturbance (Trathan et al. 2008; Perterra et al. 2017). An absence of habituation opportunities due to limited contact with humans may also make subantarctic and Antarctic wildlife more sensitive to human disturbance. While many guidelines and rules in these locations are already in place to reduce disturbance, the reasoning behind, and scientific basis for, these guidelines is often limited or lacking.

Studies have shown sensitivity to human disturbance is species-specific, yet many guidelines do not cater for the most sensitive species in the area (Blumstein et al. 2005; Holmes 2007; Tin et al. 2008; Perterra et al. 2017). Providing a sound basis for these guidelines requires a quantification of the effects of human disturbance and documenting how changes in the nature of that disturbance may impact on the animal (Møller et al. 2014; Bateman & Fleming 2017). It is recognised that the best approaches to study these effects are evidence-based assessments and controlled approach studies to scientifically evaluate guidelines and assess the appropriateness of these guidelines for reducing disturbance (Holmes et al. 2005; Weston et al. 2012).

Human disturbance has been shown to have a negative impact on a number of penguin species, including Royal Penguin *Eudyptes schlegeli*, Magellanic Penguin *Spheniscus magellanicus*, Humboldt Penguin *S. humboldti*, African Penguin *S. demersus*, Gentoo Penguin *Pygoscelis papua*, Chinstrap Penguin *P. antarctica* and Adélie Penguin *P. adeliae* (e.g. van Heezik & Seddon 1990; Martín et al.

2004; Trathan et al. 2008; Lynch et al. 2010; Barbosa et al. 2013; Reyes-Arriagada et al. 2013; Villanueva et al. 2014). These studies looked at a variety of disturbance responses, including behaviour, heart rate, levels of stress hormones, colony distribution, juvenile survival, and population trends. From this research, it is clear the magnitude and consequences of human disturbance depend on a multitude of factors including species, the level and type of human disturbance and the amount of exposure the colony has previously had to humans, demonstrating a need for species-specific guidelines to reduce human disturbance.

The Yellow-eyed Penguin (*Megadyptes antipodes*, hōiho), is one of the rarest penguins in the world (Seddon et al. 2013). It is endemic to New Zealand, occurring only on the south-east coast of the South Island, Stewart Island, Codfish Island and in the New Zealand subantarctic on the Auckland Islands and Campbell Island (**Figure 3.1**) (McKinlay 2001). Classified as 'Endangered' by IUCN and the New Zealand Department of Conservation (Birdlife International 2017; Robertson et al. 2017), the population is estimated at less than 2,000 breeding pairs, with 60% of the population thought to occur in the subantarctic (McKinlay 2001). Studies on mainland Yellow-eyed Penguins have shown it is one of the most sensitive penguin species to human disturbance (McClung et al. 2004; Ellenberg et al. 2007; Ellenberg et al. 2009). The presence of tourists decreases the likelihood an adult will come ashore to their nest, increases transit times to and from the nest and increases the likelihood of nest abandonment (Wright 1998; Ellenberg et al. 2007). This delay increases the amount of food digested before regurgitation, resulting in less food available for the chicks (Wright 1998). Unregulated tourism has been shown to decrease juvenile survival in their first year as a result of lower fledging weights, affecting population recruitment (McClung et al. 2004). Tourist presence also has a direct effect on adult penguins, causing an increase in stress induced corticosterone concentrations, which, with prolonged or frequent disturbance, is likely to result in decreased adult fitness and survival (Ellenberg et al. 2007).

The subantarctic populations are considered separate management units to the mainland due to low levels of migration (Boessenkool et al. 2009a). Because of the isolation and practical difficulties of researching in the subantarctic, comparatively little is known about the population trends, breeding success and impact of threats on these colonies (Seddon et al. 2013). Enderby Island (part of the Auckland Island archipelago) is thought to have the highest density of Yellow-eyed Penguins in the world (Moore 1990). It is also the only place in the subantarctic where tourists regularly come into contact with Yellow-eyed Penguins (Department of Conservation 2016). The beach where tourists come ashore is in the area where a large proportion of the penguin population transit to and from the sea on foraging trips daily during summer. Restrictions and guidelines are already in place, and some of these are based on an observational study of Yellow-eyed Penguins and tourists on Enderby Island (Young 2009). The current minimum approach guideline for all wildlife there is a distance of 5 m, yet the appropriateness of this has never been scientifically validated. The behavioural impact of tourism on subantarctic Yellow-eyed Penguins has also never been quantified using an experimental approach. Despite this lack of knowledge on the current impact of tourism, in 2016 the number of tourists allowed per year on the island was increased from 600 to 1,100 and the number of people allowed on the island per day increased from 150 to 200 (Department of Conservation 1998, 2016).

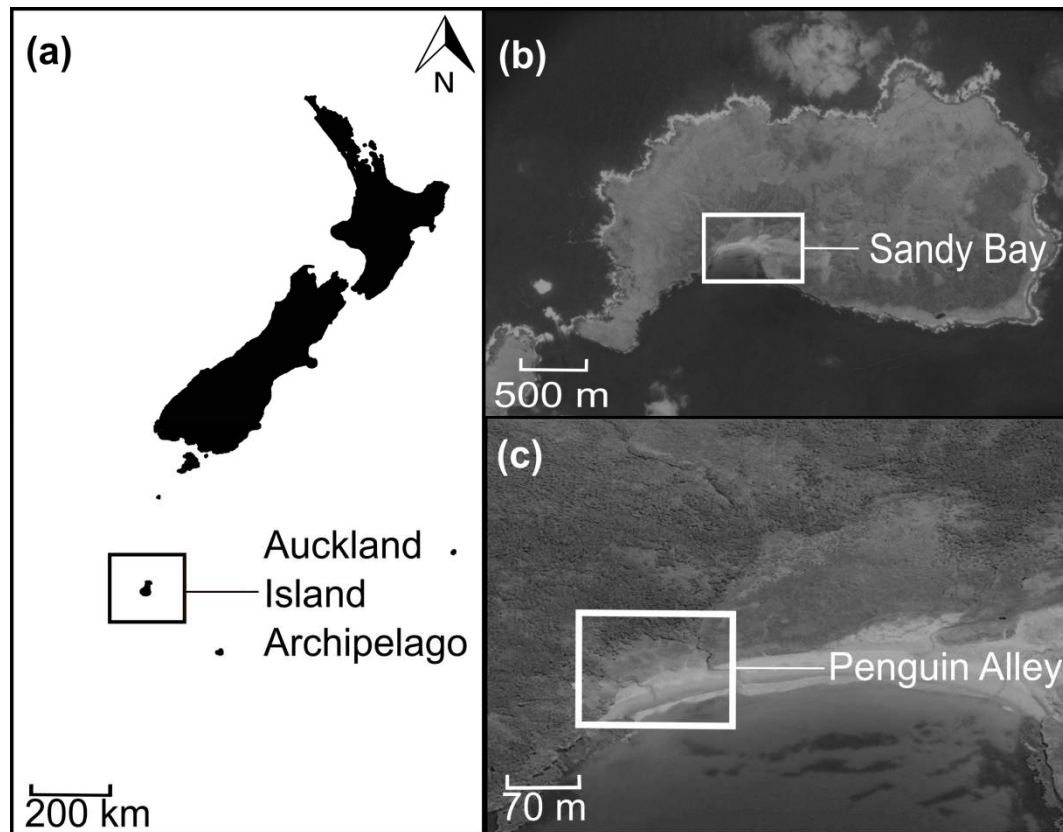


Figure 3.1. (A) New Zealand and New Zealand subantarctic islands. (B) Enderby Island. (C) Penguin Alley on Sandy Bay, Enderby Island

In this study we sought to evaluate the effectiveness of current approach guidelines in reducing disturbance to Yellow-eyed Penguins on Enderby Island. Disturbance responses can be challenging to measure without the research itself becoming a source of disturbance, particularly for a sensitive species such as the Yellow-Eyed Penguin. This study was conducted using behavioural measures only due to practical and ethical restrictions preventing the gathering of physiological data. This has some limitations; studies have shown physiological changes can occur without any measurable changes in behaviour, such as in Magellanic Penguin chicks (Walker et al. 2005). In our study it is therefore possible that physiological responses may occur even when no behavioural change is observed. Our results should thus be viewed as a minimum measure of disturbance effects. We quantified behavioural responses to human presence through controlled approaches and monitoring penguin behaviour in the presence and absence of tourists. Based on penguin behaviour and movement

data, we evaluate the appropriateness of the current minimum approach guidelines and determine more effective distances for tourists interacting with Yellow-eyed Penguins.

Methods

Fieldwork was conducted during the 2016–2017 breeding season (November – February) on Enderby Island, Auckland Island archipelago (50°29'45"S 166°17'44"E; **Figure 3.1**). The Yellow-eyed Penguin is non-colonial and nests under cover away from conspecifics (Seddon & Davis 1989). They begin to nest in August/September, in forest or dense scrub up to 1 km inland from shore (Darby & Seddon 1990). Normally two eggs are laid, which are incubated for between 39 and 51 days prior to hatching (Darby & Seddon 1990; Seddon et al. 2013). During the incubation and guard phase (September to January), both partners take it in turns to incubate the eggs and care for the young chicks, undertaking frequent foraging trips while their partner is guarding the nest (Seddon 1989). Hatching occurs in November/December. In the post-guard phase (January to March), both parents undertake foraging trips at the same time, and return for brief periods to the nest to feed the chicks (Darby & Seddon 1990). On Enderby Island, foraging trips begin and end with a transit through the forest and across the beach to get to the sea. This transit may involve contact with people and may also involve transiting through a New Zealand Sea Lion *Phocarctos hookeri* breeding area.

We collected all behavioural data at Penguin Alley, a section of Sandy Bay, Enderby Island, that is frequently used by penguins transiting to and from their nests and tourists arriving/departing and setting off/returning from walks on the island (**Figure 3.1**). Penguin Alley is currently the only area that has a penguin-specific restriction (the 'no stopping' rule), in addition to the 5 m minimum approach guideline that is applied across the subantarctic and across all species (Department of Conservation 2013).

Unlike on the New Zealand mainland, tourism in the subantarctic is highly regulated by the Department of Conservation. The main source of tourists is from cruise ships which visit Enderby at a rate of approximately one per week over part of the breeding season of the Yellow-eyed Penguin.

These vessels can hold between 50 and 200 tourists, who visit Enderby Island for one day per trip. During the 2016–2017 breeding season 12 tourist vessels visited Enderby Island at an average of one ship every nine days; at the peak period (early January) three ships visited in eight days.

Behavioural observations of penguin-tourist interactions

We used behavioural observations in the presence and absence of tourists to study the impact of tourist activity on the behaviour of penguins. We recorded behaviour of penguins, New Zealand Sea Lions and tourists using an ethogram adapted from a set of behaviours identified and previously used for similar projects on the mainland and on Enderby Island (Young 2009). Specifically, we recorded the following behaviours: walking (walking at a regular pace), preening (preening feathers, shaking head and/or stretching flippers out), alert (scanning or frequent head turning) and fleeing (also referred to as 'running highly alert', running stumbling, hopping or tobogganing at a fast pace). We recorded the start and stop times of each behaviour, so that a total time spent on each behaviour could be calculated. For example, 'time spent preening' is the total time a penguin (or penguins) spent preening during a transit. Adult and juvenile penguins were differentiated by the yellow crown present on adults but absent in juveniles (Darby & Seddon 1990). In addition, we recorded the distance between the penguin(s) and the tourist(s) where possible, using a digital rangefinder (Nikon Forestry 550), a compass to measure distance and angles to each target (human or penguin), and used trigonometry to calculate the unknown distance between the targets.

Controlled approaches

We carried out controlled approaches using a single observer, when tourists were not present. Approaches were limited to a 10-minute period every hour to minimise disturbance. Two different approaches were made:

- (i) A stationary approach where a single observer stood in the middle of Penguin Alley, so that the penguin(s) must approach the observer in order to transit across the sward.
- (ii) A moving approach, where a single observer moved slowly (approximately 0.5 m/s) towards the penguin(s) parallel to the shoreline and perpendicular to the penguin's line of travel.

When approaching, the observer used a laser range finder to measure the distance from them to the penguin(s) every 30 seconds or 5 m, including recording the distance when the penguin(s) was first disturbed. Another observer out of sight of the penguin(s) (not on Penguin Alley) recorded penguin behaviour using the ethogram mentioned above. Disturbance was defined as avoidance behaviour: either a change in direction of travel by more than 45 degrees away from the observer, or a change in the speed of travel from walking/stationary to fleeing. The time the penguin(s) was first sighted leaving a refuge (surf or forest) and the time the penguin(s) entered a refuge was recorded to calculate total transit time in the open. To investigate the impact of sea lion disturbance, we also recorded penguin-sea lion interactions on days when tourist-penguin interactions were being observed, or when controlled approaches were being undertaken. We also conducted a count of adult sea lions each observation day, where the whole of Sandy Bay was divided into five sections and the number of sea lions was counted using binoculars. In addition, we recorded the number of active sea lions (classed as active when doing any behaviours except resting) for every observation. These were used as covariates in the models described below.

Analysis

We used general linear models to analyse the continuous response variables (time spent alert, time preening, time walking and transit time). To meet the assumption of normality, all these response variables were log-transformed. We analysed disturbance type as a fixed factor with four levels: control (no disturbance), stationary (stationary controlled approach), moving (moving controlled approach) and tourist (observations of actual tourist-penguin interactions). The predictor variables

were treatment (a fixed factor with four levels), direction (whether the penguin(s) were leaving or returning from the nest), penguin group size, time (expressed as days since mean hatch date: 27 November), sea lion count and sea lion behaviour. Direction, group size, time and sea lion count were all consistently not significant and did not improve the fit of the models, so they were removed from the models. All continuous predictor variables were centred by subtracting the mean from each observation to avoid multicollinearity and to obtain meaningful odds ratios. We used a generalised linear model with binomial family and logit link for the binomial response variable 'outcome'. The transit was classed as successful if the penguin(s) completed the journey in the direction it was originally travelling. The moving approach was excluded from this analysis because the penguin(s) had to be half-way up the shore before the approach could begin. Fleeing behaviour was also expressed binomially and analysed in the same way. To model the optimum minimum approach distance, we used mixed generalized linear models for the binomial response variable 'disturbed' with the predictor variable being distance from penguin to human. The distance was recorded multiple times for each trial, so a trial was classed as a random effect and distance a fixed effect. We generated graphs in R studio, using 'ggplot2' (Wickham 2016, R Core Team 2017). Models were created using the R packages MASS and 'lme4' (Venables and Ripley 2013, Bates et al. 2015).

Results

Behaviour

We conducted a total of 95 controlled approaches (to groups of one or more penguins), 32 observations of penguin-tourist interactions and 81 observations where no humans were present (control). Human presence caused a significant drop in the probability of a successful transit compared to the control group for the stationary and tourist groups, from 0.99 (SE 0.01) for the control to 0.77 (0.06) and 0.76 (0.15) for the stationary and tourist groups respectively; $Z = -2.9$ and -2.8 , $P < 0.005$. The presence of an active sea lion caused a decrease in the probability of a successful transit from 0.99 (SE 0.01) with no active sea lion to 0.75 (0.09); $Z = -2.5$, $P = 0.01$. The probability of

a bird fleeing did not increase in the presence of a human, from 0.02 (SE 0.01) for the control to 0.05 (0.03) and 0.07 (0.04) for the stationary and tourist groups respectively $Z = 1.1$ and 1.3 , $P > 0.05$, but did increase in the presence of an active sea lion, from 0.02 (SE 0.01) for the control to 0.53 (SE 0.15) in the presence of an active sea lion; $Z = 5.9$, $P < 0.001$. Sea lion presence was not significant in any other models. The time spent alert increased with the stationary approach and in the presence of tourists ($t = 2.5$ and 5.3 , $P < 0.05$), as did time spent walking ($t = 3.2$ and 2.7 , $P < 0.01$). The time spent preening decreased with the moving approach and in the presence of tourists ($t = -4.0$ and -3.6 , $P < 0.001$). Moving human presence significantly decreased transit time ($t = -2.0$ $P = 0.04$), and tourist presence significantly increased transit time ($t = 2.1$ $P = 0.03$) compared to the control (**Figure 3.2**).

Minimum approach guideline

The distance from human to penguin had a significant effect on the likelihood of disturbance behaviour being displayed ($Z = -4.0$, $P < 0.001$, **Figure 3.3**). At the current minimum approach guideline (5 m), the probability of disturbance is 0.99 (99%). At 50 m the probability of disturbance drops to less than 0.03 (3%).

Tourist behaviour

A total of 32 penguin-tourist interactions were recorded. The distance between penguin and tourist was recorded for 18 of these interactions. The minimum distance tourists approached penguins ranged from 3 to 113 m, with a median minimum approach distance of 27 m. Thirty-nine percent of tourist groups approached Yellow-eyed Penguins to a distance of < 21 m (**Figure 3.4**). The mean group size was three tourists (SE 2.67).

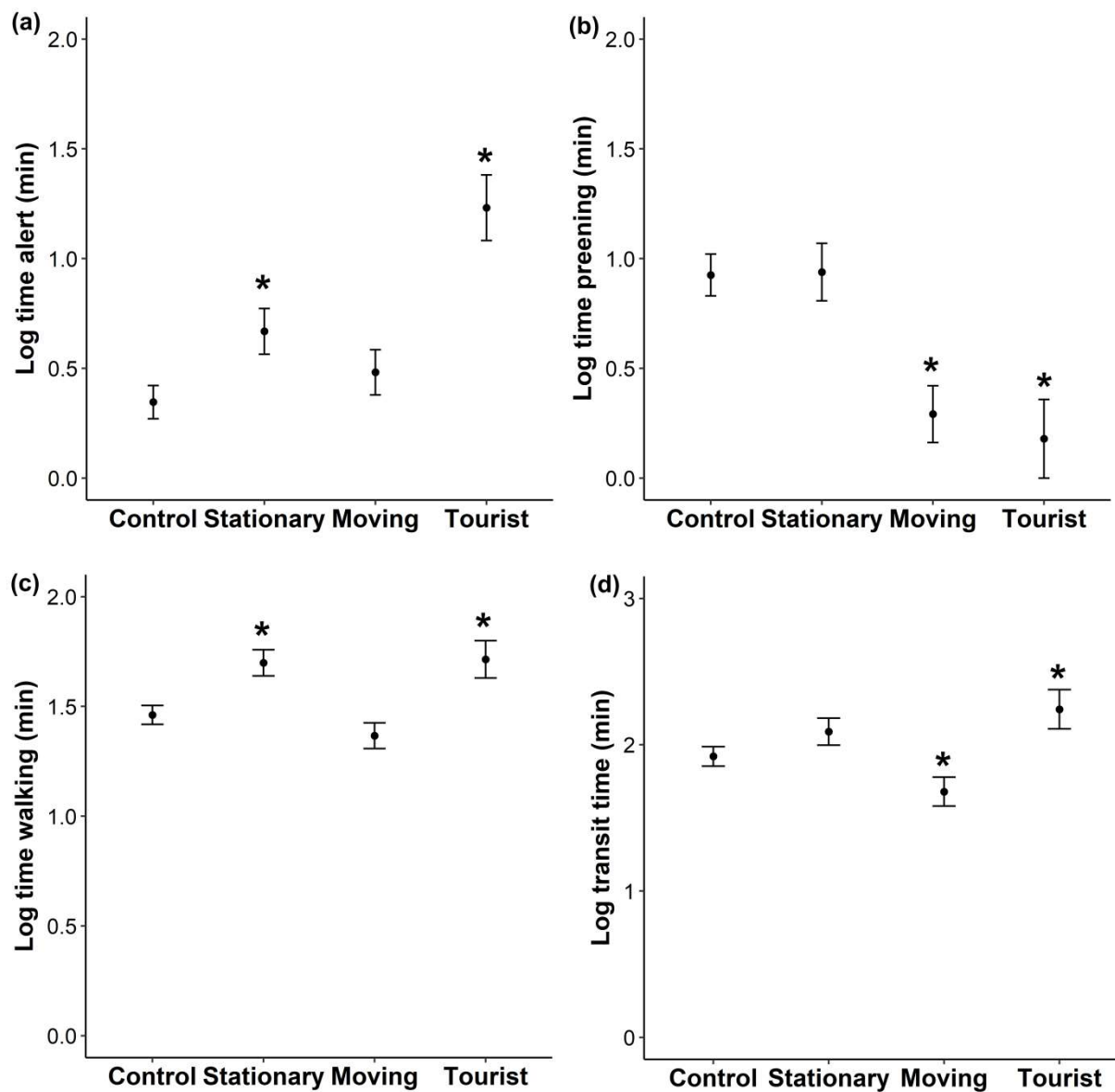


Figure 3.2. Effect of controlled approaches and tourist presence on behaviour of Yellow-eyed Penguins. Plots show (A) time spent alert, (B) time spent preening, (C) time spent walking and (D) transit time. Categories across the x-axes are when there is no human presence (Control), stationary human presence (Stationary), moving human presence (Moving) and in the presence of tourists (Tourist). Asterisk denotes significance from control. $n = 208$ for all comparisons.

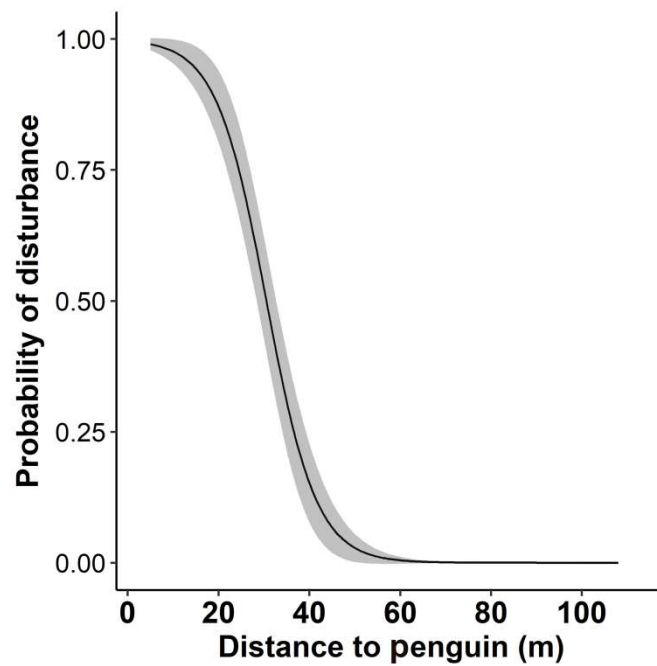


Figure 3.3. The probability of disturbance for Yellow-eyed Penguins as a function of approach distance by a human. The fitted line is from a generalized linear mixed model, grey shading is standard error; $n = 212$.

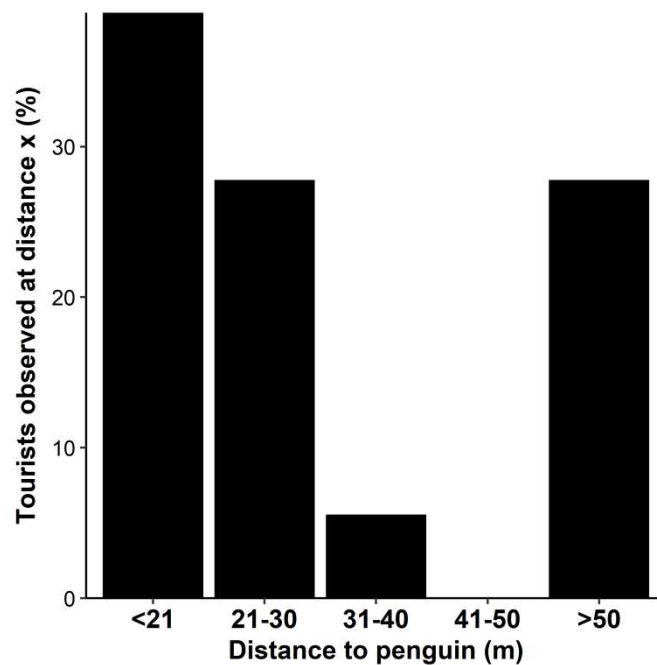


Figure 3.4. Percentage of tourists observed approaching to a minimum distance of < 21, 21–30, 31–40, 41–50 and > 50 m to a Yellow-eyed Penguin; $n = 18$.

Discussion

Our results showed that human presence on the beach on Enderby Island when Yellow-eyed Penguins were transiting caused the birds to alter their behaviour, and that the type of human presence had an impact on the nature of the behavioural change. The presence of a human caused the probability of a transit being successful to decrease, with around a fifth of the attempted transits being aborted when people were present. Transit times (in successful transits) decreased with the moving controlled approach by the observer, whereas they increased when a tourist group was present. This may be because the moving controlled approach caused an increase in speed towards the refuge (the forest or sea), whereas the tourist group often blocked the penguin(s) from the refuge. Nonetheless, both events result in a change of movement behaviour which is likely to be negative – the increased transit time results in less food regurgitated to the chicks and the decreased transit time may increase stress levels and energy expenditure (Wright 1998; Ellenberg et al. 2007).

Other behaviours were affected differently by stationary and moving controlled approaches. The stationary controlled approach resulted in an increase in the time spent alert, while the moving controlled approach resulted in a decrease in the time spent preening. Both may reflect a change in vigilance by the bird and a consequent change in alternative maintenance behaviours.

Consequences of disturbance

While increases or decreases in these behaviours may not be that important in themselves, they are a reflection of the behavioural impact of human presence, which may contribute to physiological or population-level changes. An increase in the time spent alert may indicate an increase in the levels of stress hormones (such as corticosterone). Increases in base-level corticosterone may, over the lifetime of the bird, decrease fitness and survival (Ellenberg et al. 2007). In Humboldt Penguins, alert

behaviour is correlated with an increase in stress hormones (Ellenberg et al. 2006). Alert behaviour is also a strong predictor of increased heart rate in Royal Penguins (Holmes et al. 2005).

Physiological data are difficult to collect in the wild and are one of the biggest gaps in understanding of wildlife tourism worldwide (Trave et al. 2017). There is evidence to suggest that behavioural changes do not always indicate a decrease in the health of the animal, physiological changes or population-level effects (Gill et al. 2001; Tarlow & Blumstein 2007). Conversely, physiological changes can occur as a result of human presence when no behavioural changes are observed (Beale & Monaghan 2004a; Bejder et al. 2009). Magellanic Penguin chicks exposed to humans showed evidence of lower behavioural responses to humans but higher physiological stress responses, compared to chicks not exposed to humans (Walker et al. 2005). However, as methods for gathering physiological data are often invasive and stressful themselves, it can be difficult to separate the effects of capture and sampling from the effects of tourist disturbance (Trave et al. 2017). It may also be more difficult to link specific physiological data (such as peaks in corticosterone) to specific behaviours or events. Other metrics including heavy metal levels, genotoxic damage and immunological responses can also be useful in determining human disturbance effects, as has been found in Gentoo Penguins when comparing disturbed and non-disturbed sites (Barbosa et al. 2013). The isolated and harsh conditions of the subantarctic make studying physiology extremely challenging, however several studies of mainland Yellow-eyed Penguins have shown higher base-level corticosterone at unregulated tourism sites, and an increase in heart rate of nesting birds when exposed to an approaching human (Ellenberg et al. 2007; Ellenberg et al. 2013). An increase in transit time and the number of aborted transits is likely to decrease the food available to chicks, which may lead to decreased fledgling weight. Studies on mainland Yellow-eyed Penguins have found lower fledging weights in areas of high levels of unregulated tourism (McClung et al. 2004; Ellenberg et al. 2007). Low fledging weight leads to decreased juvenile survival, meaning that lower fledging weights can have long-term population consequences (McClung et al. 2004). The increased number of aborted transits observed on Enderby Island could therefore have negative repercussions

for population recruitment. This effect has also been seen in other penguins: in Gentoo Penguins some sites frequently visited by tourists had a significant decline in breeding pairs, and in Humboldt Penguins, breeding success was found to be significantly reduced at tourist sites due to the foraging partner being prevented from returning to the nest and feeding the chicks (Ellenberg et al. 2006; Trathan et al. 2008).

Is habituation possible for Yellow-eyed Penguins?

The results of this study also indicate that sea lions may cause a similar level of disturbance to human presence. The endangered endemic New Zealand Sea Lion has a similar distribution to the Yellow-eyed Penguin, with 18% of pups born on Sandy Bay, Enderby Island (Childerhouse et al. 2017). These two species have co-existed on Enderby Island for thousands of years, indicating the Yellow-eyed Penguin is able to tolerate some level of disturbance (Collins et al. 2014). However, as this natural disturbance already exists penguins may be more vulnerable to additional disturbance by humans. By avoiding a human, they may also increase the likelihood of an interaction with a sea lion. Trade-off scenarios may also occur, where fleeing from a human then results in the penguin moving closer to an active sea lion. Trade-offs were found to affect fleeing behaviour in juvenile Chinstrap Penguins, where a trade-off existed between fleeing from the predator (a human) and entering a colony where they may be attacked by adults (Martín et al. 2004). Yellow-eyed Penguin behaviour in this study indicates a lack of habituation to sea lion behaviour, likely due to occasional land predation by sea lions (personal observation). New Zealand Sea Lions have also been shown to depredate Eastern Rockhopper Penguins (*E. chrysocome filholi*) on Campbell Island (Morrison et al. 2017). Some studies have shown habituation can have positive effects on the ability of the animal to adapt to the presence of human disturbance, by reducing stress levels and preventing negative changes in behaviour (Walker et al. 2005; Baudains & Lloyd 2007). The capability and degree of habituation appears to vary greatly among penguin species, for example there is evidence of behavioural and physiological habituation in Magellanic Penguins but not in Humboldt Penguins

(Ellenberg et al. 2006; Walker et al. 2006; Villanueva et al. 2012). As tourist visitation is infrequent and at low levels on Enderby Island, these penguins may not have had the opportunity to become habituated to humans. However, the lack of habituation by Yellow-eyed Penguins on mainland New Zealand (where the level of tourism is much higher and continuous year-round) indicates that habituation to tourism may not be possible. There is some evidence of habituation by Yellow-eyed Penguins to invasive research (including frequently approaching the nest and taking blood samples) (Ellenberg et al. 2009). However, this effect appears to be restricted to nest visits only, as Yellow-eyed Penguins exposed to unregulated tourism were observed to have a higher hormonal response than birds from undisturbed sites (Ellenberg et al. 2007).

Management implications

The results of this study indicate that human presence has an impact on behaviour of the subantarctic Yellow-eyed Penguin. This has also been found for the mainland Yellow-eyed Penguin (McClung et al. 2004; Ellenberg et al. 2007; Ellenberg et al. 2009) and other penguin species (e.g. Ellenberg et al. 2006; Villanueva et al. 2014). The mere presence of humans will have some behavioural impact on most species, so a key question which is often not addressed is what level of impact is considered acceptable (Trave et al. 2017). At one extreme, mortality or abandoned breeding attempts could result from disturbance, a far more serious impact than conservation managers would accept. Given the serious declines of Yellow-eyed Penguins on mainland New Zealand and the suite of stressors faced by birds there, a precautionary approach should be taken with the subantarctic population to prevent a similar decline (Boessenkool et al. 2010; Seddon et al. 2013). One approach could be to prevent all visible signs of disturbance, such as alert and avoidance behaviour, as has been proposed for Royal Penguins (Holmes et al. 2005).

On Enderby Island, tourists approached to a median minimum distance of 27 m, where the probability of disturbance is 0.65, and 39% of tourists approached to a minimum distance of < 21 m,

where the probability of disturbance is > 0.87 (see **Figure 3.3**). At the current minimum approach distance (5 m), the probability of disturbance is 0.99. These disturbance probabilities imply that a new minimum approach guideline is warranted. Due to the small size of the area (the length of penguin alley is approximately 70 m), reducing the probability of disturbance to near-zero (a distance of c. 50 m) may be impractical, but our results can help managers to decide on and justify a distance that is acceptable. At 40 m for example, the probability of disturbance is still low (0.15) so this distance may be an acceptable compromise between minimising disturbance and practical limitations.

To our knowledge this is the first research using controlled approaches on transiting Yellow-eyed Penguins, and the first research to evaluate minimum approach guidelines. There are many minimum approach guidelines for mainland breeding sites of the Yellow-eyed Penguin. However, to our knowledge none of these guidelines has been based on controlled approach experiments, and none has been tested for appropriateness. There is a clear need for a scientifically-validated minimum approach guideline that caters for sensitive species such as the Yellow-eyed Penguin.

The minimum approach modelling conducted in this study was based on experimental approaches, which was a single observer quietly and slowly approaching. In general, tourist groups are likely to be larger in numbers and noisier. Different movement behaviours can affect the magnitude of disturbance, such as walking and jogging (Lethlean et al. 2017; Radkovic et al. 2017). Group sizes can also have an effect; it has been shown in other colonial seabirds (Kittiwake *Rissa tridactyla* and Guillemot *Uria aalge*) that the effects of disturbance increase with numbers of visitors (Beale & Monaghan 2004b). The behavioural results from this study concur: observations of penguin behaviour in the presence of tourists (with an average group size of three) showed a greater reaction (more time alert, less time preening) than during the experimental approaches by a single observer. Therefore, the minimum approach modelling is likely to be an underestimate of the actual reaction a penguin may have in the presence of a group of tourists.

Researchers also visit the island for weeks to months at a time and have done so annually for at least the last 25 years. Like tourists, they follow the 'minimum impact code' so are bound by the same guidelines and restrictions as tourists when not conducting research (Department of Conservation 2013). All research is also subject to the New Zealand Department of Conservation and animal ethics approval. While researchers are in lower numbers than tourists and may be expected to behave differently and have a lesser impact (Stein et al. 2017), they have a constant presence throughout a large portion of the Yellow-eyed Penguin breeding season. In particular, New Zealand Sea Lion researchers must cross penguin alley multiple times each day to access the sea lion breeding area. It has been shown with mainland New Zealand Yellow-eyed Penguins that researcher disturbance at nests has no short- or long-term effects on breeding success or lifetime reproductive success (Stein et al. 2017). However, researchers on Enderby Island would mostly be disturbing penguins in a similar way to tourists (i.e. on their transit rather than at their nest). Therefore, researcher impact must not be ignored by policy makers when considering the number of people visiting the island and activities conducted.

Recommendations

Properly managed tourism can be effective at reducing the negative impacts of human disturbance (Trave et al. 2017). Tourism in the New Zealand subantarctic is presently at low levels, so the current effect is likely to be low. However, the negative impact of human presence shown in this study indicates the importance of minimising the number of human-penguin interactions. This can be done by keeping the total number of tourists visiting the island to low levels, regulating the timing of tour boats landing and departing to avoid peak penguin activity, and limiting the number of tourists ashore at one time. In addition, regulations such as a suitable minimum approach distance are important for reducing the disturbance during a penguin-human interaction. Modelling from this study indicates the current guideline needs to be revised from 5 m to ensure disturbance is minimised. Modelling the appropriateness of minimum approach guidelines by predicting the

probability of disturbance is a useful technique that could be applied to other species and systems.

With the number of participants in wildlife tourism worldwide expected to double in the next 50 years (French et al. 2011), regulations and guidelines with a scientific basis will become more important than ever for reducing human disturbance in wildlife.

Chapter 4:

Breeding Biology of Subantarctic

Yellow-eyed Penguins in Areas of High

and Low Levels of Human Disturbance



Abstract

To effectively manage bird populations, understanding population parameters such as nesting success, reproductive output and fledgling health are essential. However, there is often a bias towards populations that are easy to access or study, resulting in underinformed management decisions for understudied populations. The endemic Yellow-eyed Penguin (*Megadyptes antipodes*) is one of the rarest penguins in the world, occurring only on the south-east coast of the South Island/Te Wai Pounamu, Stewart Island/Rakiura, Codfish Island/Whenua Hou and in the New Zealand subantarctic on the Auckland Islands/Motu Maha and Campbell Island/Motu Ihupuku. Because of the isolation and practical difficulties of undertaking research in the subantarctic, comparatively little is known about the population trends, breeding success and impact of threats on these colonies. In this study I report for the first time a detailed study of Yellow-eyed Penguin breeding biology on Enderby Island (Auckland Islands group, 450 km south of New Zealand). I studied the breeding success, fledging body size and fledging weight of penguins in areas with and without disturbance of adults when leaving/returning to the island from the sea, and present other aspects of their ecology such as nesting habitat and brood-size, and the effect this may have on reproductive output. I found a strong significant effect of brood-size on fledging weight and fledging body size, with chicks from single-brood nests weighing significantly more and being significantly smaller than chicks from double brood nests (across both the disturbed and undisturbed sites, with no difference between sites). There was no difference in nesting success (expressed as eggs, chicks and fledglings per pair) between the disturbed and undisturbed site and no significant difference in the average weight and body size of fledglings at the disturbed site compared to fledglings at the undisturbed site. These results indicate the current level of disturbance caused by humans and New Zealand Sea Lions at Enderby Island may not be having an impact on the breeding success of Yellow-eyed Penguins. The highly regulated nature of tourism of Enderby Island may therefore be an example of sustainable eco-tourism and successful management, although more research including multi-year studies would be needed to confirm this.

Introduction

It is vital to understand population parameters such as nesting success, reproductive output and fledgling health to successfully manage bird populations (Armstrong et al. 2002). They can be used to study the resilience of a population to threats such as human disturbance and food quantity or quality, or to determine the effectiveness of management and help make informed management decisions (Williams & Croxall 1990). An understanding of the breeding biology of a population is also essential for long-term monitoring, and determining population change (Miller et al. 2017). However, breeding biology can be time consuming and expensive to study, particularly in isolated areas such as the subantarctic, and for cryptic species (Innes et al. 1999). Often this results in a bias towards populations that are easy to access or study, and uninformed management decisions for understudied populations (Trathan et al. 2015).

The Yellow-eyed Penguin (*Megadyptes antipodes*, hōiho) is endemic to New Zealand, and classified as endangered by the IUCN and the New Zealand Department of Conservation (Birdlife International 2017; Robertson et al. 2017). It occurs only on the south-east coast of the South Island/Te Wai Pounamu, Stewart Island/Rakiura, Codfish Island/Whenua Hou and in the New Zealand subantarctic on the Auckland Islands/Motu Maha and Campbell Island/Motu Ihupuku (**Figure 4.1**) (McKinlay 2001). The population is estimated at less than 2000 breeding pairs, with 60% of the population thought to occur in the subantarctic (McKinlay 2001). The well-monitored mainland populations have suffered adult mortality events, high chick mortality and nest failure as well as low recruitment and high fluctuations in population size, with grave concerns for their future (Seddon et al. 2013).

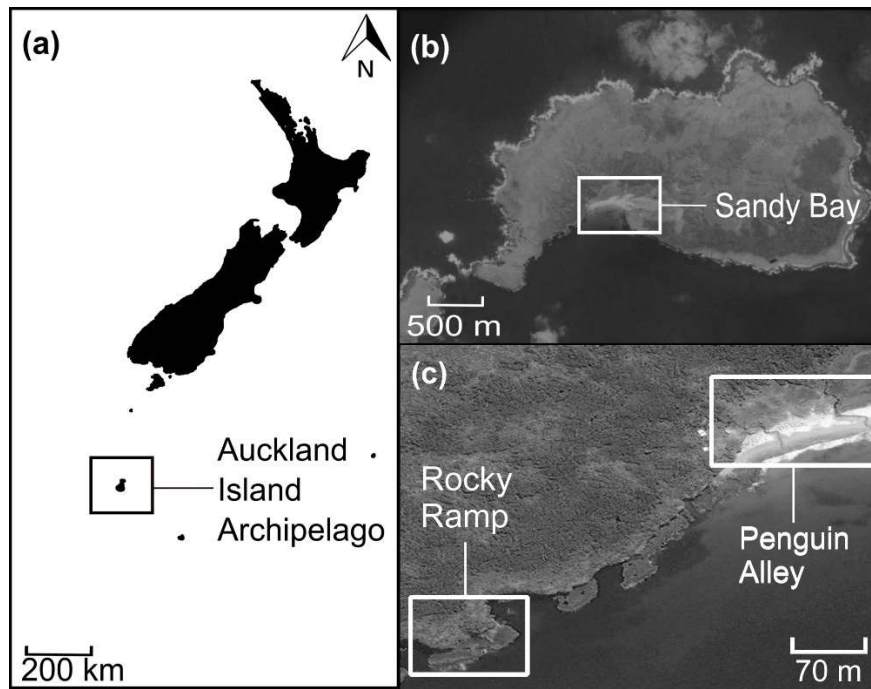


Figure 4.1. (A) New Zealand and New Zealand subantarctic islands. (B) Enderby Island. (C) Rocky Ramp and Penguin Alley (part of Sandy Bay).

The subantarctic and mainland populations are genetically and geographically distinct (Boessenkool et al. 2009b). Low levels of migration mean these populations are expected to remain distinct, and thus the subantarctic populations are considered separate management units to mainland New Zealand (Boessenkool et al. 2009b). This may mean that population trends, reproductive output and nesting success observed on mainland New Zealand are not the same as those occurring in the subantarctic population (Seddon et al. 2013), and therefore separate monitoring and research for each management unit is required for effective conservation of the species.

However, due to the isolation and practical difficulties of researching in the subantarctic there has been little research on the population trends, breeding success and impact of threats on these colonies (Seddon et al. 2013). The only comprehensive study of Yellow-eyed Penguin breeding biology in the subantarctic was over 30 years ago, on Campbell Island, finding a low chick mortality rate (15%) and high nest success rate compared to mainland New Zealand (Moore 1992a).

It is thought that Enderby Island (50°29'45"S 166°17'44"E, in the Auckland Island archipelago, **Figure 4.1**) has the highest density of Yellow-eyed Penguins in the world (Moore 1990). However, the only research on breeding success conducted on Enderby Island was a study of chick mortality in 2007/2008 (Argilla et al. 2013). In contrast to the findings of Moore (1992a), high chick mortality rates were observed (over 50%), attributed to starvation and possibly sub-clinical effects of *Leucocytozoon*, an avian haemoparasite (Argilla et al. 2013). Human disturbance from tourists was also hypothesised to have played a role in the high mortality rates observed in the 2007/2008 season (Young 2009). Despite the high levels of chick mortality recorded, breeding success has not been studied in the subantarctic since 2008. In addition, subantarctic Yellow-eyed Penguin chicks have never been monitored up to fledging, or weighed at fledging, so the condition of live chicks beyond a few weeks of age on Enderby Island is unknown. Fledging weight is an important metric used in mainland New Zealand to predict the ability of the chick to survive post-fledging, and therefore can be an indicator of population recruitment (McClung et al. 2004).

On mainland New Zealand, nesting success and fledging weights have also been used as an indicator of the impacts of human disturbance, by comparing reproductive output and fledging weights between sites of high and low disturbance stimuli (McClung et al. 2004; Ellenberg et al. 2007). These and other studies on mainland Yellow-eyed Penguins have also shown it to be one of the most sensitive penguin species to human disturbance stimuli (McClung et al. 2004; Ellenberg et al. 2007; Ellenberg et al. 2009). Behavioural studies have shown that human presence on Sandy Bay, Enderby Island significantly increases alert behaviour and the probability of an aborted beach transit (Chapter 3; Young 2009). However, the potential impact of this change in behaviour on breeding success and reproductive output has never been studied. Despite this lack of knowledge on the current impact of tourism (and the importance of the Enderby Island population for the species), in 2016 the number of tourists allowed per year on the island was increased from 600 to 1100 (Department of Conservation 1998, 2016). The number of visitors allowed on the island per day has also been increased from 150 to 200 (Department of Conservation 1998, 2016).

On the south-west coast of Enderby Island there are two key land-sea access points used by Yellow-eyed Penguins transiting between their nest site and foraging areas in the ocean (Houston & Thompson 2013). The first access point is Sandy Bay, a large sandy beach with a grassy sward area directly behind. In this bay tourists have relatively free access to the sward area behind the beach, and often interact with penguins in 'Penguin Alley'. Penguin Alley is an area between two streams that most tourists cross to get to the boardwalk, and where large numbers of penguins transit to and from the sea (**Figure 4.1**). There is also a breeding colony of New Zealand Sea Lion (*Phocarctos hookeri*) present on the beach and sward from December until March (Chilvers et al. 2007). Penguins that exclusively use this access point are therefore regularly exposed to tourist and sea lion activity. The other access point is a rocky slope leading directly into the forest, called 'Rocky Ramp' (west of Sandy Bay). This access point is not accessible to tourists, and there is virtually no sea lion activity in this nesting area. Therefore, birds that exclusively use Rocky Ramp are not exposed to tourist or sea lion activity. There is a small chance that penguins from Rocky Ramp (as well as those from Sandy Bay) are occasionally exposed to disturbance at sea when a boat is anchored in Sandy Bay. However, if this does occur it would be at the same rate for penguins from both sites, and much less frequent than the disturbance Sandy Bay penguins are exposed to on land.

For the purposes of this study, I treat penguins that habitually use Sandy Bay for access to and from the sea as being in a disturbed site, and those that use Rocky Ramp habitually as being in an undisturbed site. Data from the automatic microchip reader situated at Rocky Ramp showed penguins microchipped in the Sandy Bay site did not use the Rocky Ramp access point, indicating they display fidelity to one access point (Chris Muller pers. comm). There is little land predation at nests on Enderby Island, with no introduced mammals. Brown Skua (*Catharacta antarcticus*) may occasionally predate penguin nests, but this appears to be very rare as they do not enter the forest or scrub areas (pers. obs.). Therefore, the predator environment at the two sites is similar. Preliminary GPS data indicates penguins from both sites forage in the same location (Chris Muller pers. comm), indicating they are essentially one population with two access points to the sea.

In this study I report a detailed study of Enderby Island Yellow-eyed Penguin breeding biology, for the 2016/17 season. Concurrently, I also studied for the first time the effect of disturbance on breeding success, fledging body size and fledging weight (by comparing nests and fledglings from Sandy Bay and Rocky Ramp) and examined environmental effects such as habitat and brood-size on reproductive output. I compare these results to the well-studied mainland Yellow-eyed Penguin populations (Roberts & Roberts 1973; Seddon 1989; Seddon & Davis 1989; Darby & Seddon 1990; van Heezik & Davis 1990; Ratz & Thompson 1999; McClung et al. 2004; Ellenberg et al. 2007; Ellenberg et al. 2009; Stein et al. 2017).

Methods

Fieldwork was conducted during the 2016–17 breeding season (November – February) on Enderby Island, Auckland Island archipelago (**Figure 4.1**). The Yellow-eyed Penguin begins to nest in August/September, nesting away from conspecifics under forest or dense scrub up to 1 km away from the shore (Darby & Seddon 1990). One or (usually) two eggs are laid, which are incubated for between 39 and 51 days before hatching in November/December (Darby & Seddon 1990; Seddon et al. 2013). Between September and January the parents take it in turns to incubate the eggs or chicks and undertake foraging trips (known as the incubation and guard phases). From January to March both parents undertake foraging trips simultaneously, returning only briefly to feed their chicks before heading out to sea again (known as the post-guard phase) (Darby & Seddon 1990). The chicks fledge between late January and March. In the well-studied mainland Yellow-eyed Penguin populations, juvenile survival and population recruitment is low (between <10% and 60% probability of surviving 1–2 years post fledging, depending on fledging weight) (McClung et al. 2004).

From 18 November 2016 the areas behind Rocky Ramp and Sandy Bay were searched for Yellow-eyed Penguin nests. For each nest found the GPS position was noted, the adult was scanned for a microchip and the contents of the nest are checked. 83% of adult penguins were microchipped.

Penguins at both sites were exposed to a similar level of researcher disturbance, which was kept to a minimum.

The habitat of each nest was recorded, according to classifications used by Seddon and Davis (1989), with scrub being woody vegetation dominated by shrubs (stem <10 cm in diameter), and forest being woody vegetation dominated by trees (stem >10 cm diameter). Overhead nest cover (the percentage cover directly above the nest) and the degree of cover surrounding the nest were also visually estimated. An automatic microchip reader placed at Rocky Ramp determined which of the two access points (Rocky Ramp and Sandy Bay) the birds from each nest were using. As there is no other access point in the Sandy bay area, if the bird is not detected at Rocky Ramp it can be assumed to be using the Sandy Bay access point. The majority of nests had both partners using the same access point exclusively. Hybrid nests (where one parent used Rocky Ramp and one Sandy Bay, n=4) were excluded from analyses comparing the two sites.

To obtain accurate hatch dates for as many nests as possible, the status of the nests was checked every three to eight days. Chicks not observed hatching were aged by appearance as per Darby and Seddon (1990); van Heezik and Davis (1990) (**Table 4.1**). As the nests were visited frequently, even when a chick was seen at more than three days old the hatch date could be approximately determined based on when the nest was last seen with eggs. In this case, the median of the range of dates was selected as the approximate hatch date. Hatch dates could not be determined for nests that were first found with chicks aged at three or more days old.

Table 4.1. Estimated age based on chick appearance, used to determine hatch dates. Based on previous research (Darby & Seddon 1990; van Heezik & Davis 1990).

Chick appearance	Estimated age
Wet feathers, eyes closed	1 day
Dry feathers, eyes closed	2 days
Dry feathers, eyes partially open	3 days
Dry feathers, eyes fully open	3+ days

To reduce the possibility of disturbance by researchers once the chicks had hatched, nest visits were decreased to twice a month in December and January, to monitor chick mortality and nest failure. From 1st – 17th February, 129 fledglings (48 from Sandy Bay, 81 from Rocky Ramp) were weighed and measured. The measurements were skull length (from the bulge of the occipital condyle to the tip of the culmen) and foot length (tarsus plus the middle toe, not including the claw) (van Heezik & Davis 1990). The number of ticks attached to skin was counted. Chicks were weighed and measured at an average age of 71 days old (range 60–85), but due to logistical reasons most at Sandy Bay were weighed approximately five days earlier than Rocky Ramp nests. To correct for potential bias created by the date the chicks were weighed and measured, the slope of the linear regression line for the relationship between fledging weight or fledging skull length versus date at each site was determined (**Figure 4.2**). Where there was a significant change in size with date, measures were standardised to the mean date (6th of February). As there was no relationship between measure date and foot length for either site (**Table 4.2**) foot length was not corrected for date.

Table 4.2. Linear regression equations, p-values and R-squared values for fledging weight, skull length and foot length at the undisturbed site (Rocky Ramp) and the disturbed site (Sandy Bay).

Measurement	Site	Linear regression	p-value	R ² value
Weight	Rocky Ramp	$y = 0.026x + 4.506$	0.262	0.016
	Sandy Bay	$y = 0.089x + 4.211$	0.031	0.099
Skull length	Rocky Ramp	$y = 0.154x + 127.45$	0.324	0.010
	Sandy Bay	$y = 0.813x + 123.38$	0.004	0.171
Foot length	Rocky Ramp	$y = -0.009x + 127.14$	0.949	<0.001
	Sandy Bay	$y = -0.180x + 128.465$	0.580	0.007

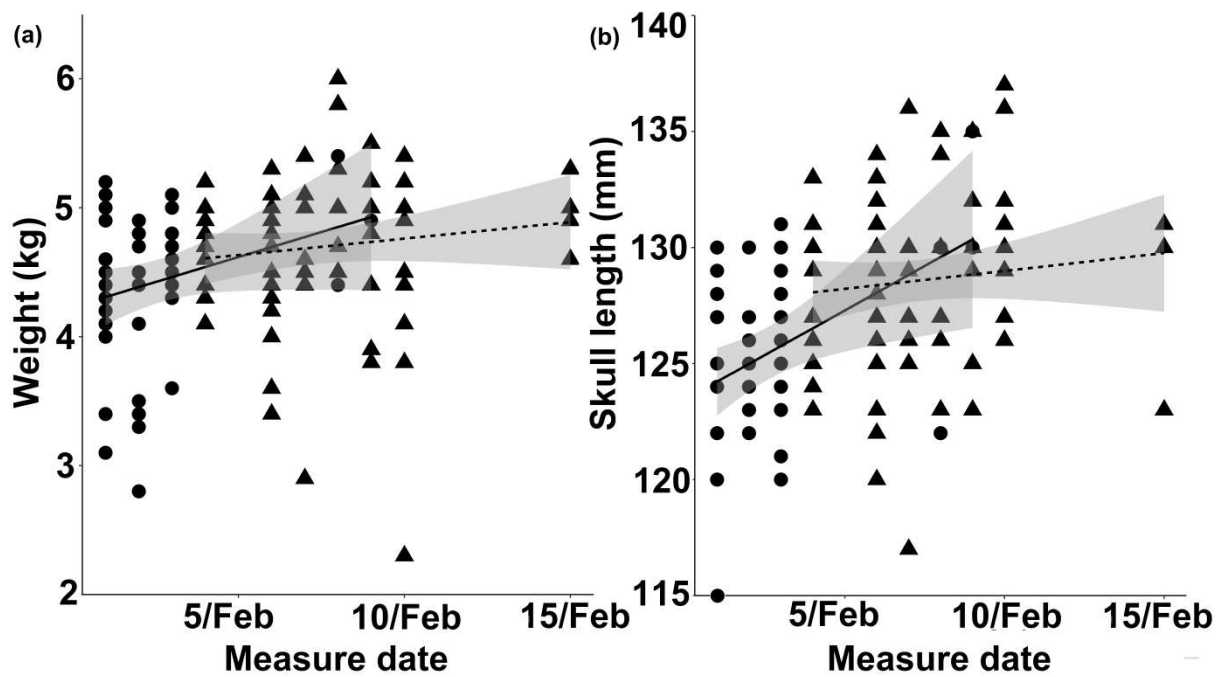


Figure 4.2. The relationship between fledging (a) weight (kg) and (b) skull length (mm) and the date they were measured, with a linear regression fitted for each site individually (solid line = Sandy Bay, dotted line = Rocky Ramp). Circle = fledglings from Sandy Bay, triangle = fledglings from Rocky Ramp

For chicks with known hatch dates, the relationship between fledging weight, skull length, foot length and age could be modelled. This produced similar results to **Figure 4.2**. Measure date was used to make the correction instead of age because it allowed fledglings without known hatch dates to be used in the analysis, thereby increasing the sample size considerably.

Analysis

The effects of site on fledging weights and sizes were analysed using linear mixed effect models, with the following predictor variables: brood-size (fixed factor with 2 levels – 1 chick and 2 chicks per nest), site (fixed factor with 2 levels – Rocky Ramp and Sandy Bay), habitat (fixed factor with 2 levels – scrub and forest), overhead nest cover (fixed effect), fledging body size (fixed effect, when analysing fledging weight as the response variable), fledging weight (fixed effect, when analysing fledging size as the response variable) and nest ID (random effect). Nest ID was added as a random

effect with a random intercept to avoid pseudo-replication in two-chick nests. A random slope model was not used because there were not enough observations to support the model. Brood-size was originally split into three levels – 2 chicks per nest, 1 chick per nest from hatching (where only one egg hatched), and 1 chick per nest at fledging (where either only one egg hatched or two chicks hatched and one died) – however there was no difference between the two single-chick categories so they were pooled.

Fledging body size is the first principle component from a principle component analysis with two variables: skull length and foot length. Principle component analysis was conducted to create a better overall measure of size than using each measurement individually or adding the measurements together (which is useful for sexing adult Yellow-eyed Penguins (Setiawan et al. 2004)). Axis 1 provided a general measure of size (loadings = 0.80 for both skull length and foot length) and accounted for the most variation (62%), whereas axis 2 represented a measure of proportional differences between the two size measures (loadings = -0.61 for skull length, 0.61 for foot length), and accounted for less variation (37%). Therefore, the first component of the PCA (axis 1) was used as a measure of size in the subsequent analyses. Interactions were only retained when they significantly improved the model. Models were compared using likelihood ratio tests, and AICc scores.

The numbers of eggs, chicks and fledglings were analysed as count data using generalised linear models with a poisson family and log link, using the same predictor variables as described above. Hatch date (fixed effect) was tested as a predictor variable but was not significant and did not improve the AICc score so was removed from the models. Unlike in the models above (where all chicks were included in the analysis), only nests with hatch dates were included to avoid bias towards successful nests. This is because successful nests are considerably easier to find after hatching than failed nests due to smell and noise (Armstrong et al. 2002).

Analyses were conducted in R studio (R Core Team 2017). The mixed linear models were analysed using the R package lme4, and graphs were made using ggplot2, and ggbiplot (Wickham 2009; Vu 2011; Bates et al. 2015).

Results

Ninety-one nests were found – 31 at Sandy Bay, 51 at Rocky Ramp, 4 hybrid nests and 5 where the landing site used by the adults was unknown. Forty-nine of these were found early enough to be monitored throughout the season. As I did not conduct a complete search of the area, this number should not be interpreted as a population estimate. Sixty-eight nests (75%) were located in the scrub, and 23 (25%) were located in the forest. The percentage of overhead cover ranged from 0–100%, with an average of 57% cover (\pm SE 3.30, **Figure 4.3**). The back and roof of the nests were commonly *Hebe spp.*, but many were also under ferns (*Polystichum vestitum*, *Asplenium scleroprium*, or *Blechnum durum*), juvenile and adult rātā (*Metrosideros umbellata*) and *Myrsine divaricata* (**Figure 4.4**).

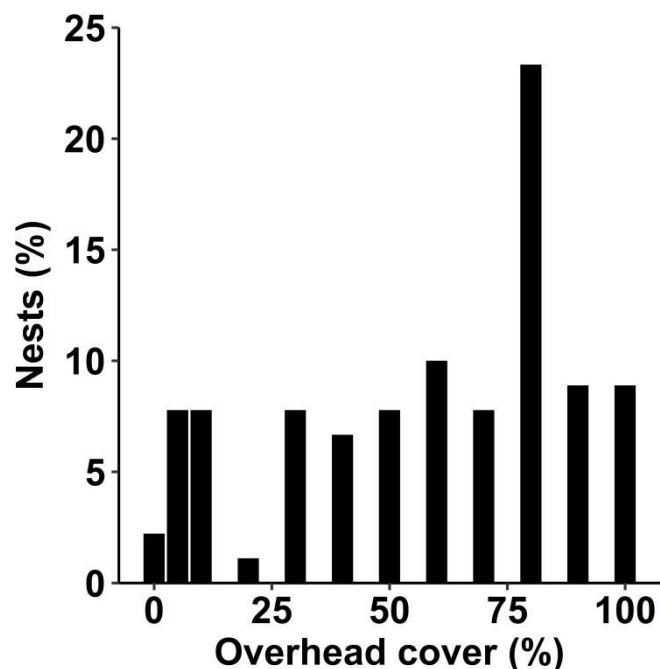


Figure 4.3. Percentage overhead cover of nests, n=90.

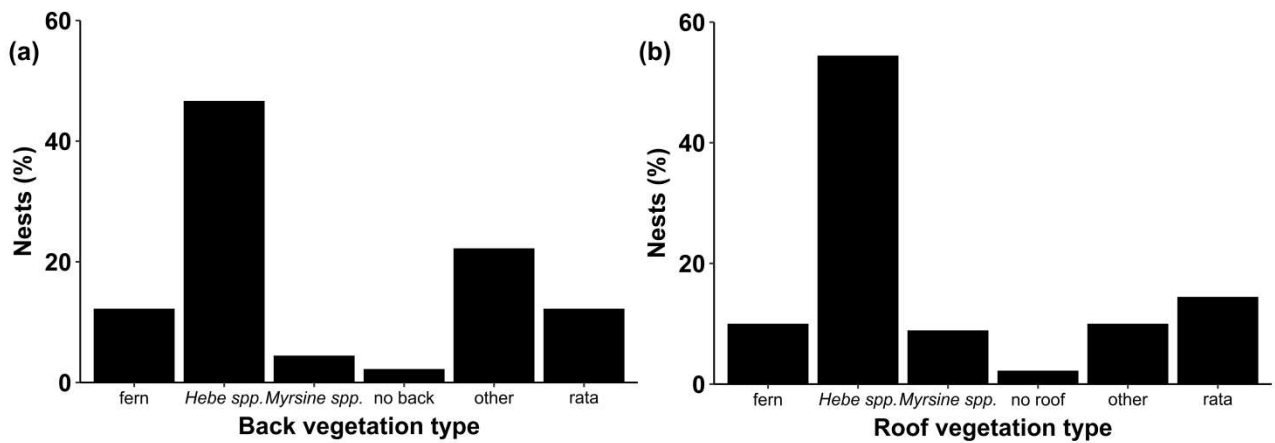


Figure 4.4. (a) Back and (b) roof vegetation type of nests as a percentage. 'Fern ' refers to *Polystichum vestitum*, *Asplenium scleroprium*, or *Blechnum durum*. 'Rata' refers to the Southern rātā *Metrosideros umbellata*. 'Other' included objects other than vegetation such as earth and tree logs, and also plants such as reeds and grasses, *Anisotome latifolia* and *Dracophyllum spp.* n=90.

Of the 49 nests monitored throughout the season, most pairs (90%) laid two eggs. Six nests (12%) failed at the egg stage, where both eggs failed to hatch. In total, 15 eggs failed to hatch out of 93 eggs laid (16%, **Table 4.3**). Hatch dates ranged from 18 November to 4 December, with a mean hatch date of 27 November (\pm SE 0.43 days, **Figure 4.5**).

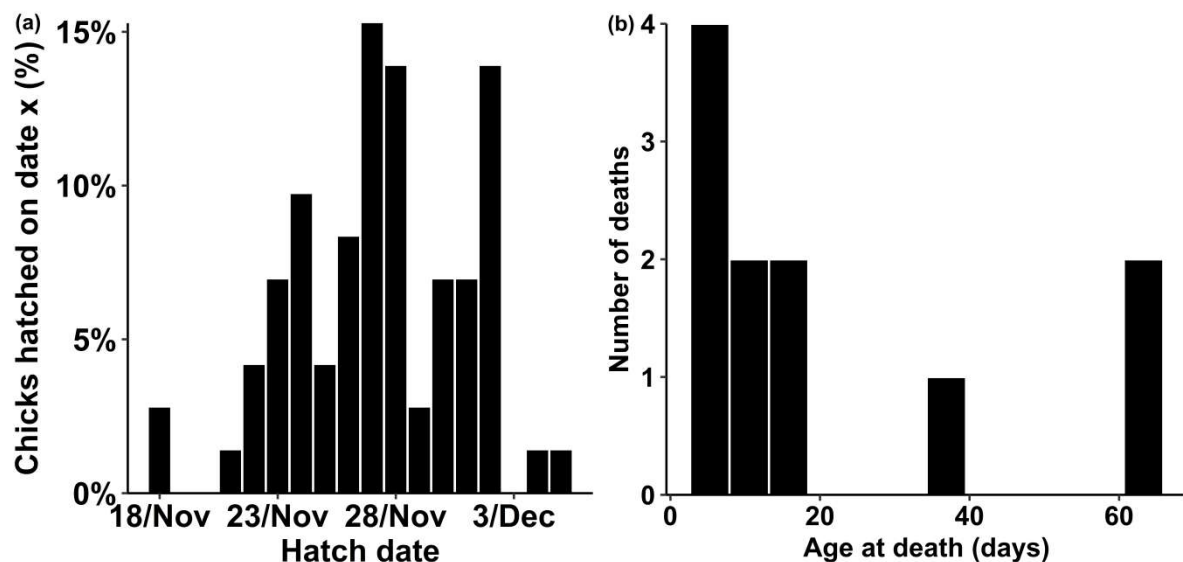


Figure 4.5. (a) Percentage of chicks that hatched on each date, n=61 (b) Number of chicks that died at 6–10 days, 11–15 days, 16–20 days, 36–40 days and 60–64 days old, n=11.

Eleven chicks died out of 78 hatched eggs (14%) (**Table 4.3**). Most chick deaths (73%) occurred within 20 days of hatching (**Figure 4.5**). The causes of the deaths were not able to be determined. 86% of chicks survived to fledging (**Table 4.3**). When weighed at fledging, 58% of chicks had at least one tick attached to their skin, with an average of $1.78 (\pm SE 0.29)$ ticks overall, mostly on the top and back of the head and around the eyes and mouth (**Figure 4.6**).

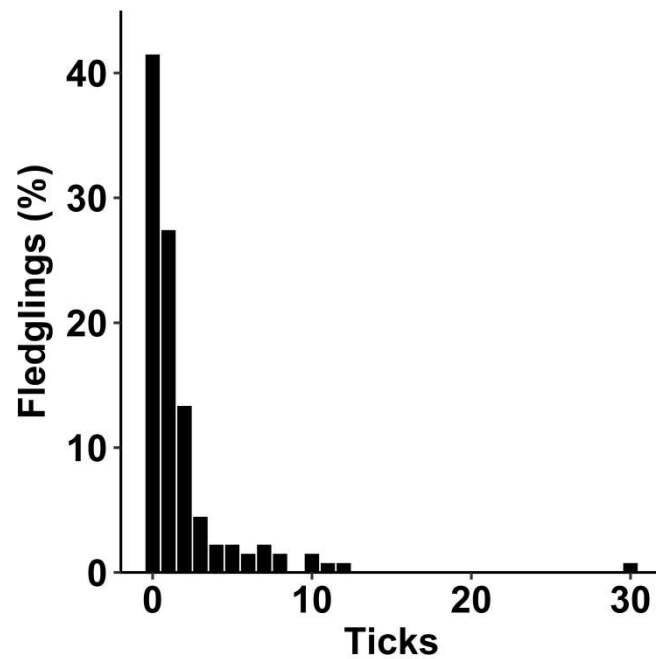


Figure 4.6. Percentage of fledglings found with ticks, n=125.

There was no significant difference in number of eggs, chicks or fledglings per nest between sites (**Table 4.3**). Habitat, overhead cover and hatch date also had no significant effect on any of these response variables.

A PCA was carried out on skull length and foot length (see methods) (**Figure 4.7**). Chick size (PC1) was positively related to fledging weight, habitat, (with chicks in the forest being larger on average than chicks in the scrub) and brood-size, with chicks from single-chick nests smaller in size than chicks from double chick nests (**Figure 4.8, Table 4.4**). The model also showed no significant effect of site or overhead cover, but these variables considerably improved the AICc score so were left in the model (**Table 4.4**).

Table 4.3. Total and average number of eggs laid, chicks hatched and fledglings (chicks that survived to mid-February) for the Rocky Ramp (RR) site (no disturbance stimulus present, n=27) and Sandy Bay (SB) site (disturbance stimuli present, n=17) and all nests (n=49). 'All' is the total, including 'hybrid' nests (where one parent used Rocky Ramp and one Sandy Bay, n=3) and nests where the landing site of the parent(s) was unknown (n=2). Model results are the Z values (degrees of freedom) and p-values of the generalised linear models for the effect of site (with site as the predictor variable). Hybrid nests and nests where the landing site is unknown were excluded from this analysis. Only nests with known hatch dates are displayed in this table and were used in the model.

	Total			Average per nest (\pm SE)			Model results (effect of site)
	RR	SB	All	RR	SB	All	
Eggs laid	51	33	93	1.89(\pm 0.02)	1.94(\pm 0.03)	1.90(\pm 0.01)	$Z_{43} = 0.12, p=0.90$
Chicks hatched	44	29	78	1.63(\pm 0.03)	1.71(\pm 0.05)	1.59(\pm 0.02)	$Z_{43} = 0.19, p=0.85$
Fledglings	39	25	67	1.44(\pm 0.03)	1.47(\pm 0.05)	1.37(\pm 0.02)	$Z_{43} = 0.07, p=0.94$

Table 4.4. Model results from the linear mixed model Chick Size ~ Chick Weight + Brood-size + Habitat + Overhead nest cover + Site + (1 | Nest ID).

Response variable	Model results
Fledging weight	$X^2_1 = 11.55, p < 0.001$
Habitat	$X^2_1 = 11.55, p < 0.001$
Brood size	$X^2_1 = 5.09, p = 0.002$
Site	$X^2_1 = 0.0009, p < 0.1$
Overhead cover	$X^2_1 = 3.71, p = 0.054$

Chick mass was related to brood-size, with chicks from two-chick nests estimated to be on average 0.54 kg (SE \pm 0.10) lighter than chicks from single-chick nests (**Figure 4.8, Table 4.5**). Chicks mass was also positively related to fledging body size, and overhead nest cover (**Table 4.5**). Nest habitat was also related to chick mass, (with chicks from nests in the forest lighter on average than chicks from the scrub) and there was a significant interaction between site, overhead cover and nest habitat, suggesting the effect of overhead cover varied with site and habitat type (**Table 4.5**). Site was not statistically significant as a main effect (**Table 4.5**). Other predictor variables (surrounding vegetation

cover and tick number) were consistently non-significant when added to both fledging body size and fledging weight models, and did not improve the AICc score so were removed.

Table 4.5. Model results from the linear mixed model Chick Mass ~ Site*Overhead nest cover*Nest habitat + Brood-size + fledging body size + (1 | Nest ID).

Response variable	Model results
Fledging body size	$X^2_1 = 71.95$, $p < 0.0001$
Habitat	$X^2_1 = 11.43$, $p < 0.001$
Brood size	$X^2_1 = 26.50$, $p < 0.0001$
Site	$X^2_1 = 0.17$, $p = 0.68$
Overhead cover	$X^2_1 = 5.37$, $p = 0.02$
Site*Overhead cover*nest habitat	$X^2_1 = 17.42$, $p < 0.0001$

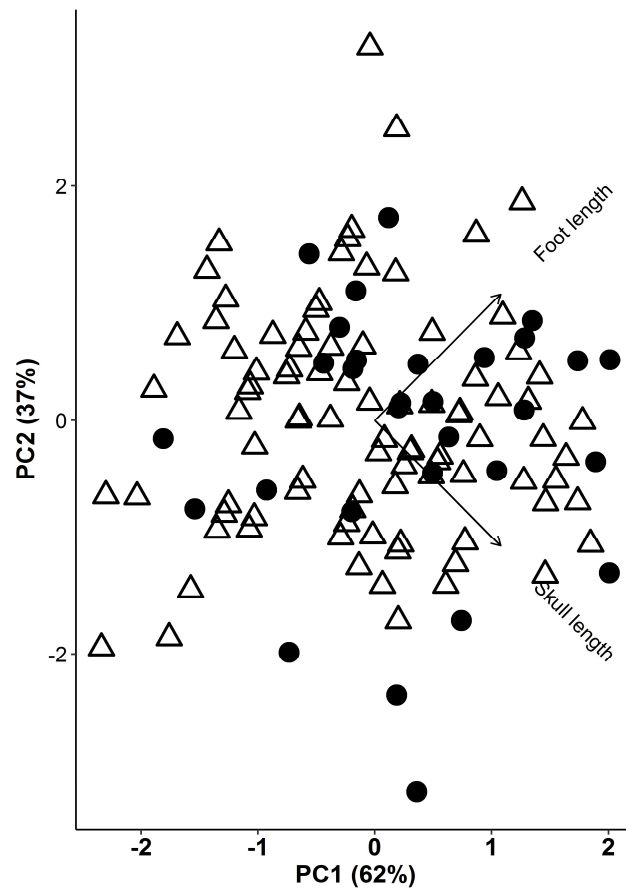


Figure 4.7. Principle Component Analysis of skull length and foot length. The amount of variation explained by each component is shown in brackets on the axes. Chicks from nests in the scrub are marked with a circle, chicks from the forest with a triangle, $n=148$.

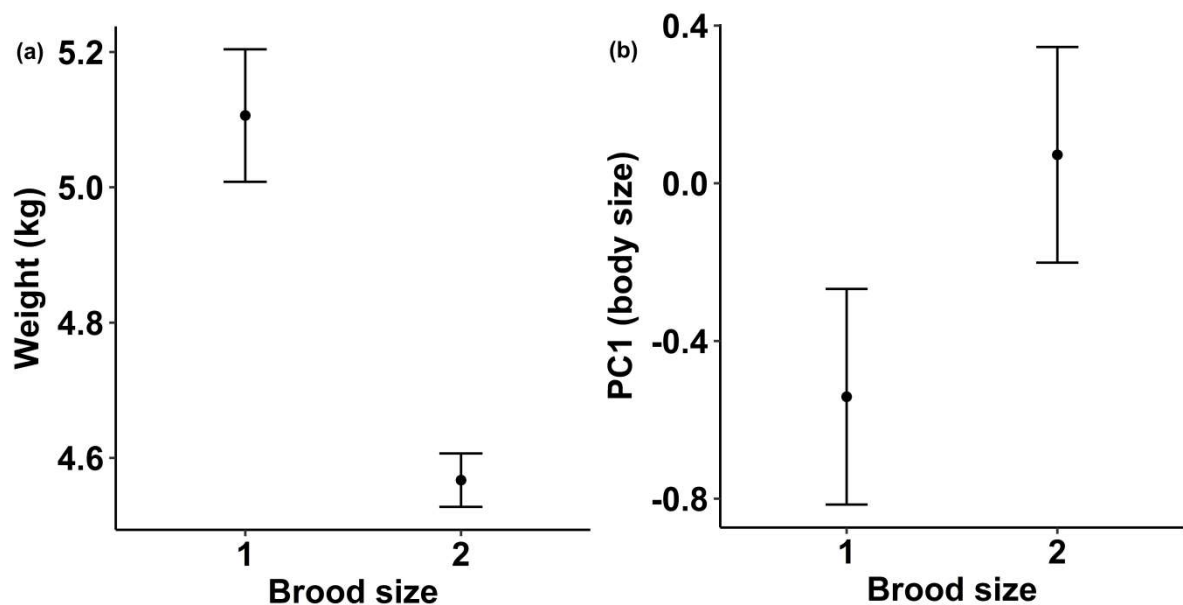


Figure 4.8. Results of linear mixed effects models. The effect of brood-size on (a) fledging weight (kg) and (b) fledging body size, $n=129$, with standard error bars.

Discussion

In my results, I reported a comprehensive study of Enderby Island Yellow-eyed Penguin breeding biology and investigated for the first time potential effects of brood-size, habitat and disturbance stimuli on nesting success, fledging weight and fledging body size. I found strong significant contrasting effects of brood-size on fledging weight and fledging body size, with chicks from single-brood nests weighing significantly more yet being significantly smaller in size than chicks from double brood nests. There was no difference in nesting success (expressed as eggs, chicks and fledglings per pair), fledging weight or fledging body size between the disturbed and undisturbed site nests, suggesting disturbance by tourists may not be having a detectable effect on Yellow-eyed Penguin breeding. Habitat affected fledging weight and fledging body size differently, with chicks in the forest being larger in fledging body size but lighter than chicks in the scrub. I also found ticks present on many of the fledglings but this did not affect fledging weight or fledging body size.

My results are similar to that found by Moore (1992a) on Campbell Island, with similar chick mortality (14% and 15% respectively) and reproductive output (1.37 and 1.40 respectively). However, fledging weight was lower in my study ($4.69 \text{ kg} \pm \text{SE } 0.05$) compared to Moore (1992a) (5.1 kg). This may be due to differences in age at weighing – in my study I weighed fledglings at an average of 71 days old whereas Moore (1992a) weighed fledglings at 108 days old – although growth studies have shown chick weights do not change much in the last month before fledging (van Heezik & Davis 1990). In contrast, my results differed considerably from the chick mortality reported in Argilla et al. (2013) at the same site, with much lower chick mortality in my study (14% compared to 55%). This demonstrates a high degree of annual variability, which has also been found on mainland New Zealand (Seddon et al. 2013).

When the fledging weights of this study are compared to mainland studies (McClung et al. 2004; Ellenberg et al. 2007), subantarctic fledglings appear on average lighter than mainland Yellow-eyed Penguin fledglings, which may indicate lower food quality, quantity, or a greater energy expenditure

required to access food. Conversely, the number of chicks fledged per pair was high compared to mainland New Zealand (Ellenberg et al. 2007). This low level of chick mortality on Enderby Island compared to mainland New Zealand may mean that lighter chicks are more likely to survive than chicks of the same weight on the mainland. These lighter chicks may lower the mean weight, resulting in a lower average weight, as has been suggested for Gentoo Penguins (*Pygoscelis papua*) by Williams and Croxall (1990). Mainland Yellow-eyed Penguins also face terrestrial threats such as mammalian predators and disease that may disproportionately affect lighter chicks, caused by a reduced ability to defend against predators and weakened immune systems (Seddon et al. 2013). This may cause an increased mortality of smaller and lighter chicks, increasing the mean weight of fledgling chicks.

Brood-size

I found brood-size had a significant effect on fledging weight, with single chicks weighing significantly more than chicks from two-chick broods. This has also been found in mainland Yellow-eyed Penguins by McClung et al. (2004) and Ellenberg et al. (2007), yet is considered unusual for this species, which is thought to be able to adjust parental effort according to brood-size. Previous research on mainland Yellow-eyed Penguins has shown no difference between single- and double-chick broods, even in years of low food availability (van Heezik & Davis 1990; Edge et al. 1999). The effect of brood-size was found across both sites in my study, in contrast to Ellenberg et al. (2007) who found in mainland Yellow-eyed Penguins this effect was significant only at one site (Sandfly Bay), which had high levels of unregulated tourist disturbance stimuli. I also found no significant difference in brood-size (expressed as number of eggs laid, and number of chicks per pair) between sites. This suggests that the brood-size effect on fledging weight is not site-specific, and may indicate lower food availability or quality where parents at both sites cannot supply the optimum amount of food to two chicks. Studies of foraging and diet of subantarctic Yellow-eyed Penguins would shed further light on this.

Salihoglu et al. (2001) modelled Adélie Penguin (*Pygoscelis adeliae*) chick weights and showed that quantity, quality and timing of food provided to chicks was critical for chick mass, and that the amount of food delivered to the chick was most important late in chick development when the chicks have increased growth and food demands. This might suggest that the amount of food delivered to the chicks only became sub-optimal later in the breeding season, which may have resulted in the difference in fledging weights between double- and single-chick broods. While differences in fledging weight may be considered less threatening to population survival than chick or adult mortality, lower fledging weight may still have a detrimental effect on population recruitment in the long-term. McClung et al. (2004) showed that chicks fledging at lower weights had a lower probability of surviving into adulthood. Chicks with a larger fledging weight may be better able to cope with food shortages when first learning to forage, making them less susceptible to starvation. Heavier chicks may also be less likely to take risks since missing opportunities to get food carries less cost, lowering their likelihood of predation (Eccard & Liesenjohann 2014). This indicates lower fledging weights can have long-term consequences for the population as a whole. The relatively low fledging weights recorded on Enderby Island (compared to mainland New Zealand) and differences in fledging weight between single- and double-brood chicks may therefore be cause for concern if this is a long-term effect. It is also possible that the differences in fledging weight between the subantarctic and mainland populations are due to differences in population density. This could increase competition and affect food availability, reducing chick growth. Future research including multi-year studies, and studies on juvenile survival, diet and foraging would shed light on this and should therefore be a high priority.

Surprisingly, fledging body size was not affected by brood-size in the same way as fledging weight. Although there was a strong positive relationship between fledging body size and fledging weight, there were also significant contrasting effects of brood-size on fledging body size and fledging weights, where fledglings from single-chick nests weighed significantly more but were significantly smaller (based on head and foot measurements) than chicks from double chick nests. While there

have been a number of studies measuring fledging weight (McClung et al. 2004; Ellenberg et al. 2007), to my knowledge only one study of mainland Yellow-eyed Penguins has studied the effect of brood-size on fledging size (van Heezik & Davis 1990). This study found no significant differences between single- and double-fledgling broods for fledging weight, skull length or foot length. Single chicks have no competition for food, in contrast to chicks from two-chick nests who are competing with their sibling. Chicks from two-chick nests (which were larger and lighter) may therefore benefit from prioritising growth in fledging body size over fat reserves, as being larger in size may help them better compete with their sibling for food. While sibling competition is common in other species of penguins such as Rockhopper Penguins (*E. chrysocome filholi*) (Poisbleau et al. 2011; Poisbleau et al. 2013), it is thought to be low in Yellow-eyed Penguins, due to similar-sized eggs, synchronous hatching and relatively equal growth rates (van Heezik & Davis 1990). However my results may suggest there is some degree of competition, along with Ellenberg et al. (2007) and McClung et al. (2004) who found that brood-size affected fledging weight. Single chicks may also benefit from prioritizing fat over fledging body size once the parent stops incubation, as they may have increased heat loss when in the nest alone, compared to chicks with siblings. This would only be important in the subantarctic where temperatures are lower; mainland Yellow-eyed Penguins chicks are known to suffer heat stress due to the high temperatures over summer so heat loss is unlikely to be an issue (Seddon & Davis 1989).

Alternatively, changes in body size could be a result of differences in sex ratio. Yellow-eyed Penguin adults and juveniles can be differentiated by measuring skull and foot length, therefore fledglings may also differ significantly in their measurements (Setiawan et al. 2004). If this were the case it would suggest single-chick broods had more female offspring than double chick broods. It is possible that male chicks are more demanding for the parents to raise, and therefore adult females with poor body condition may be more likely to produce female chicks, and vice versa. This has been observed in a number of other bird species (e.g. Trewick 1997; Whittingham & Dunn 2000; Whittingham et al. 2002). However, to my knowledge this has not been observed in mainland Yellow-eyed Penguins,

and as Yellow-eyed Penguins are monogamous and have little sexual dimorphism, the benefits of skewing sex ratios are likely to be small (Setiawan et al. 2004; Seddon et al. 2013). In my study it was not possible to determine sex or sex ratios in fledglings, but this could be a useful measure to include in future studies.

Habitat

I also found contrasting effects of habitat on fledging body size and fledging weight, with fledglings from nests in the forest being significantly lighter and larger than fledglings from nests in the scrub. There was no significant difference in brood-size between habitats. Indigenous forest is thought to be the preferred nesting habitat of Yellow-eyed Penguins, with the suggestion that deforestation on mainland New Zealand has resulted in more Yellow-eyed Penguins nesting in scrub and exotic plants (Seddon & Davis 1989; Darby & Seddon 1990; Seddon et al. 2013). While there has been some clearing on Enderby Island this is only still evident in a small area (known as the sward, described in Chapter 1) (Taylor 1971). Thus, large areas of Enderby Island are covered in forest (Taylor 1971). Only 25% of the nests in my study were in the forest, but this may be due to the forest habitat being smaller in my study area, and having a greater line of sight through the undergrowth. Yellow-eyed Penguins strongly prefer to nest out of sight of conspecifics (Seddon & Davis 1989), so the forest habitat may have a lower nest capacity than scrub.

Forest may be preferred because nests are more sheltered from environmental factors such as wind and rain. Roof cover had a significant positive effect on the fledging weight of chicks, indicating shelter from weather is important. In the forest, the nest would have a second canopy from the rātā trees above the roof of the nest (which was not included in the estimation of roof cover), which may provide more effective shelter from rain, and the forest is also likely to shelter them more effectively from wind than the much shorter scrub. This may mean the need for fat reserves to reduce heat loss is greater for chicks in the scrub, who prioritise fat reserves over body growth. Gentoo Penguins are

also affected by weather; they have a lower breeding success when colonies are small, or surrounded by short grassland (Holmes et al. 2006). This is thought to be related to exposure to wind and rain. In contrast, mainland Yellow-eyed Penguins are thought to be at risk of heat stress when incubating, so forest habitats are considered desirable as they are cooler and provide more shade (Seddon & Davis 1989).

The effect of disturbance on fledging weight

I found no significant effect of site (meaning access via the disturbed Sandy Bay or undisturbed Rocky Ramp) on fledging weight or fledging body size, suggesting the current level of disturbance may not be having an impact on breeding success of Yellow-eyed Penguins on Enderby Island. During the guard and post-guard phase, the parents must return regularly to the nest to feed their chicks. A behavioural study of Yellow-eyed Penguins on Enderby Island (Chapter 3) showed that human and/or sea lion presence significantly increased the likelihood of an aborted transit at Sandy Bay. This means the adult either returns to the forest and delays or abandons the foraging trip, or returns to the sea and delays the return to the nest. A delayed or abandoned foraging trip could reduce the frequency of feeding the chicks would receive, and a delayed return to the nest could increase the amount of digestion of the food and reduce the amount regurgitated to the chicks (Wright 1998). Increased stress levels and longer foraging trips could also lead to higher energy expenditure for the parents, resulting in less food being available to the chicks (Ellenberg et al. 2007). Any of these outcomes could result in a chick receiving less food, and if repeated over the breeding season could cause the chick to fledge at a lower weight. My results suggest that any delays in foraging trips are not long enough to cause a reduced amount of food regurgitated to the chicks, or abandoned foraging trips caused by disturbance stimuli are not frequent enough to cause a sufficient reduction in food provided over the season.

My results differ from studies on mainland Yellow-eyed Penguins, where human disturbance was shown to result in lower fledging weights (McClung et al. 2004; Ellenberg et al. 2007). Human disturbance on mainland New Zealand generally consists of constant disturbance stimuli over a long period. Many popular beaches such as Sandfly Bay have humans constantly on the beach causing disturbance throughout the day (Seddon et al. 2003). The mainland tourists are also often not monitored or guided, so there is little to prevent bad behaviour such as approaching transiting and nesting penguins. In contrast, tourism on Enderby Island is comparatively infrequent (less than once per week), and consists of a large number of people present over a short period of time (approximately 8 hours, most of which is not in the penguin transit area), with many days of little/no human disturbance stimuli at all. The timing of tour boats landing and departing is regulated to avoid peak penguin activity, and the number of tourists allowed per day and over the entire season is also regulated (Department of Conservation 2016). The behaviour of the tourists is also regulated, with guides required to be present to ensure compliance. The results of my study suggest the low levels of highly regulated tourism on Enderby Island may be sustainable, and that regulation of tourist activities appears to be effective at reducing the impact of disturbance on Yellow-eyed Penguins. This regulation reduces the number of human-penguin interactions and is likely to play an important role in reducing the impact.

As disturbance by researchers occurred at both sites, it is possible that this effect 'swamped' the effect of disturbance by tourists. However, if this was the case it may be expected that nests with known hatch dates (that were found early, and therefore experienced more disturbance by researchers) would have a lower fledging weight than chicks from nests that were found later in the season. However, there was no significant difference between fledging weights of these two groups ($t_{120} = 0.36$, $p\text{-value} = 0.72$) suggesting researcher disturbance at nests did not have a detectable effect. Microchipping of adults may also have caused disturbance, but this occurred only once per bird.

It is also possible that this study did not have the power to detect the differences caused by human disturbance. When conducting similar studies on mainland New Zealand, Ellenberg et al. (2007) and McClung et al. (2004) found significant effects of human disturbance on fledging weight, with differences of 0.76 kg and 0.41 kg. Power analysis showed my study had an 82% chance of detecting a minimum difference of 0.3 kg in fledging weight between sites. This suggests that if there was an effect of human disturbance on Enderby Island, the difference in fledging weights between sites was less than 0.3 kg.

Disturbance from sea lions

My behavioural study on Enderby Island has shown sea lion disturbance stimuli has a similar effect to human disturbance stimuli on Yellow-eyed Penguin behaviour, increasing the probability of an aborted transit (Chapter 3). However, my results from this study indicate that disturbance stimuli (human and sea lion) is not having a detectable effect on the breeding success of the Yellow-eyed Penguin on Enderby Island.

The New Zealand Sea Lion has a similar distribution to the Yellow-eyed Penguin, with the majority of pups born in the subantarctic, and 18% of pups born on Sandy Bay, Enderby Island (Chilvers & Meyer 2017). Penguins using the Sandy Bay access point therefore regularly come into contact with New Zealand Sea Lions, thus it is impossible to separate these two types of disturbance stimuli. Penguins using the Rocky Ramp access point will not come into contact with either humans or sea lions. New Zealand Sea Lion disturbance occurs every day over the entire breeding season, and the sea lions occur in high concentrations due to the presence of the sea lion colony on Sandy Bay (Chilvers & Meyer 2017). Their behaviour is also more threatening (even occasionally resulting in predation) than the regulated tourist behaviour (pers. obs.; Morrison et al. 2017). As they are both endemic and endangered species (Baker et al. 2016; Robertson et al. 2017), little can be done to avoid

disturbance or predation of Yellow-eyed Penguins by sea lions, but human disturbance can be minimised to lower the total amount of disturbance stimuli the penguins are subjected to.

Recommendations

This study showed potential effects of brood-size and habitat on fledging weight and fledging body size. I found no evidence of disturbance having an impact on the breeding success on Enderby Island, indicating the current levels of tourism appear to be sustainable. The total number of tourists visiting the island should therefore be kept to low levels, and the frequency and timing of tour boats landing and departing should continue to be regulated to avoid peak penguin activity. In addition, regulations such as a suitable minimum approach distance are important for reducing the disturbance during a penguin-human interaction (Chapter 3). There is also still comparatively little research on the subantarctic Yellow-eyed Penguin. Studies on foraging and diet are urgently needed to assess food availability and quality. In addition, this study was conducted over just one breeding season, and therefore does not show changes in breeding success or fledging weight over time. Long-term studies of this population would be extremely useful in monitoring population health and effects of disturbance stimuli, particularly given so little is known about these populations.

Chapter 5:

General Discussion



Human disturbance stimuli have been demonstrated to have behavioural, physiological and population-level impacts in a number of penguin species (e.g. Ellenberg et al. 2006; Holmes et al. 2006; Holmes 2007; Lynch et al. 2010). On mainland New Zealand, the Yellow-eyed Penguin (*Megadyptes antipodes*) is particularly vulnerable to human disturbance stimuli, and unlikely to habituate to tourism (McClung et al. 2004; Ellenberg et al. 2007; Ellenberg et al. 2009). Subantarctic Yellow-eyed Penguins are also subjected to human disturbance stimuli through tourism but it was not known whether the current management guidelines were effective at reducing disturbance, or whether the current level of tourism had any population-level impact on the species. My study aimed to address these knowledge gaps, with the goal of aiding in future management of the species and improving our knowledge of the impacts of human disturbance stimuli on animals.

In Chapter 2, I reviewed the current disturbance literature and described the different research techniques used to measure and quantify disturbance. Behavioural responses were the most studied disturbance response in penguins, and therefore the basis for most evidence-based management decisions aiming to reduce human impact. However, behavioural or physiological responses alone do not give a measure of long-term impact, meaning that population-level effects are also important to give a clear indication of the long-term impact of disturbance (or lack thereof). Behavioural and physiological responses measure the mechanisms of disturbance, whereas population-level responses can be used to measure the conservation implications of disturbance stimuli, or changes in management. Ideally, all three (behavioural, physiological and population) levels of response would be studied to give a well-rounded view of disturbance impacts on a species. However, this is rare in penguin studies. Due to logistical and ethical constraints it was not feasible to measure physiological effects in my research. The New Zealand Department of Conservation only permit essential research in the subantarctic islands that has minimal impact. The invasive nature of physiological research (and the availability of other less invasive behavioural and population-level options) meant these requirements would not have been met.

In Chapter 3, I quantified the behavioural impact of human disturbance on Yellow-eyed Penguins at Enderby Island. Human presence caused a significant drop in the probability of a Yellow-eyed Penguin successfully transiting to or from their nest, and significantly increased the time penguins spent alert and decreased the time spent preening.

Given the population on Enderby is estimated at between 200 and 290 pairs (and many of those would be using other access points around the island), it is likely some individual birds were sampled more than once in my behavioural study. As the birds were not individually identifiable without capture, this could not be avoided. The number of birds transiting each day is highly variable depending on time of year and weather conditions, and varied from 20 to over 70 birds transiting per day in the penguin alley area (unpublished data).

Disturbance stimuli from New Zealand Sea Lions (*Phocarctos hookeri*) also had an impact, increasing the likelihood of a penguin to flee and decreasing the probability of a successful transit. This indicates that Yellow-eyed Penguins perceive humans in a similar way to how they perceive their natural predators, the New Zealand Sea Lion, which provides evidence for the risk-disturbance hypothesis (Frid & Dill 2002). It's possible that viewing humans as predators was originally adaptive; Yellow-eyed Penguin bones have been found in middens from early Polynesian settlers in New Zealand, suggesting they were hunted (Boessenkool et al. 2009a). However, studies indicate hunting pressure was greatest on the extinct species (*M. waitaha*), and there is little evidence that Maori hunted *M. antipodes* when the penguin recolonised the mainland following the extinction of *M. waitaha* (Boessenkool et al. 2009a; Boessenkool et al. 2009b). This is thought to be either due to a local reduction in human population around the coast of the South Island of New Zealand, or a cultural shift resulting in increased awareness of environmental management (Boessenkool et al. 2009a).

Modelling showed that with closer human approaches the likelihood of a bird displaying disturbance behaviour increased, and that the current minimum approach guideline of 5 m is not sufficient for

preventing disturbance (Chapter 3). To my knowledge, this guideline was set arbitrarily and based on guidelines from other areas (as with many other similar guidelines around the world). For example, 5 m is also applied in Antarctica and on Macquarie Island (Tasmania Parks and Wildlife Service 2008; IAATO 2017b). My study shows that for Yellow-eyed Penguins at Enderby Island the minimum approach guideline would be improved if it was increased to at least 40 m where the probability of disturbance is much lower (0.15 compared to 0.99 at 5 m). This shows the importance of scientifically evaluating the effectiveness of management guidelines; if guidelines are set arbitrarily or based on work from other areas or species, it is possible that they will be ineffective or even potentially harmful.

One issue with using flight initiation distances to set a minimum approach distance is that the distance at which an animal flees varies according to many environmental factors (see Chapter 2). This means the highly variable nature of flight initiation distances are not incorporated into the guidelines, which are often (for simplicity) a single minimum approach distance (Blumstein 2003, 2006). In addition, for certain sites the ideal minimum approach distance may not be suitable; due to topography or vegetation visitors may not be able to maintain the distance safely (Holmes et al. 2008). The topography of Sandy Bay, Enderby Island, may make Yellow-eyed Penguins more likely to flee than in other areas, due to the relatively short distance to a refuge (either the forest or the sea), and good visibility due to the lack of tall vegetation (Frid & Dill 2002; Stankowich & Blumstein 2005). Hides and other structures that may reduce disturbance would be unlikely to be approved in this world heritage area, and would be difficult to maintain in such an isolated place. The small size of the area also makes tourists more likely to interact with transiting penguins, and may make a large minimum approach distance impractical. This creates a trade-off between tourist experience and penguin conservation/welfare. As discussed in Chapter 1, ecotourism may have some benefits to conservation, so guidelines reducing disturbance need to be practical to avoid unintentionally making tourism in the area unviable. This trade-off will need to be managed carefully to keep tourism on Enderby Island feasible, while minimising disturbance. This could be further enhanced if

visitor experience was measured in conjunction with their approach distance. A minimum approach distance that optimises the trade-off between tourist experience and wildlife disturbance could then be generated.

In Chapter 4, I describe the breeding biology of Yellow-eyed Penguins on Enderby Island in 2016/17. I applied the understanding I gained on breeding success, fledgling body size and fledgling weight to study the effects of disturbance (by comparing a disturbed and undisturbed site), as well as presenting other aspects of their ecology such as nesting habitat, tick numbers, brood-size, and the effect these factors may have on reproductive output. I found a strong significant effect of brood-size on fledging weight and fledging body size, with chicks from single-brood nests weighing significantly more and being significantly smaller than chicks from double brood nests (across both the disturbed and undisturbed sites). This was a surprising result, given that sibling competition is thought to be almost non-existent in Yellow-eyed Penguins, and adults are thought to modify their parental effort based on brood-size (van Heezik & Davis 1990; Edge et al. 1999). There was no difference in nesting success (expressed as eggs, chicks and fledglings per pair) between the disturbed and undisturbed site and no significant difference in the average weight and body size of fledglings at the disturbed site compared to fledglings at the undisturbed site. These results indicate the current level of disturbance caused by humans and New Zealand Sea Lions at Enderby Island may not be having a measurable impact on breeding success of Yellow-eyed Penguins, but further multi-year studies would be needed to confirm this. In studies of other penguin species, finding no effect of tourism on breeding success is common (e.g. Yorio & Boersma 1992; Hull & Wilson 1996; Patterson & Fraser 1998; Cobley & Shears 1999; Patterson 2003; Trathan et al. 2008; Lynch et al. 2010). This indicates that penguin species are reasonably resilient to low levels of controlled human disturbance stimuli such as on Enderby Island, and able to maintain reproductive output.

Ideally in my study adult mortality, juvenile mortality, immigration and emigration would have been measured as well as breeding success, which could have been used to create a population model to

determine the effects of different management strategies. I focussed on breeding success for two reasons. Firstly, breeding success is the only indicator of population-level effects than can be measured in one breeding season, and thus for practical reasons the other measures were not feasible to include in this study. Secondly, changes in breeding success had been observed in mainland Yellow-eyed Penguins as a result of unregulated tourism (McClung et al. 2004; Ellenberg et al. 2007), as well as in a number of other penguin species (**Table A.1**) so studying the same indicator of disturbance allowed direct comparison with these studies.

When planning Chapter 4, I had originally aimed to model nesting success using the program MARK, to determine daily survival probabilities and examine the effects of different environmental factors (including comparing the disturbed and undisturbed site) on these daily survival probabilities (Dinsmore & Dinsmore 2007). However, a number of issues prevented this from being a viable option. Firstly, while six nests failed at the egg stage, it was impossible to know when they failed. Many penguins would continue to incubate the eggs long after most eggs from other nests had hatched, and would only abandon the nest late in the season. I was also not able to open or candle the eggs. Therefore, although I knew at what point the nest was abandoned, I had no way of knowing when the eggs had failed. Modelling daily survival probabilities during the incubation stage would be more useful in species where predation or destruction of the nest are the common causes of failure (as opposed to infertility or temporary exposure), as then the approximate date of failure could be determined. Secondly, modelling daily survival probabilities for the chick stage was not very informative because so few nests failed. Eleven chicks died out of 78 hatched eggs, but in most cases the other chick survived, so the nest was ultimately successful. Only four nests failed at the chick stage, which is clearly not a large enough sample size to do any meaningful modelling.

Research implications

My results indicate that while human and sea lion disturbance stimuli have a behavioural impact on Yellow-eyed Penguins at current levels and control measures, this disturbance does not result in a

measurable impact of human disturbance stimuli on breeding success. This shows the importance of studying population-level impacts as well as behavioural or physiological impacts. Thus, from a management perspective while I did show the minimum approach distance needs to be revised to minimise disturbance to individual birds, I found no evidence that the current level of tourism on Enderby Island is unsustainable. The regulated tourism of Enderby Island may therefore be an example of sustainable eco-tourism and successful management. However, my study of behavioural responses showed humans do cause disturbance on a behavioural level, even if this does not reduce breeding success. This indicates that the lack of population-level effects is not due to habituation. The nature of this tourism (irregular, intermittent, whole-day visits) means that habituation is unlikely. Some penguins such as Magellanic Penguins (*Spheniscus magellanicus*) habituate to human presence, but this was to short, intense and regular visits (Walker et al. 2005). This type of visit is not feasible in the New Zealand subantarctic, and even if it was it may not result in habituation by Yellow-eyed Penguins. It is therefore important that the number of interactions continues to be kept to a minimum by ensuring the number of tourists allowed to visit Enderby Island is kept at low levels, and by restricting landing hours during peak penguin transit times (early morning and evening) (Young 2009).

The lack of evidence of population-level impacts on Enderby Island contrasts with the findings of studies on mainland Yellow-eyed Penguins, where unregulated tourism reduces indicators of population dynamics such as breeding success and fledging weights (McClung et al. 2004; Ellenberg et al. 2007). This may be due to the decreased pressure from other threats on Enderby Island, such as a lack of predation from introduced mammals (Darby & Seddon 1990). However, it is more likely due to the differences in the nature of the tourism including the frequency of tourist visits, the high degree of regulation to reduce the number of penguin-tourist interactions, and the supervision of tourist behaviour in the New Zealand subantarctic compared to mainland New Zealand. Self-regulation (as opposed to supervision by guides) requires tourists to be able to judge their own impact, which requires knowledge of animal behaviour (Holmes 2007). The tourists also need to care

whether they are having an impact or not. Research on Humboldt Penguins (*S. humboldti*) showed that tourists informed of the potential negative impacts of their behaviour were more likely to choose visiting options that reduced penguin stress (compared to those not informed) (Lavín et al. 2016). This indicates self-regulation can be effective in some cases. In contrast, research on a popular New Zealand Fur Seal (*Arctocephalus forsteri*) attraction has shown that self-regulation facilitated by signs was not effective at reducing negative tourist behaviour (Acevedo-Gutiérrez et al. 2011a). However, the presence of an official-looking volunteer significantly reduced the frequency of harassment (Acevedo-Gutiérrez et al. 2011b). On some beaches on mainland New Zealand, tourists have been observed "running, shouting and chasing penguins" (Ellenberg et al. 2007). During my observations of tourists on Enderby Island, this type of behaviour was never seen, which may be because they were permanently supervised by either guides or Department of Conservation representatives, or are predisposed to acting positively around wildlife because they have chosen to pay large sums of money to see wildlife. Predator-like behaviour by tourists on mainland New Zealand beaches may have contributed to the greater population-level responses compared to the subantarctic population where tourists displayed more suitable behaviour. The unpredictable and threatening nature of this behaviour on the New Zealand mainland may also lead to sensitisation, causing greater responses to all forms of human disturbance stimuli (Ellenberg et al. 2007; Weston et al. 2012). However, while I did not observe tourists behave in highly disturbing ways, I did observe frequent approaches closer than 5 m. This may be because wildlife photography and birdwatching are key interests for tourists visiting the New Zealand subantarctic, which motivates tourists to approach closer (pers. obs). In African birds, approaches by people displaying birdwatching behaviour resulted in longer escape distances than approaches by pedestrians, indicating some species perceive birdwatching behaviour as more threatening (Radkovic et al. 2017). Codes of conduct encourage minimising stress when approaching closely (e.g. Birds New Zealand 2017), but as discussed above, self-regulation such as these codes of conduct require positive intentions and knowledge of animal behaviour to be effective.

Alternatively, the lack of impact on Enderby Island may be because the large majority of Yellow-eyed Penguin nests are not accessible to tourists, and the only exposure to humans is during their transit to or from the sea. Two nests were located very close to the boardwalk, and were subjected to prolonged disturbance stimuli during days tourists visited. Both nests hatched two chicks each but one chick of the four died. While it is possible this was a result of human disturbance stimuli, there was no evidence to confirm this. In mainland New Zealand, Yellow-eyed Penguins often have nests accessible to tourists, particularly in areas without dense bush. Ellenberg et al. (2013) observed unregulated visitors frequently spending 20 minutes or more close to penguin nests, and showed human approaches to Yellow-eyed Penguin nests caused a large increase in heart rate. Therefore, it is possible that the population-level effects of disturbance stimuli observed in mainland New Zealand are due to disturbance on the nest, which subantarctic Yellow-eyed Penguins are very rarely subjected to.

The current level of regulation of tourism on Enderby Island means there is a greater chance of successful implementation of measures to reduce tourist impact, compared to mainland New Zealand. This also means Enderby Island could be viewed as a model system with which to study and test possible avenues for reducing tourism impact. For example, the minimum approach guideline recommended in my study (at least 40 m) could be applied on Enderby Island, then monitored for effectiveness. Compliance and feasibility could also be monitored. These could then be applied to mainland sites, where practical. If the impact of tourism on mainland Yellow-eyed Penguins is to be reduced, it may be effective to adopt some of the measures applied in the subantarctic, such as closing the beaches to the public early in the morning and in the evening to reduce the number of penguin-tourist interactions. This measure has also been recommended for Magellanic Penguin colonies exposed to disturbance stimuli (Scioscia et al. 2009). Closing vulnerable areas completely may also be an option, as occurs in the Galápagos Islands (Burger & Gochfeld 1993). For the subantarctic islands, the Department of Conservation selects areas that are less vulnerable for tourists to visit; this could be applied to mainland New Zealand (Department of Conservation 2016).

However, while this eliminates impact in the closed areas, it can result in increased pressure on the open areas.

Future research

My study was conducted over only one breeding season, which considerably limits my ability to draw conclusions on population stability. The mainland Yellow-eyed Penguin population size and breeding success is extremely variable, meaning subantarctic breeding success could also vary considerably between seasons (Seddon et al. 2013). My results are therefore a preliminary snapshot only, and long-term monitoring and research should be a high priority for the subantarctic Yellow-eyed Penguin. This is particularly important given I found fledglings had a low weight compared to mainland Yellow-eyed Penguin fledglings, and I also found a large effect of brood-size on fledging weight and fledging size, both of which indicate juvenile mortality could be high and population recruitment low.

It is important that management guidelines are either species-specific (if species can be easily identified), or cater for the most sensitive species in the area (Blumstein et al. 2005; Holmes 2007; Tin et al. 2008). This can be prevented by a lack of data on the current impact of tourism on the species, or the lack of scientific evaluation of the effectiveness of guidelines (Møller et al. 2014; Trave et al. 2017). Using my research, management guidelines could now be changed to reduce behavioural impacts on the Yellow-eyed Penguin on Enderby Island. However, the Yellow-eyed Penguin is probably not the most sensitive species in the area – that is most likely the Northern Giant Petrel (*Macronectes halli*). Northern Giant Petrels nest on the edge of the vegetation on Enderby Island, including around the edges of Sandy Bay, and also gather in large numbers on the beach (Parker et al. 2016). de Villiers et al. (2006) showed on Marion Island that the heart rate of nesting Northern Giant petrels increased upon detection of a human 40 m away. However, from my observations I would estimate that the Northern Giant Petrel on Enderby Island is much more sensitive to disturbance stimuli (particularly when off the nest), and approaches caused them to flee

from much further than 40 m. The chicks will also regurgitate stomach oil when disturbed (Warham et al. 1976). If this occurs frequently it may carry a significant cost, and their nests are much more accessible to tourists than Yellow-eyed Penguin nests which are hidden in thick scrub. Therefore, to reduce impact on all species on Enderby Island, research into the impact of disturbance on other species such as the Northern Giant Petrels should be considered.

Conclusion

My research indicates that when carefully managed, even species known to be vulnerable to disturbance stimuli can be viewed by tourists without apparent long-term impact. It shows that reducing the number of interactions between animals and humans should be a high priority, as well as managing tourist behaviour during an interaction. It also demonstrates the value of studying both individual (behavioural or physiological) and population-level effects, and scientifically evaluating management guidelines. The New Zealand subantarctic is an incredibly special place, valued for its isolation, biodiversity, endemism and pristine nature. The fact that tourists are able to visit and appreciate these areas without appearing to have any long-term impact on Yellow-eyed Penguins is commendable.

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Appendix

Table A.1. Current published literature on behavioural, physiological and population-level impacts on wild penguins. The key results of each paper are summarised under 'outcome' as either habituation (defined as a reduced response to disturbance stimuli following previous exposure), negative, or 'none detected' (where no statistically significant impact was detected). Literature is listed more than once where multiple responses, species or disturbance stimuli are studied within one paper. UAVs are unmanned aerial vehicles.

Response measured	Penguin Species	Disturbance stimulus	Outcome	Reference
Behavioural	Yellow-eyed	Controlled pedestrian approach	Habituation	Ellenberg et al. (2009)
	African	Controlled pedestrian approach	Habituation	van Heezik and Seddon (1990)
	Magellanic	Human presence	Habituation	Walker et al. (2006)
	Gentoo	Tourism	Habituation	Holmes et al. (2006)
	African	Tourism	Habituation	Pichegru et al. (2016)
	Magellanic	Tourism	Habituation	Villanueva et al. (2012)
	Magellanic	Tourism	Habituation	Walker et al. (2005)
	Magellanic	Tourism	Habituation	Yorio and Boersma (1992)
	Magellanic	Tourism	Habituation	Villanueva et al. (2014)
	Magellanic	Tourism/human presence	Habituation	Fowler (1999)
	African	Controlled pedestrian approach	Negative	Hockey and Hallinan (1981)
	Adélie	Controlled pedestrian approach	Negative	Giese (1998)
	King	Controlled pedestrian approach	Negative	Holmes (2007)
	Gentoo	Controlled pedestrian approach	Negative	Holmes (2007)

Response measured	Penguin Species	Disturbance stimulus	Outcome	Reference
Physiological	Royal	Controlled pedestrian approach	Negative	Holmes (2007)
	Royal	Controlled pedestrian approach	Negative	Holmes et al. (2005)
	Chinstrap	Controlled pedestrian approach	Negative	Lee et al. (2017)
	Gentoo	Controlled pedestrian approach	Negative	Lee et al. (2017)
	Adélie	Helicopter overflights	Negative	Culik et al. (1990)
	Emperor	Helicopter overflights	Negative	Giese and Riddle (1999)
	King	Helicopter overflights	Negative	Hughes et al. (2008)
	Adélie	Human presence	Negative	Wilson et al. (1991)
	Fiordland Crested	Disturbance by researchers	Negative	Ellenberg et al. (2015)
	Adélie	Disturbance by researchers	Negative	Wilson et al. (1989a)
	Emperor	Tourism	Negative	Burger and Gochfeld (2007)
	Little Blue	Tourism	Negative	Shaughnessy and Briggs (2009)
	Yellow-eyed	Tourism	Negative	Young (2009)
	Adélie	UAV overflights	Negative	Rümmeler et al. (2016)
	Macaroni	UAV overflights	Negative	Weimerskirch et al. (2018)
	Gentoo	UAV overflights	Negative	Weimerskirch et al. (2018)
	Chinstrap	Controlled pedestrian approach	None detected	Martín et al. (2004)
	Adélie	Helicopter overflights	None detected	Southwell (2005)
	Emperor	Helicopter overflights	None detected	Southwell (2005)
	Yellow-eyed	Tourism	None detected	Ratz and Thompson (1999)
	Gentoo/Skua	Tourism	None detected	Crosbie (1999)
	Adélie	UAV overflights	None detected	Korczak-Abshire et al. (2016)
	Rockhopper	UAV overflights	None detected	Weimerskirch et al. (2018)
	Yellow-eyed	Controlled pedestrian approach	Habituation	Ellenberg et al. (2009)
	King	Controlled pedestrian approach	Habituation	Viblanç et al. (2012)
	Magellanic	Human presence	Habituation	Walker et al. (2006)
	Magellanic	Disturbance by researchers	Habituation	Walker et al. (2006)
	Gentoo	Tourism	Habituation	Barbosa et al. (2013)
	Magellanic	Tourism/human presence	Habituation	Fowler (1999)
	Humboldt	Controlled pedestrian approach	Negative	Ellenberg et al. (2006)
	Snares	Controlled pedestrian approach	Negative	Ellenberg et al. (2012)
	Yellow-eyed	Controlled pedestrian approach	Negative	Ellenberg et al. (2013)

Response measured	Penguin Species	Disturbance stimulus	Outcome	Reference
	Adélie	Controlled pedestrian approach	Negative	Giese (1998)
	Royal	Controlled pedestrian approach	Negative	Holmes et al. (2005)
	King	Controlled pedestrian approach	Negative	Viblanç et al. (2015)
	Adélie	Helicopter overflights	Negative	Culik et al. (1990)
	Adélie	Helicopter overflights	Negative	Wilson et al. (1991)
	Adélie	Human presence	Negative	Culik et al. (1990)
	Humboldt	Human presence	Negative	Ellenberg et al. (2003)
	Emperor	Human presence	Negative	Regel and Pütz (1997)
	Adélie	Human presence	Negative	Wilson et al. (1991)
	Adélie	Disturbance by researchers	Negative	Boyd and Sladen (1971)
	Emperor	Disturbance by researchers	Negative	Boyd and Sladen (1971)
	Little Blue	Disturbance by researchers	Negative	Carroll et al. (2016)
	Adélie	Disturbance by researchers	Negative	Cockrem et al. (2009)
	Emperor	Disturbance by researchers	Negative	Cockrem et al. (2009)
	Magellanic	Disturbance by researchers	Negative	Hood et al. (1998)
	Little Blue	Disturbance by researchers	Negative	Larcombe (2015)
	King	Disturbance by researchers	Negative	Viblanç et al. (2012)
	King	Disturbance by researchers	Negative	Viblanç et al. (2015)
	King	Disturbance by researchers	Negative	Viblanç et al. (2016)
	Yellow-eyed	Tourism	Negative	Ellenberg et al. (2007)
	Magellanic	Tourism	Negative	Walker et al. (2005)
	King	UAV overflights	Negative	Weimerskirch et al. (2018)
	Rockhopper	Human presence	None detected	Poisbleau et al. (2009)
	Magellanic	Tourism	None detected	Villanueva et al. (2012)
	Rockhopper	Disturbance by researchers	None detected	Ludynia et al. (2012)
	Gentoo	Tourism/Disturbance by researchers	None detected	Trathan et al. (2008)
Breeding success and Population size	Adélie	General human activities	Negative	Thomson (1977)
	Adélie	General human activities	None detected	Patterson and Fraser (1998)
	Royal	Disturbance by researchers	None detected	Hull and Wilson (1996)
	Rockhopper	Disturbance by researchers	None detected	Hull and Wilson (1996)
	Adélie	Tourism	None detected	Patterson (2003)

Response measured	Penguin Species	Disturbance stimulus	Outcome	Reference
	Magellanic	Tourism	None detected	Villanueva et al. (2012)
	Yellow-eyed	General human activities	Negative	Roberts and Roberts (1973)
	Adélie	Helicopter overflights	Negative	Wilson et al. (1991)
	African	Human presence	Negative	Hockey and Hallinan (1981)
	Adélie	Disturbance by researchers	Negative	Giese (1996)
	Humboldt	Tourism	Negative	Ellenberg et al. (2003)
	Yellow-eyed	Tourism	Negative	Ellenberg et al. (2007)
	Adélie	Tourism	Negative	Giese (1996)
	Little Blue	Tourism	Negative	Larcombe (2015)
	Gentoo	Tourism	Negative	Lynch et al. (2010)
	Yellow-eyed	Tourism	Negative	McClung et al. (2004)
	Humboldt	Tourism	Negative	Ellenberg et al. (2006)
	Adélie	Tourism/Disturbance by researchers	Negative	Woehler et al. (1994)
	Yellow-eyed	Disturbance by researchers	None detected	Stein et al. (2017)
	Little Blue	Disturbance by researchers	None detected	Vertigan et al. (2012)
	Adélie	Tourism	None detected	Carlini et al. (2007)
	Gentoo	Tourism	None detected	Cobley and Shears (1999)
	Gentoo	Tourism	None detected	Holmes et al. (2006)
	Adélie	Tourism	None detected	Lynch et al. (2010)
	Magellanic	Tourism	None detected	Yorio and Boersma (1992)
	Adélie	General human activities	Negative	Bricher et al. (2008)
	Little Blue	General human activities	Negative	Giling et al. (2008)
	Adélie	General human activities	Negative	Muller-Schwarze (1985)
	Gentoo	General human activities	Negative	Muller-Schwarze (1985)
	Chinstrap	General human activities	Negative	Muller-Schwarze (1985)
	Adélie	Helicopter overflights	Negative	Thomson (1977)
	Adélie	Disturbance by researchers	Negative	Wilson et al. (1990)
	Adélie	Disturbance by researchers	Negative	Young (1990)
	Humboldt	Tourism	Negative	Reyes-Arriagada et al. (2013)
	Magellanic	Tourism	Negative	Reyes-Arriagada et al. (2013)
	Humboldt	Tourism	Negative	Simeone and Schlatter (1998)

Response measured	Penguin Species	Disturbance stimulus	Outcome	Reference
	Magellanic	Tourism	Negative	Simeone and Schlatter (1998)
	Gentoo	General human activities	None detected	Cobley et al. (2000)
	Adélie	General human activities	None detected	Fraser and Patterson (1997)
	Adélie	General human activities	None detected	Patterson and Fraser (1998)
	Adélie	Disturbance by researchers	None detected	Micol and Jouventin (2001)