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Factors affecting the population dynamics of Eastern Rockhopper Penguins
(*Eudyptes chrysocome filholi*) on Campbell Island, New Zealand

A thesis presented
in partial fulfilment of the requirements
for the degree of

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ABSTRACT

The population dynamics of seabirds may be influenced by ‘top-down’ predation effects, or from the ‘bottom-up’ by environmental limitations on food availability. Southern Rockhopper Penguin (*Eudyptes chrysocome*) populations have declined hugely at multiple sites across their circumpolar, sub-Antarctic range in recent decades, resulting in an extinction risk of ‘Vulnerable’. They are a small-bodied penguin, adapted to exploit seasonally abundant, pelagic prey by being migratory and having prolonged fasting periods onshore and foraging offshore during breeding. Mysteriously, like other *Eudyptes* penguins they lay an extremely dimorphic two-egg clutch in which the first-laid egg is smaller and less successful, and rarely fledge two chicks.

The world’s largest population (c. 620,000 pairs) of the Eastern sub-species (*E. c. filholi*) of Rockhopper Penguin formerly bred at Campbell Island, New Zealand. Prior to the current work, the only previous intensive research at this site in the mid-1980s revealed the population had declined by a startling 94% since the early 1940s as local sea-surface temperatures (SSTs) increased. It was hypothesized that climate change had reduced the availability of the penguins’ preferred zooplankton prey, so that the Campbell population’s decline was caused by its unusual reliance on a fish-based diet which resulted in low body masses and demographic rates. I examined this hypothesis of bottom-up population regulation by estimating the population growth rate from 1984–2012 and assessing links between SST, diet quality, chick-provisioning rates, chick and adult body masses, egg masses, reproductive success, and first-year and adult survival rates. Additionally, I considered whether top-down predation effects were causing the recent, unusually rapid population decline in a relatively small, fragmented colony. I assessed the population growth rate using digital imagery analysis of current and historic colony photographs, dietary trophic level using stable isotope analysis of blood samples, and chick-provisioning and adult survival rates using an automated gateway to record the colony-sea transit times of individual transponder-tagged penguins breeding at closely monitored nest sites.

I estimated the total Campbell Island population size to be 33,239 breeding pairs in 2012, a 21.8% decrease from an adjusted estimate of 42,528 pairs in 1984. However, the recent decline occurred before 1996 with most colonies stable or growing thereafter under cooler SSTs and more abundant prey. My results supported the previous assertion that the overall population size declined during periods of warm SST and that a zooplankton-based diet was a higher quality diet, resulting in heavier adults and chicks. However, the primary

determinant of chick growth was how often they were fed, and the rigid division of labour between parents during early-chick rearing reduced potential chick-provisioning rates, especially from males in a poor-food year. The ongoing, localized decline of my study population was caused by high rates of predation on adults by sea lions, as well as on eggs by skuas. I did not find support for overlap between migration and egg-formation underlying egg-size dimorphism.

This study emphasizes the constraints that a species' genotype and ecological context place on the degree of behavioural plasticity it exhibits when faced with environmental variability. My results highlight the vulnerability of Eastern Rockhopper Penguins, and likely other *Eudyptes* penguins, to the more variable and warmer environment and less predictable food supply in a future under climate change.



Figure i Eastern Rockhopper Penguin, Campbell Island. Photo by Kyle Morrison.

DEDICATION

*For Sarah, my island girl who is now my wife, now my son's mother, always my foundation
when I'm far out at sea*



Figure ii Sarah Jamieson and Finnigan Morrison at 6 months old. Photo by Kyle Morrison.

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Figure iii Clockwise from top-left: Neil Morrison, Ray Buchheit, Andy Whittaker and Phil Battley, Leigh Torres and David Thompson and Paul Sagar, Henk Haazen, Rob Dunn. Photos by Kyle Morrison.

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CO-AUTHORS

I wrote all parts of this thesis, designed and led all data collection, and performed all analyses. However, I have recognized the essential contributions of eight collaborators by their inclusion as co-authors in specific research chapters.

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Sarah supervised the stable isotope analysis of blood samples for Chapter 3, which she also revised and is a co-author.

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Rob Dunn

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Chapter 1

GENERAL INTRODUCTION



Figure 1.0 Top: Eastern Rockhopper Penguins coming ashore in a breaking wave. Bottom: Recently landed penguins in Smoothwater Bay, Campbell Island. Photos by Kyle Morrison.

SEABIRD ECOLOGY

The Earth is primarily covered in salt water, and seabirds have evolved a diversity of forms and strategies to exploit marine prey over most of that vast area to meet their own energy demands and those of their offspring. For example, terns and storm petrels are adapted to surface feeding, while the larger auks and penguins routinely dive to 100 m depth and beyond (Gaston 2004). Most marine productivity originates with phytoplankton which provide food for zooplankton, cephalopods, and fish; these in turn feed fish, seabirds, and marine mammals, notwithstanding the predator-prey relationships amongst these taxa. Phytoplankton and zooplankton productivity is determined by sunlight, nutrients, and sea temperature. The duration and intensity of solar radiation varies predictably by latitude and through each year, but currents, stratification, terrestrial inputs, and bathymetry create dynamic levels of nutrients and sea temperature that can vary greatly through space and time (Hunt et al. 2001). Consequently, phytoplankton, zooplankton, and therefore fish and cephalopod productivity and distributions may be predictable at certain times and locations, but are often sparsely or patchily distributed and intermittent or highly seasonal (Mackas et al. 2001; Murphy et al. 2001).

The marine prey of seabirds are patchily distributed and abundances vary through time. Seabirds' shared challenges of locating and obtaining prey have been fundamental to the evolution of a similar breeding ecology and slow life history strategy across most seabird taxa (Williams 1995; Gaston 2004). Colonial breeding facilitates information transfer between individuals on foraging locations. High breeding site fidelity allows familiarization with neighbouring pairs and foraging locations and synchronized breeding. High mate fidelity may increase breeding success through better synchronization of foraging trips and prevent delays in laying or missing breeding seasons. A late age at first breeding allows development of the foraging proficiency and body condition required to successfully rear offspring. A small clutch size and low annual fecundity represent conservative investments in eggs and chick-provisioning by parents reluctant to risk their own survival and future breeding attempts for the uncertain outcome of breeding in any given year. A high adult survival rate allows for multiple breeding attempts over an individual's lifetime, most of which will occur under inadequate foraging conditions, causing egg or chick failure or the mortality of those offspring which do fledge before they recruit into the breeding population years later.

SEABIRD POPULATION DYNAMICS

The slow-life history strategy of most seabirds, including delayed recruitment, low annual fecundity, and a high adult survival rate, results in their population growth rate being most sensitive to changes in adult survival. Seabird populations can remain stable with semi-regular mass breeding failures, but a single mass mortality event of adults immediately causes a decrease in population size that will take years to recover from. Adult mass mortality events are rare and difficult for seabirds to adapt to or avoid because they are associated with irregular events such as severe storms, extreme El Niño years, disease epidemics, and oil spills. Typically, seabird adult survival rates are high and stable relative to reproductive success, as adults buffer their own survival rates by limiting their investment in reproduction under poor feeding conditions (Drent and Daan 1980; Sandvik and Einar Erikstad 2008). Hence, reproductive success is generally more closely associated with oceanographic indices reflecting food availability such as sea-surface temperature (SST) or chlorophyll levels reflecting phytoplankton densities, than are adult survival rates (Gjerdrum 2003; Morrison et al. 2011). Regulation of seabird population dynamics through the availability of prey in lower trophic levels is called “bottom-up control”, and is more common than “top-down control” from predation of seabirds or their eggs or chicks (Frederiksen et al. 2006; Ainley and Hyrenbach 2010). Survival of sub-adult pre-breeders from fledging until recruitment as (“adult”) breeders is the least-studied seabird demographic rate, owing to the long-term studies required to measure it. First-year survival is typically lower than subsequent survival of pre-breeders, as the latter may have a similar survival rate to that of adults (Guinard et al. 1998; Dehnhard et al. 2014). The challenge of developing the foraging skills required to sustain themselves appears to select against low-quality first-year seabirds or those in poor condition at independence (Morrison et al. 2009). The result is that although the population growth rate of seabirds is most sensitive to changes in adult survival, it may be the more variable rates of reproductive success and first-year survival that largely determine the population trend (Jenouvrier et al. 2009a).

HUMAN-INDUCED CHANGE IN MARINE ECOSYSTEMS

Human activities are having profound effects on marine ecosystem in each of the world’s oceans. Seabird demographic rates may be affected by humans directly and conspicuously through by-catch mortality in commercial fisheries and oil spills (Votier 2008; Barbraud et al. 2012), but more often anthropogenic effects are indirect and harder to quantify and mitigate

against. For example, competition for prey with commercial fisheries may be associated with seabird population declines (Crawford 2007), but demonstrating a causative link is challenging because of the confounding effects of environmental effects on prey availability (Engelhard et al. 2014), and legislating for an ecosystem-based approach to fisheries management that allocates a portion of fish stocks to wildlife even more difficult (Cury et al. 2011; Katsanevakis et al. 2011). Human exploitation of the oceans can have positive effects for seabirds (at least in the short-term), as offal from deep-sea fish species may be an important source of food for scavenging procellariids (James and Stahl 2000; Xavier et al. 2004). Additionally, the historic over-exploitation of pinnipeds and whales in the Southern Ocean appears to have resulted in a 'krill surplus' and growth in penguin populations, some of which are now in decline as marine mammal populations recover (Trathan et al. 2012; Emslie et al. 2013). Humans may directly harvest seabird eggs, chicks, or adults for food or fishing bait, but most human-induced predation of seabirds occurs through the introduction of alien terrestrial mammals to islands (Trathan et al. 2014). Alien mammals can rapidly cause the local or global extinction of a seabird population, but mammal eradication and seabird reintroduction techniques have improved rapidly in recent years (Howald et al. 2007; Deguchi et al. 2012).

One of the most serious and challenging threats to seabird populations is climate change. Climate change affects seabirds at multiple levels, the most important of which is for the potential to reduce the abundance, availability, or quality of prey species (Barbraud et al. 2011; Quillfeldt and Masello 2013). Seabird prey, or the zooplankton and phytoplankton their prey relies upon, may be sensitive to changes in water temperature, resulting in lower prey availability to seabirds through range shifts or lower rates of reproduction and survival (Frederiksen et al. 2006; Richardson 2008). Warm water is less dense than cold water, so that warmer temperatures can cause water stratification and prevent upwelling of cold, nutrient-rich water that stimulates marine productivity. It has already been shown that climate change is creating not only a warmer world, but a more variable climate in which severe storms, heat waves, and extreme climate events such as El Niño occur more frequently (Meehl and Washington 1996; Timmermann et al. 1999). Such events are linked not only to poor breeding success of seabirds, but more importantly to low adult survival rates that can cause rapid and dramatic population declines (Vargas et al. 2007). More variable temperatures may also create mismatches between the timing of peak prey availability and the energetic requirements of seabirds (Hipfner 2008; Gaston et al. 2009). Such mismatches are likely to occur when seabirds and their prey use different phenological cues (e.g., SST vs. photoperiod) or differ in their response to the same cue (Durant et al. 2007; Dawson 2008). Climate change is also the least

tangible and manageable threat to seabirds, given humanity's reliance on fossil fuels and projections that global temperatures will continue to rise for centuries even if greenhouse gas pollution was stopped today (Meehl 2006). Furthermore, most of our seabird knowledge has been accumulated over the past 75 years, during a very narrow range of the past and future climate conditions, so that we have a limited understanding of the resilience and adaptability of seabirds to climate change and what conservation management actions might help buffer seabird populations against climate change.

BEHAVIOURAL PLASTICITY, CONSTRAINTS, AND CANALIZATION

The ability of seabirds to adapt to natural and human-induced changes in the marine environment is largely determined by their degree of behavioural plasticity. Behavioural plasticity is the expression of different behaviours under various environmental conditions (Nussey et al. 2007). Certain seabirds behaviours are very plastic, such as chick-provisioning rates, whereas others might be canalized and invariable regardless of environmental change, like the fixed one-egg clutch size of procellariids (Gaston 2004; Saraux et al. 2011). The degree of behavioural plasticity a seabird is able to express is determined in part by its genotype (there is no evidence that a two-egg clutch genotype exists within the Procellariidae), and in part by ecological constraints (a mutant two-egg clutch genotype is unlikely to be successful because procellarid parents struggle to provision one chick, let alone two). Given that individuals will vary genetically, physiologically and in the environmental conditions they encounter, constraints on behavioural plasticity will also vary between individuals, populations and species (Nussey et al. 2007; Gremillet and Charmantier 2010). This may limit the ability of individuals and species to respond to current threats such as climate change.

PENGUINS

The extant penguins include 18 species in six genera. Penguins evolved from flying seabirds c. 71 million years ago (Baker et al. 2006). Penguin wings are highly adapted flippers that allow more efficient diving than either wing- or foot-propelled flying seabirds (Elliott et al. 2013). The smallest and most tropical penguins, the Little Penguin (*Eudyptula minor*) and Galapagos Penguins (*Spheniscus mendiculus*) are heavier than the heaviest flying auks of the northern hemisphere (≥ 1 kg), whereas the most polar breeding bird in the world, the Emperor Penguin (*Aptenodytes forsteri*) is c. 30 times heavier (Gaston 2004). This pattern and the energetic trade-off between efficient wing-propelled diving and flight suggests that the evolution of

flightlessness allowed penguins to become larger and occupy otherwise inhospitable regions. Larger animals lose less heat through their lower surface-area to volume ratio, allowing a slower metabolism and lesser energy requirements than smaller animals would have in environments where the ambient temperature is below body temperature. Thus, a large body size also facilitates the unique penguin trait of a rapid and complete moult (Williams 1995). Such a moult jeopardizes penguin's water-proofing and thus occurs on land, thereby requiring substantial body reserves and relatively low metabolic rate to survive a multi-week fast and to fuel feather growth. Some penguin species also have prolonged periods of fasting during the breeding season, over one or more stages of courtship, incubation, and chick-rearing.

Like most other seabirds, penguins generally have a slow life-history strategy, but as in other animals, the larger-bodied penguin species tend to have a later-age at first-breeding, lower-fecundity, and higher adult-survival rates than the smaller-bodied species. For example, the *Aptenodytes* penguins (Emperor and King Penguins) are the largest, the only genus that lays a one-egg clutch, and have among the latest age at first breeding and highest adult survival rates (Williams 1995; Davis and Renner 2003). In contrast, Little and Galapagos Penguins lay a two-egg clutch like all other penguins, but may produce two broods in a single year, and breed for the first time as early as 1-year old while surviving at a lower rate as adults. Variation in penguin life history strategies is also linked to whether the species is sedentary and exploits nearshore prey or migrates away from breeding colonies over-winter and is an off-shore forager. For example, sedentary Yellow-eyed (*Megadyptes antipodes*) and Gentoo Penguins (*Pygoscelis papua*) are larger-bodied, but breed at a younger age and have higher fecundity than sympatric and migratory *Eudyptes* penguins (Croxall and Davis 1999; Davis and Renner 2003). Migration and foraging strategies also interact with breeding ecology, as migratory species tend to arrive at breeding sites with large body reserves and make extended fasts during a shorter breeding season. They do so by exploiting seasonally abundant prey over a larger foraging area, supporting larger breeding population sizes and enabling them to recover from fasts and raise chicks in a shorter time than sedentary, nearshore foragers.

EUDYPTES PENGUINS

There are currently seven recognized extant species of *Eudyptes* or crested penguin, speciated from the ancestral Eudyptid within the past c. eight million years (Baker et al. 2006). The crested penguins are so-named for their yellow/orange superciliary crest feathers. *Eudyptes* penguins are the most diverse penguin genus, and occur over the largest geographic area,

having a circumpolar distribution including islands of the sub-tropics south to the Polar Front. *Eudyptes* rival *Pygoscelis* penguins for the largest total population size of c. eight million individuals (Borboroglu and Boersma 2013). This large total population is mostly accounted for by Macaroni Penguins, but these and all other Eudyptids have threat rankings of 'Vulnerable' or 'Endangered' because of substantial population declines and/or restricted breeding ranges (IUCN 2014). The New Zealand region, including New Zealand's South Island and sub-antarctic island groups and Australia's Macquarie Island, was the origin of the genera's species radiation, and retains the greatest diversity (five species including four endemics, Baker et al. 2006).

Eudyptes penguins range in body size from small to intermediate relative to other penguins, but have the slow life history strategy of the much larger *Aptenodytes* penguins, undoubtedly driven in large part by their migratory and offshore-foraging strategies (Croxall and Davis 1999; Stein and Williams 2013). Macaroni (*Eudyptes chrysolophus*) and Rockhopper Penguins (*E. chrysocome filholi*, *E. c. chrysocome*, *E. moseleyi*) travel 1,500-2,500 km from breeding colonies during their five-six month over-winter period at sea (Thiebot et al. 2013; Ratcliffe et al. 2014), and may travel c. 300 km away on incubation foraging trips and \leq c. 50 km on daily foraging trips (Sagar et al. 2005; Ludynia et al. 2013). *Eudyptes* penguins have a two-egg clutch, but fledging two chicks is very rare and has never been observed in the three largest-bodied species which only hatch one egg (St. Clair 1998). In the four smaller-bodied species that may hatch both eggs, typically only the second-laid 'B-egg' results in a fledged chick, as first-laid 'A-eggs' are smaller, hatch later, and A-chicks are outcompeted for regurgitated food and space under the brooding parent. B-eggs are preferentially incubated, and A-eggs may be 'deliberately' ejected around the time of B-egg laying in the larger species, or displaced just before hatching by movements of the B-chick and parent in the smaller species (St Clair et al. 1995; St. Clair and St. Clair 1996). The mismatch between the clutch size and fecundity of *Eudyptes* penguins suggests their two-egg clutch is a maladaptive canalized trait, but what caused the evolution of a smaller A-egg, rather than a smaller B-egg, remains uncertain (Stein and Williams 2013). *Eudyptes* penguins are also exceptional in the long 5-7 week courtship/incubation fast of both sexes, and the 3-5-week incubation/guard stage fast of males (Williams 1995). All other penguin species alternate chick guarding (brooding) duties between the sexes daily or every few days, so that males do not have a second long fast during breeding. Furthermore, it is typical in other penguin species that females make the first incubation foraging trip soon after laying, but Eudyptids have a prolonged shared incubation period initially, followed by males going to sea for 9-16 days, and then females on a shorter

trip before hatching. Observations of unusual male-first incubation trips in Adélie (*Pygoscelis adeliae*) and Chinstrap (*P. antarctica*) Penguins suggests this occurs when males have spent considerably more time ashore than females before laying, so that males have depleted their body reserves to a greater degree than females (Ainley et al. 1983; Trivelpiece and Trivelpiece 1990). This observation, that the degree of protandry determines incubation-shift order, is supported by the male-first pattern in Fiordland Penguins (*E. pachyrhynchus*) described below.

Most species of *Eudyptes* penguins breed on the surface in dense colonies, often on rocky slopes above the shoreline. However, two New Zealand endemic species behave differently. Snares Penguins (*E. robustus*) often breed on flat ground under tree cover, and Fiordland Penguins nest in isolation or in small/loose colonies under forest and in small caves (Warham 1975). The migration and foraging ecology of Fiordland Penguins is unknown, but they are suspected of foraging in more nearshore waters than other Eudyptids (Warham 1974b). A unique foraging ecology, closer to that of a nearshore foraging penguin species, is suggested by Fiordland penguins being distinct among Eudyptids in having less synchronous laying, the least dimorphic eggs, and the highest rate of rearing both chicks from a nest (St. Clair 1992). Also uniquely, males and females in a pair appear to occupy nest sites at a similar date instead of males arriving before females by c. 1 week, and have a longer period before laying than in other Eudyptids (Grau 1982). The sexes similar pre-laying fast durations likely leads to females making the first incubation foraging trip and males the second before hatching, thereby reducing the second long fast of males to just the guard period. The large breeding aggregations and predictable transits between sea and shore of other Eudyptids attract avian and pinniped predators that may decrease penguin demographic rates.

STUDY SPECIES

Eastern Rockhopper Penguins (*Eudyptes chrysocome filholi*) are given full species status (*E. filholi*) and have a 'Nationally Critical' threat status in New Zealand (Robertson et al. 2013), but are classified as a sub-species of the 'Vulnerable' Southern Rockhopper Penguins (*E. c. chrysocome*) by the International Union of the Conservation of Nature (IUCN; BirdLife International 2012). Eastern Rockhopper Penguins breed at sub-Antarctic islands of the Indian Ocean and in the New Zealand Region, the latter including small remnants of historically large populations at Antipodes Island and the Auckland Islands (< 3,000 pairs each), and larger populations at Campbell Island and Macquarie Island (> 30,000 pairs each, Chapter 2 and references therein). Southern Rockhopper Penguins breed on islands of Southern South

America along the coasts of Chile and Argentina, and at the Falkland Islands. Only recently were Northern Rockhopper Penguins recognized as a separate species from Southern/Eastern Rockhopper Penguins, but their distinctness is more readily apparent, including an earlier timing of breeding in warm, sub-temperate waters, exceptionally long crest feathers, and different vocalizations (Jouventin et al. 2006; de Dinechin et al. 2009). Southern and Eastern Rockhopper Penguins are very similar in their breeding ecology and morphology, the most obvious difference being the white/pink skin around the base of the bill of Eastern Rockhopper Penguins and white/pink colouration on the lower mandible in the New Zealand region, whereas the “black-faced” Southern (and Northern) Rockhopper Penguin has black skin around the bill and solid orange/brown lower and upper mandible (Morrison 2013; Pütz et al. 2013).

Rockhopper Penguins have evolved a body size and breeding pattern that places them at the boundary of success and failure and relies upon predictably abundant food around breeding colonies. They are the third-smallest penguin species after Little and Galapagos Penguins (Borboroglu and Boersma 2013). The small body size of Little Penguins increases their vulnerability and that of their nests to avian predators, so that they breed in isolation or in loose colonies in burrows or dense vegetation and are the only penguin species that transits between sea and shore only at night. Therefore, if Rockhopper Penguins were any smaller their colonial surface nests and diurnal colony transits would likely cause high predation rates that would challenge population persistence. At their present body size they are still more vulnerable to predation than larger penguin species. Female Rockhopper Penguins may lose c. 40% of their arrival body mass over their courtship/incubation fast of > 6 weeks duration (Chapters 3 and 5). The pre-fasting body composition of Rockhopper Penguins (26% lipid) and proportion of mass loss during breeding fasts are similar to those of Emperor Penguins, the largest penguin species whose greater size results in a slower metabolic rate and lessened risk of starvation (Cherel et al. 1993; Robin et al. 1998). Perhaps more remarkably, female Rockhopper Penguins make this large investment in reproduction (including clutch production) without up-to-date knowledge on the current season’s local food availability. Females initiate egg formation on migration 1-2 weeks before arriving to breed (Chapter 6), resulting in highly repeatable lay dates and little behavioural plasticity within populations for matching their timing of reproduction to changes in peak food availability (Dehnhard et al. 2015). Additionally, feeding conditions at females’ arrival > 6 weeks previously may not closely reflect those on their incubation foraging trip when they must regain some of their lost reserves before exclusively provisioning their chick(s) for ≥ 3 weeks. In contrast to their relatively fixed breeding schedule, Rockhopper Penguins may have a generalist diet, including various species

of zooplankton, cephalopods, and fish (Cooper et al. 1990). However, in a given year at a particular site, one or two species of zooplankton may dominant the diet fed to chicks (Tremblay and Cherel 2003).

All three Rockhopper Penguin taxa have experienced dramatic population declines, primarily in the second-half of the 20th century, some of which may be ongoing (BirdLife International 2010). Reduced food availability and/or quality because of climate change is suspected as an important cause of the declines, given their broad geographic area and largely simultaneous timing in conjunction with major oceanographic changes (Cunningham and Moors 1994, Guinard et al. 1998; Pütz et al. 2006). A retrospective study of Rockhopper Penguin diet through stable isotope analysis of feathers suggested no change in diet quality, but marine productivity decreased at some sites as SST warmed (Hilton et al. 2006). Alternative, but non-exclusive hypotheses include disease epidemics, mass mortality during blooms of toxic algae, and competition for prey with, and predation by pinniped populations recovering following historic exploitation (BirdLife International 2010).

STUDY SITE

Campbell Island New Zealand (52° 32' 12" S, 169° 2' 10" E) is New Zealand's southern-most sub-Antarctic island group. It is part of New Zealand's sub-Antarctic World Heritage Area, is an ecological preserve, and in 2014 had a restricted-use marine protected area created around a portion of its circumference out to 12 nautical miles (Peat et al. 2006). The island was perhaps first discovered by a sealing ship in 1810, as prior Polynesian visitation has yet to be confirmed. Sealers introduced Norway rats (*Rattus norvegicus*) which affected the ecosystem heavily until their eradication in 2001. Sheep and cattle farming was tried early in the 20th century, but abandoned, the last feral stock to be eliminated were sheep on the western peninsula in 1989. WWII coast watchers lived year-round on the island in the 1940s and provided important observations and photographs of the much larger southern elephant seal (*Mirounga leonina*), Campbell (*Thalassarche impavida*) and Grey-headed (*T. chrysostoma*) Albatross, and Eastern Rockhopper Penguin populations of that time (Bailey and Sorensen 1962). A small population of Erect-crested Penguins (*E. sclateri*) formerly bred at Campbell Island, but appear to have been extirpated during the Eastern Rockhopper Penguin population decline. Currently, the only other penguin species breeding on the island, Yellow-eyed Penguin, breeds at isolated nests in the *Dracophyllum* scrub forest around much of the island, but form a comparably small population, estimated to be 1,034 individuals in 1992 and of unknown recent trend

(Moore et al. 2001). Meteorological staff lived on the island year-round from the 1970s to 1995 and created infrastructure still useful to the only current island visitors – researchers and cruise ship tourists that are strictly controlled by the New Zealand Department of Conservation (DOC).

Campbell Island is a long-extinct volcano, now heavily eroded and indented by deep harbours because of the regions strong swells, winds, and frequent rain (Bailey and Sorensen 1962). The tallest cliffs occur on the island's western peninsula because of the predominantly south-westerly swells. The talus and boulder slopes below these western cliffs between Mount Paris and Mount Yvon are where the largest breeding colonies of Eastern Rockhopper Penguins occur (Chapter 2). The only readily accessible, but relatively small colony occurs nearby at Penguin Bay. A two-bunk field hut, 'The Penguin Bay Hilton', was erected at this site in the early 1980s to support the only previous intensive study of Eastern Rockhopper Penguins from 1984/1985 to 1986/1987. It was this study that estimated that the population had crashed by 94% from 1942 to 1984. Resident breeding avian predators of Eastern Rockhopper Penguin eggs and small chicks include Brown Skuas (*Catharacta antarctica lonnbergi*), and Northern Giant Petrels (*Macronectes halli*) predate larger chicks, pre-breeders, and adults. There is a growing population of New Zealand sea lions (*Phocarctos hookeri*) at Campbell Island, which are known to depredate other penguin species. Resident New Zealand fur seals (*Arctocephalus forsteri*) have been recorded to depredate Eastern Rockhopper Penguins at Campbell Island. The fur seal population size and trend is unknown, but is likely still much lower than before the sealing era in the early 19th century.

AIMS OF THIS THESIS

Previous research had established a dramatic population decline of Eastern Rockhopper Penguins at Campbell Island, and suggested the decline resulted from warm SST reducing the availability of zooplankton prey (Cunningham and Moors 1994). In the mid-1980s penguins were feeding on a more-fished based diet and chick fledging masses were lower than recorded at other breeding sites. The aims of this thesis are to more fully explore the factors affecting penguin population dynamics through a further examination of the hypothesized relationships between population dynamics, SST, diet quality, and chick growth. In addition, I evaluated adult body masses and provisioning rates in relation to diet quality and chick growth, the effects of predation on the population growth rate of the Penguin Bay study population, and potential determinants of the relative masses of the species' extremely dimorphic eggs. I

employed a variety of recent technological advances to facilitate data collection and analysis, while decreasing the risk of detrimental research effects to the penguins. Such technologies included digital photography and analysis of colony size, stable isotope analysis of penguin blood samples, individually marking penguins with passive integrated transponder (PIT) tags, and the use of an automated gateway to record PIT tag codes to determine survival and provisioning rates.

RESEARCH CHAPTERS

My three field research seasons on Campbell Island, 2010–2011, 2011–2012, and 2012–2013, occurred between mid-October and mid-January, and so considered the penguin's courtship, incubation, and the first-half of the chick-rearing period. My opportunity to spend time in Penguin Bay in the 2010–2011 season was limited, so it acted as a pilot year that set up more intensive research during the following two seasons.

This thesis is written in the style of five stand-alone scientific journal articles, two of which (Chapters 2 and 3), have been published in *Polar Biology*, and *Marine Biology*, respectively. In the five research chapters I considered the following focal questions, by chapter number:

2. What were the 1984–1996 and 1996–2012 population growth rates of Eastern Rockhopper Penguins on Campbell Island and were they associated with patterns of SST?
3. Was a higher-trophic level, more fish-based diet, a higher quality diet for Eastern Rockhopper Penguin adults and chicks, in that individuals with a higher trophic level diet had a greater body mass than those feeding at a lower trophic level?
4. Does the canalized division of labour strategy of Eastern Rockhopper Penguins during early chick-rearing reduce their potential provisioning rates relative to a strategy of shared parental roles?
5. Is the localized decline of the Eastern Rockhopper Penguin population in Penguin Bay being caused by predation?
6. Does a carry-over effect of migration underlie individual variation in extreme egg-size dimorphism in Eastern Rockhopper Penguins?



MASSEY UNIVERSITY
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**STATEMENT OF CONTRIBUTION
TO DOCTORAL THESIS CONTAINING PUBLICATIONS**

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Kyle William Morrison

Name/Title of Principal Supervisor: Dr. Phil Battley

Name of Published Research Output and full reference:

Morrison KW, Battley PF, Sagar PM, Thompson DR (2014) Population dynamics of Eastern Rockhopper Penguins on Campbell Island in relation to sea surface temperature 1942–2012: current warming hiatus pauses a long-term decline. *Polar Biology*. Available online. doi:10.1007/s00300-014-1575-x

In which Chapter is the Published Work: 2

Please indicate either:

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and / or
- Describe the contribution that the candidate has made to the Published Work:
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Chapter 2

POPULATION DYNAMICS OF EASTERN ROCKHOPPER PENGUINS ON CAMPBELL ISLAND IN RELATION TO SEA SURFACE TEMPERATURE 1942–2012: CURRENT WARMING HIATUS PAUSES A LONG-TERM DECLINE

Morrison KW, Battley PF, Sagar PM, Thompson DR (2015) *Polar Biology* 38 (2):163-177.



Figure 2.0 Yvon Villarceau Eastern Rockhopper Penguin colony looking northeast (top) and southwest (bottom). Photos by Kyle Morrison.

ABSTRACT

Major population changes of marine mega-fauna are ongoing as global warming and other anthropogenic drivers affect prey availability. The historical stronghold of the Eastern Rockhopper Penguin (*Eudyptes chrysocome filholi*) was New Zealand's sub-Antarctic Campbell Island, but the population declined by 94% between 1942 and 1984. The apparent mechanism of collapse was warm ocean temperatures causing an inadequate food supply. *Eudyptes* penguin population declines are ongoing at some breeding sites, highlighting the need to investigate the population trend on Campbell Island since 1984. We estimated the Eastern Rockhopper Penguin breeding population size through physical and photo-counts of birds and nests in 2012, and changes in colony area relative to 1984 and 1996 photos. We estimated the 2012 population size at 33,239 breeding pairs, a 21.8% decrease from an (adjusted) estimate of 42,528 pairs in 1984. Although substantial, the recent 1984–2012 decline occurred at a much slower rate ($\lambda = 0.991$) than the 1942–1984 decline ($\lambda = 0.940$). Despite great variation in trends between colonies ostensibly linked to differences in predation rates, the recent decline occurred primarily between 1984 and 1996, and thereafter the overall population grew. A 100-yr time series of extended reconstructed sea surface temperatures (ERSST) confirmed that the population declined during warm periods and increased during cool periods, but that the initial decline began before increases in regional ERSST. Population growth after 1996 appears related to the current global warming hiatus, lower ERSST, and increased abundance of a key prey species. We predict a continuation of the long-term population decline after warming resumes.

INTRODUCTION

Global warming, fisheries, habitat degradation, and historical and contemporary over-exploitation are altering predator-prey dynamics and species' distributions, causing rapid population changes in many marine mega-fauna (Hucke-Gaete et al. 2004; Rolland et al. 2008; Trivelpiece et al. 2011; Hazen et al. 2012). Most penguin populations have declined in recent decades, with 11 of 18 species designated by BirdLife International as being threatened with extinction (Vulnerable or Endangered), four as Near Threatened, and three as Least Concern (BirdLife International 2014). Although considerable attention has been given to the future of the two strictly Antarctic-breeding penguin species, Adélie Penguins (*Pygoscelis adeliae*), and Emperor Penguins (*Aptenodytes forsteri*), in a warming world (Barbraud and Weimerskirch

2001; Croxall et al. 2002; Jenouvrier et al. 2009b), those of greatest immediate concern are the less studied species of lower latitudes, some of which have been declining rapidly for decades. For example, all seven crested penguins of the genus *Eudyptes* are ranked as Vulnerable or Endangered (BirdLife International 2014).

Rockhopper Penguins have a circumpolar distribution, breeding on 25–30 island groups of the southern regions of the Atlantic, Indian, and Pacific Oceans. Northern Rockhopper Penguins (*Eudyptes moseleyi*) were recently recognized by BirdLife International as a separate species from Southern Rockhopper Penguins (sometimes called Western Rockhopper Penguins, *E. chrysocome chrysocome*), and some researchers support full species status for Eastern Rockhopper Penguins (*E. c. filholi*; Banks et al. 2006; de Dinechin et al. 2009). In the past 37 years the global populations of Southern/Eastern and Northern Rockhopper Penguins have declined by 34 and 57%, respectively (BirdLife International 2010), resulting in IUCN Red List rankings of 'Vulnerable' and 'Endangered' (BirdLife International 2014; but see Robson et al. 2011; Baylis et al. 2013). At many Rockhopper Penguin breeding sites the population record extends back only 30 years (BirdLife International 2010), but where the record extends back further to the mid-20th century, declines of c. 90% representing millions of birds have been documented (Cunningham and Moors 1994; Pütz et al. 2003; Cuthbert et al. 2009). Suggested causes of Rockhopper Penguin population declines vary from lower food availability related to warmer (Cunningham and Moors 1994) or cooler (Guinard et al. 1998; Pütz et al. 2006) sea surface temperatures (SSTs), oiling and negative fisheries effects (Bingham 2002; Pütz et al. 2006), direct mortality from humans and introduced pests (Cuthbert et al. 2009), and predation by or competition with growing pinniped populations (Cuthbert et al. 2009). The widespread and largely simultaneous declines of Rockhopper Penguin populations throughout their range might signal a single shared cause. A longitudinal study of stable isotope signatures of Rockhopper Penguin feathers at seven breeding sites supported an overall decline in marine productivity through the 20th Century, and suggested Rockhopper Penguins had a lower-quality diet in years of warm SST (Hilton et al. 2006, but see Morrison et al. 2014 – hereafter 'Chapter 3').

Campbell Island (52° 32' 24" S, 169° 8' 42" E), New Zealand's southernmost sub-Antarctic territory, formerly held the world's largest breeding colony of Eastern Rockhopper Penguins ('Rockhopper(s)'), but a dramatic decline between 1942 and 1984 reduced the population by an estimated 94% (Moors 1986; Cunningham and Moors 1994). Researchers typically represent penguin population size as the number of breeding pairs, equal to the number of nests actually counted during the incubation period or estimated by nest

density*colony area (Trathan 2004; Cuthbert et al. 2009; Baylis et al. 2013). Cunningham and Moors (1994) measured nest density in a photo of one historical colony and by sub-sampling in two contemporary colonies, and estimated or measured colony areas to derive estimates of 814,550 breeding pairs on Campbell Island in 1942 and 51,550 pairs in 1985. The authors suggested that the decline was linked to warming SSTs that may have reduced availability of preferred prey around Campbell Island, leading to reduced reproductive success and survival. Prior to our study the current size of the Rockhopper Penguin population on Campbell Island was unknown, but the rate of decline at some other colonies may have accelerated in recent years (BirdLife International 2014).

The steep, rocky, and generally inaccessible Rockhopper Penguin colonies on Campbell Island make traditional methods of physically measuring colony areas and nest densities extremely difficult at most sites. However, recent technological advances in photographic and digital image analysis allowed our development of alternative methods based on counting penguins in high resolution digital photo mosaics ('photo-counts') in 2012, and comparing change in relative colony area in oblique photos taken from standardized locations ('photopoints') in 1984, 1996, and 2012. Throughout our study we refer to Cunningham and Moors (1994) population estimate in 1985 as the 1984 estimate to coincide with the photopoint photos we used that were taken in 1984.

The primary objectives of the current study were to estimate the size of the Rockhopper breeding population on Campbell Island in 2012 and rates of population change from 1984–1996 and 1996–2012. Secondly, we related population dynamics from 1942–2012 to a 100-yr time series of SST. Thirdly, we surveyed the current occupation status of 20 of 23 former colony sites and summarized historical information on colony occupancy. Additionally, we examined inter-colony differences in rates of population change, revised the 1942 and 1984 population estimates by suggesting alternative, colony-specific nest densities, and suggested methods to use for future population estimates.

MATERIALS AND METHODS

Study species

Southern/Eastern Rockhopper Penguins are among the world's smallest penguin species, being 45–55 cm in length, and weighing 2.2–4.3 kg (Marchant and Higgins 1990). The sexes are reliably separated by bill measurements (Warham 1972; Hull 1996), with larger-billed males

readily distinguishable in breeding pairs. Rockhopper Penguins are highly gregarious and often form large breeding colonies. They are socially monogamous and appear to form long-lasting pair bonds, renewed annually by high nest site fidelity and visual and vocal recognition (Warham 1975). The nest site is a lined scrape on rock terraces, on scree slopes, among boulders, and occasionally among tussock or in caves, sometimes 400 m from shore on Campbell Island (Marchant and Higgins 1990). The only Rockhopper Penguin colony on Campbell Island that is readily accessible to researchers is at Penguin Bay. In 2012 the Penguin Bay colony consisted of four sub-colonies including the adjacent Ravine sub-colony (Figure 2.1, Table 2.1).

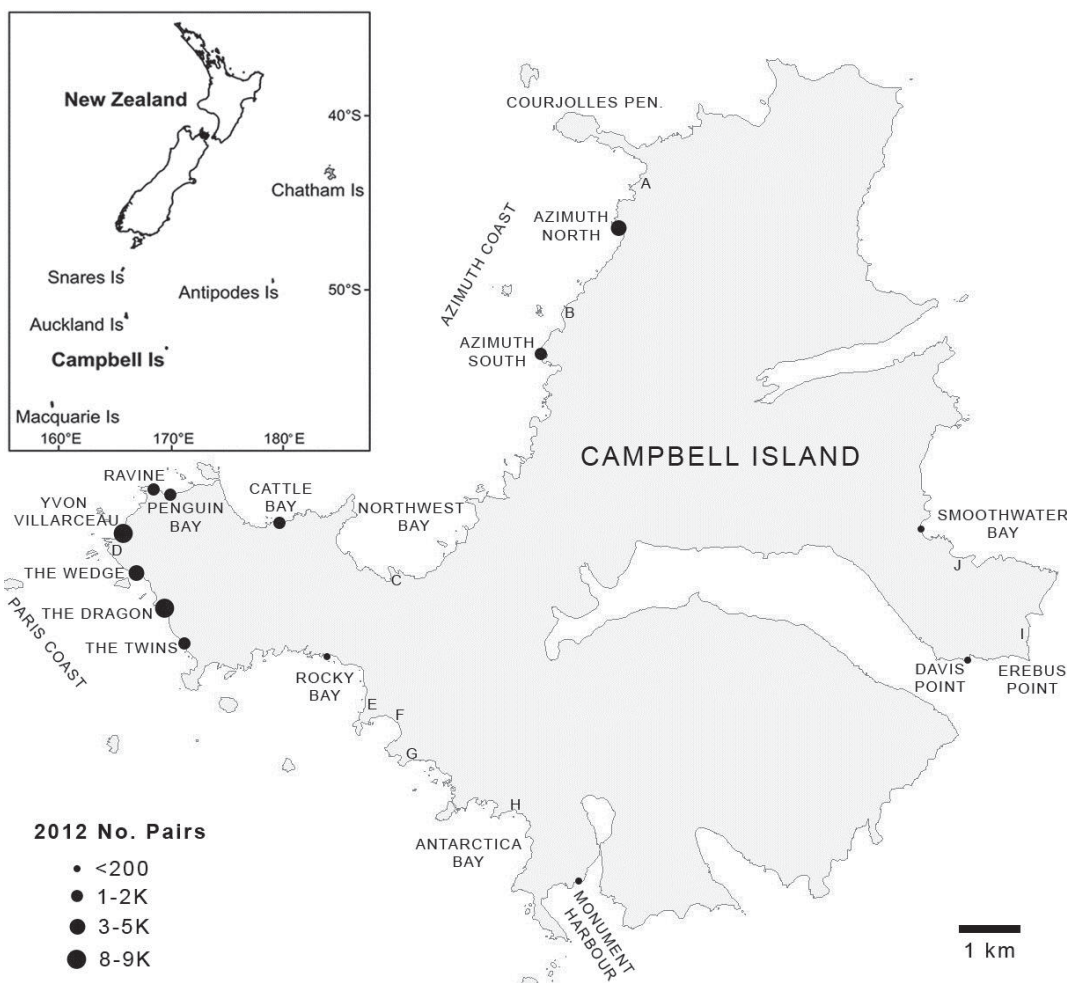


Figure 2.1 Map of Campbell Island indicating the location and size of Eastern Rockhopper Penguin colonies occupied in 2012 (circles) and colonies vacant or of unknown-status (letters). See Table 2.3 for the history of occupation status of all 23 sites since 1958. Inset map modified from Wilmschurst et al. (2004).

Table 2.1 Counts of nests and birds on 14-16 Nov 2010, 12-13 Nov 2011, and 12-13 Nov 2012 in the Eastern Rockhopper Penguin sub-colonies in Penguin Bay, Campbell Island. The late count of birds was on 24-26 Nov 2012 while the photo-count was made from a photo taken 23-Nov 2012.

	East	West	Ravine	Foreshore	Total
Count of nests 2010	34	541	1074	1546	3195
Count of nests 2011	24	460	1045	1408	2937
Count of nests 2012	19	452	1068	1473	3012
Change in nests 2010–2011	-29%	-15%	-3%	-9%	-8%
Change in nests 2011–2012	-21%	-2%	2%	5%	3%
Change in nests 2010–2012	-44%	-16%	-1%	-5%	-6%
Count of birds 2010	84	1108	2259	3248	6699
Count of birds 2011	62	989	2269	3107	6427
Count of birds 2012	52	999	2334	3254	6639
Change in birds 2010–2011	-26%	-11%	0%	-4%	-4%
Change in birds 2011–2012	-16%	1%	3%	5%	3%
Change in birds 2010–2012	-38%	-10%	3%	0%	-1%
Non-breeding males 2010	19%	2%	5%	5%	5%
Non-breeding males 2011	23%	7%	8%	9%	9%
Non-breeding males 2012	27%	10%	8%	9%	9%
Late count of birds 2012	13	409	993	1537	2952
Photo-count of birds 2012	2	349	448	949	1748
Correction factor	6.50	1.17	2.22	1.62	1.69
Nests accounted for by late count of birds 2012	68%	91%	93%	104%	98%

The spring-summer breeding period is divided into four stages – (1) arrival and courtship, (2) incubation, (3) guard, and (4) crèche stages – followed in the austral autumn by the pre-moult exodus and moult. After arriving from over-wintering areas to breed, both sexes remain ashore and fast at their nest site until after egg-laying. Males typically arrive on Campbell Island in the second week of October, females a week later (Chapter 3). Single males that have been unable to attract a mate usually continue to guard a nest site at least until breeding males depart (K.W.M. pers. obs.). In contrast, females that arrive in October rarely went unpaired at our Penguin Bay count sites on Campbell Island, suggesting a male-biased breeding population. Females lay a two-egg clutch in the first two weeks of November, about two weeks after their arrival. Very few of the birds paired in October fail to produce eggs. Males depart synchronously over a few days about a week after clutch completion on a c. 2-week long incubation foraging trip, leaving the female to take the first solo incubation shift. Pairs that lose both eggs early in incubation will continue to guard their nest site at least until males depart on their incubation foraging trip, but often both remain longer (K.W.M. pers. obs.). Returned males take over incubation duties and females go to sea for about a week, returning near hatching in the second week of December (Chapter 3). Rockhopper Penguin surveys beyond the mid-incubation period are a poor representation of the breeding population size because of the departure of failed breeders and arrival of sub-adults. The October to February breeding seasons will be referred to throughout our study using the year in which they began.

Colony occupation status

We visited or viewed from above 20 of 23 historically occupied Rockhopper Penguin colonies on Campbell Island during the 2010–2012 breeding seasons to determine their occupancy status (Figure 2.1). The 23 sites were identified from four sources in the literature extending back to a 1958 survey (Westerskov 1960; Department of Lands and Survey 1980; Moors 1986; Cunningham and Moors 1994). The three historical colonies that we did not visit or view from above were viewed from a boat with binoculars. All colonies apparently vacant 2010–2012 were viewed multiple times without observing breeding Rockhopper Penguins, except for the bays below and east of Mt. Dumas, and Antarctica Bay, which were viewed only once in 2011, when no penguins were seen.

Population estimation

Our estimation of the Rockhopper Penguin breeding population size and trends on Campbell Island consists of four parts: 1) Penguin Bay counts – census counts of the Penguin Bay sub-colonies in three consecutive years to measure inter-annual variation and allow ground truthing of photo-counts; 2) Photo-counts – counting all penguins visible in oblique photos in 2012; 3) Adjusted nest numbers – adjusting the 1942 and 1984 population estimates based on colony-specific nest densities; 4) Relative area comparison in photos – comparing the change in relative colony area in photos taken from standardized photopoints in 1984, 1996, and 2012.

Penguin Bay counts

Penguin Bay contains the only Rockhopper Penguin colony on Campbell Island readily accessible to researchers (Figure 2.1). In 1984, Cunningham and Moors (1994) established photopoints overlooking Penguin Bay and the seven other largest colonies so that photos could be used to assess future population change. The Penguin Bay colony currently consists of four sub-colonies, including the Ravine. Census counts were made using tally counters in mid-November 2010, 2011, and 2012 (for dates see Table 2.1) in all Penguin Bay sub-colonies early in the incubation period when both pair members were attending nests. Nests were counted if containing eggs, or empty but attended by both pair members. Empty nests guarded by unpaired males were not counted as nests. Total birds were also counted. Counts were conducted only once because of time constraints and to limit disturbance.

To ensure the accuracy of counts we used a grid system composed of two yellow ropes marked with alternating red and black tags at 2.5 m intervals. The ropes were aligned in parallel at one end of the colony, 2.5 m apart, with tags of the same colour opposite each other. Counters remained at either end of the ropes at the edge of the colony and counted nests and birds in each of the grid squares formed by the ropes and coloured tags. Counters counted the grid squares closest to them, stopping at an agreed upon grid boundary towards the middle of the colony. Counters counted only their own squares, repeating counts until they were confident of the totals. After a row of squares was counted the outermost rope was lifted from either end and placed parallel to the remaining rope a further 2.5 m into the colony to create another row of squares. Only occasionally did counters have to enter the edge of the colonies to see behind large boulders, except at the larger Foreshore colony, which was too large to count from the edges, and so was divided down the middle with each half being

counted separately by having one of the counters counting from the midline.

Years in which a large proportion of the population skip breeding can lead to underestimates of breeding population size (Croxall and Rothery 1995; Baylis et al. 2013). Annual counts in Penguin Bay over three years were used to assess whether we were likely to have selected a year of “normal” breeding effort to make an island-wide population estimate.

Photo-counts were made from photos taken 23–26 (“late”) November 2012 in the first half of the female-only incubation period, soon after all breeding males and most non-breeding males had gone to sea (Chapter 3). Each bird counted was assumed to represent one breeding pair. Photo-counts in mid-November when all breeding birds were ashore would remove the potential negative bias of the departure of failed breeders. However, mid-November photo-counts are impractical because birds overlap and obscure one another. In contrast, counting non-breeding penguins that remain in late-November is a potential positive bias to the estimated number of breeding pairs. It is clear that photo-counts will underestimate the actual number of nests present because an unknown proportion of nests are hidden behind or beneath rocks and boulders. Additionally, this proportion will differ between colonies based on boulder size and number, colony topography, and photo angle and distance. We ground-truthed our late-November photo-counts by repeating census counts of total birds in the four Penguin Bay sub-colonies 24–26 November 2012. The late-November counts allowed the calculation of photo-count correction factors to account for birds not visible in the photographs. Additionally, we calculated what % of nests counted in 12–13 (mid-) November were accounted for by the late-November count of birds when we expected only one bird (incubating female) per nest. These percentages demonstrated whether the departure of failed breeders or retention of non-breeding males strongly influenced the assumption that late-November counts of birds were an appropriate proxy for the original mid-November number of nests.

The percentage of non-breeding males in mid-November (1), is given by:

$$((b_1 - 2*n_1) / b_1) * 100 \tag{1}$$

where b_1 is the mid-November count of birds and n_1 is the mid-November count of nests.

The photo-count correction factor (2) equals:

$$b_2 / b_p \tag{2}$$

where b_2 is the late-November count of birds and b_p is the photo-count of birds.

The % of nests counted in mid-November accounted for by the late-November count of birds (3) equals:

$$(b_2/n_1)*100 \quad (3)$$

Photo-counts

Photo-counts were made on “mosaic” images merged automatically in Adobe Photoshop CS6 (Adobe Systems Inc.). Images were composed of 2–35 photographs taken at focal lengths of 42–200 mm with a Nikon D7000 DSLR camera and 18–200 mm Nikon lens. Photographs were taken 23–26 November 2012 either at the cliff-edge photopoints established by Cunningham and Moors (1994) or at adjacent viewpoints offering a complementary or more vertical viewing angle. Photo-counts were made on separate images for different discrete sections of a colony as colony topography required. We used the “Count” tool of Adobe Photoshop CS6 to mark each penguin in the image with a consecutive number and to provide a running total. Photopoint photos taken in previous years were of inadequate quality to make comparable photo-counts. Photo-counts or physical counts during incubation were not possible for four small colonies amongst large boulders: Rocky Bay, Monument Harbour, Davis Point, and Smoothwater Bay (Figure 2.1). Our estimates of 100 or 200 pairs in each are based upon chick-rearing counts at Rocky Bay and Smoothwater Bay, and the limited penguin activity observed at Monument Harbour and Davis Point.

Adjusted nest numbers

In generating population estimates for 1942 and 1984 Cunningham and Moors (1994) applied a nest density of 2.0 nests/m² across all colonies regardless of inter-colony variation in topography and nest substrate. The authors’ ability to estimate density in 1942 was obviously limited, but the now extinct “Mystery” colony in the historical photo they used was one free of the vegetation and huge boulders that appear to limit nest density at some other colonies. As in the “Mystery” colony, large boulders and vegetation occur only at the peripheries of the Penguin Bay and Cattle Bay colonies where Cunningham and Moors measured a nest density of c. 2.0 nests/m² in the mid-1980s (Figure 2.1). We adjusted the nest numbers for 1942 and 1984 estimated by Cunningham and Moors based on our impression that a nest density of 1.5 nests/m² was more likely for the Yvon Villarceau, Paris Coast, and Rocky Bay colonies than the estimate of 2.0 nests/m² the authors applied across all colonies (Figure 2.1). Historical photos

from the 1940s show that a large proportion of colony area in these locations was recently colonized and still vegetated and/or amongst huge boulders, reducing the area available for nests. Similarly, remnant colonies in these areas in 1984 were amongst much larger boulders than in Penguin Bay and Cattle Bay.

Changes in the estimated number of pairs between years are presented in two forms. The % change in number of breeding pairs (4) is:

$$((p_2 - p_1) / p_1) * 100 \quad (4)$$

where p_1 is the number of pairs in the earlier year (y_1) and p_2 is the number of pairs in the later year (y_2). The annual (exponential) population growth rate (λ) is based on the equation (5):

$$p_2 = p_1 * \lambda^t \quad (5)$$

where $t = y_2 - y_1$.

Relative area comparison in photos

The inaccessibility and complex topography of the colonies and oblique angles of the photopoint photographs prevented our measurement of the actual geometric areas of the colonies. Instead, we measured the visible “area” of a colony in a photopoint photo relative to the “area” of the same colony photographed from the same photopoint in a different year. We calculated the % change in “relative area” between photopoint photos from 1984, 1996, and 2012 by first outlining the colony perimeter using the “Polygonal Lasso” tool in Adobe Photoshop CS6 (see Figure 2.2). Relative area was measured in arbitrary units defined by setting a custom measurement scale equal to the distance between specific points on two stationary boulders spaced as far apart as possible in the photograph. The “Measurement” function in Photoshop produced the “area” of the outlined colony. To account for measurement error associated with lens distortion, the precise position of the photographer, and differences in the exact placement of scale markers on the image, we set the measurement scale between two different boulders and re-measured the “area” a total of six times in each photograph. The process was repeated for each photograph of the time series from a given photopoint using the same boulders as scale markers. We calculated the % change in relative area between years as the average of the % change in relative area of the six measures.

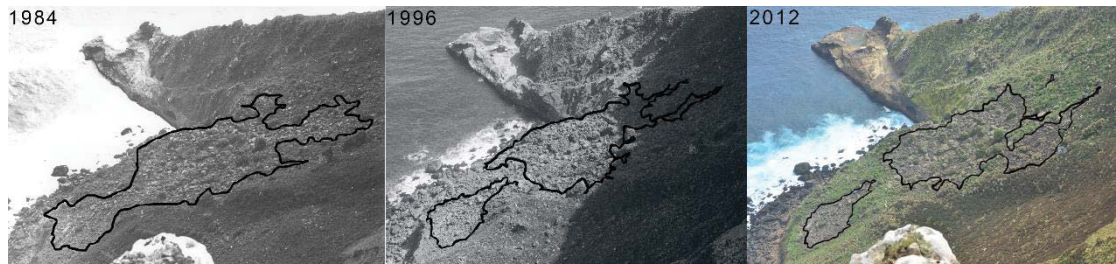


Figure 2.2 Photos taken from photopoint #10, 23-26 Nov 1984 (G. Taylor), 1996 (P. Moore), and 2012 (K.W.M.) illustrating change in area and shape of The Dragon colony (outlined in black) of Eastern Rockhopper Penguins on Campbell Island. This was the island's largest colony in 1984 (7,875 pairs), but decreased to 7,180 pairs in 2012 following contraction and expansion in area before and after 1996 (Table 2.4).

Sea surface temperature

We compared Rockhopper Penguin population trends to a 100-yr time series (1913–2012) of Extended Reconstructed SST (ERSST.v3b) data downloaded from <https://www.ncdc.noaa.gov/ersst/>. ERSST data are based on ship and buoy SST measurements prior to 1985 and include satellite measurements thereafter (Smith et al. 2008). Monthly ERSST data were downloaded for a rectangular region surrounding Campbell Island, 52–54°S, 168–170°E (222 km latitudinally by 134 km longitudinally). This region encompasses the expected foraging radius of 5–50 km for chick-rearing Rockhopper Penguins (Sagar et al. 2005; Ludynia et al. 2012). We tested whether there had been a greater proportion of anomalously warm years (annual average > 90th percentile of the 100-yr time series) during the middle period of Rockhopper Penguin population decline versus the early and late periods of population growth (see Results) using one-tailed z-tests. As per Cunningham and Moors (1994), we plotted austral summer (Dec, Jan, Feb) mean values smoothed using a 5-year moving average (Figure 2.3). In contrast to those authors we present temperature anomalies from the 100-yr average instead of actual temperatures and we include austral winter values (Jun, Jul, Aug) for comparison to summer values.

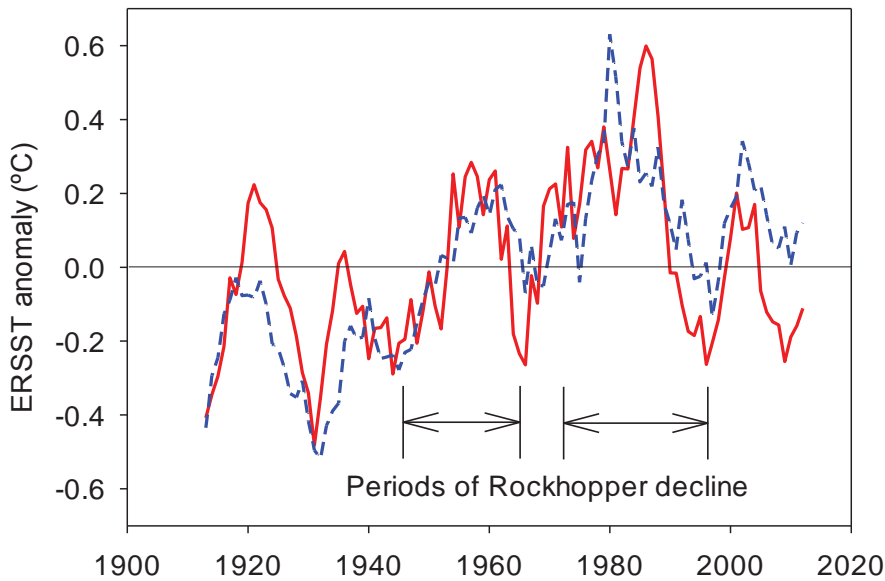


Figure 2.3 Five-year moving averages of ERSST anomalies 1913–2012 for the Campbell Island region. Data are presented for the summer (Dec, Jan, Feb) mean ERSST as red solid lines and winter (Jun, Jul, Aug) mean ERSST as blue dashed lines. The Eastern Rockhopper Penguin population on Campbell Island declined 1945–1996, with temporary growth following the cooler period in the 1960s, and growth 1996–2012.

RESULTS

The timing of changes in the occupation status of Rockhopper Penguin colonies on Campbell Island is poorly documented because of incomplete information (Figure 2.1, Table 2.2). It is likely that the number of active colonies has decreased gradually since the first survey in 1958. As of 2012, 8–11 of 23 former colony sites were vacant. There is no firm evidence that any colony has been reoccupied after becoming vacant. At the three colonies we viewed with binoculars instead of visiting (listed as “NI” for “No Information” in Table 2.1) no penguins were visible amongst the narrow band of large boulders at each site. We estimated that if these three colonies are still active they probably each contain < 200 pairs.

The total number of nests and birds in Penguin Bay decreased by 6% and 1%, respectively, from 2010–2012 (Table 2.1). The overall decrease occurred between 2010 and 2011 (nests -8% and birds -4%), followed by an increase from 2011–2012 (nests +3% and birds +3%). The greatest proportional decreases occurred in the smallest sub-colonies. The lesser decrease in the number of birds compared to nests was caused by an increase in the

proportion of non-breeding males from 2010–2011, which remained the same overall in 2012 (Table 2.1).

Table 2.2 Occupation status of 23 geographically separated Eastern Rockhopper Penguin colonies on Campbell Island, 1958–2012. Colonies occupied by breeding penguins are marked with an “x”, those with no information are shown as “NI”. Data from: Jan–Feb 1958, Westerskov (1960); Nov 1975 – Feb 1976, Department of Lands and Survey (1980); Feb 1984, Moors (1986); 1985–1987, Cunningham and Moors (1994); Oct–Jan 2010–2012, this study. Note: there was apparently never a photopoint 14. Refer to Figure 2.1 for the location of colonies.

Colony	Photopoint # or				1985–	2010–
	Fig. 2.1 letter	1958	1975	1984	1987	2012
Btwn Azimuth North and Courrejolles	A	NI	x	NI	NI	vacant
Azimuth North	13	x	x	x	x	x
Azimuth Point (below Mt. Azimuth)	B	x	NI	x	NI	vacant
Azimuth South	11	x	x	x	x	x
Limestone Point/Capstan Cove	C	x	x ^a	vacant	vacant	vacant
Cattle Bay	12	x	x	x	x	x
Penguin Bay	1-5, 15	x	x	x	x	x
Ravine	6,7	x	x	x	x	x
Yvon Villarceau	8	x	x	x	x	x
Opposite Hook Keys	D	x	NI	x	x	vacant
The Wedge	9	x	x	x	x	x
The Dragon	10	x	x	x	x	x
The Twins	10	x	x	x	x	x
Rocky Bay Boulder Beach	--	NI	NI	x	x	x
Rocky Bay Slump	E	x	x	vacant	vacant	vacant
Bay below Mt Dumas	F	x	NI	NI	NI	vacant
Bay east of Mt Dumas	G	x	NI	NI	NI	vacant
Antarctica Bay	H	NI	NI	NI	x ^b	vacant
Monument Harbour	--	x	x	x	x	x
Davis Point to Erebus Point	--	x	NI	vacant ^b	NI	NI ^c
East coast of eastern-most peninsula	I	x	NI	NI	NI	NI
Smoothwater Bay, mid south side	J	x	x	x	x	NI
Smoothwater Bay, southwest corner	--	x	NI	NI	NI	x

^a Drawn too far east

^b Unconfirmed

^c Occupied in 1996 (P. Moore pers. comm.)

For the photo-count method of population estimation we chose to apply the photo-count correction factors from either the West or Foreshore sub-colonies in Penguin Bay (Table 2.1), or the average of these (1.40) to the photo-counts of the other colonies (Table 2.3) with choice of factor based upon viewing angle and distance from the photopoint to the colony. The larger correction factors for the East and Ravine sub-colonies were not used because most birds were hidden by boulders in the exceptionally small East sub-colony and the visibility of birds in the Ravine sub-colony was poor because this colony is unique in being above its photopoint. The % difference between the mid-November count of nests and the late-November count of birds decreased with increasing sub-colony size, from birds accounting for 68% of nests in the smallest sub-colony to birds (over-) representing 104% of the nests counted in the largest sub-colony (Table 2.1). This trend occurred because of the greater nest failure rate of smaller sub-colonies and subsequent departure of breeding birds, combined with the greater retention rate of failed and non-breeders at larger colonies (K.W.M. unpub. data). We concluded that late-November bird counts were a suitable proxy for the mid-November number of breeding pairs because bird counts were only 2.0% lower than nest counts overall (Table 2.1). All of the colonies for which photo-counts were conducted were of similar or much larger size than the largest Penguin Bay sub-colony (Table 2.1 and Table 2.4), so if these colonies retained a similar or greater proportion of failed breeders or non-breeders our assumption that the late-November photo-counts of birds represent the original numbers of nests may cause a positive bias in perceived nest numbers.

Table 2.3 Estimated number of breeding pairs of Eastern Rockhopper Penguins on Campbell Island in 1942 and 1984 adjusted by multiplying colony areas in 1942 and 1984 (Cunningham and Moors 1994 and P. Moors unpub. data) by a nest density of 2.0 nests/m² as in Cunningham and Moors (1994), except 1.5 nests/m² for the Yvon Villarceau, Paris Coast, and Rocky Bay colonies. Also shown are the number of pairs counted in photos, correction factors applied, and corrected number of pairs for 2012.

Colony	1942		1984		2012		
	Area (m ²)	Adjusted pairs	Area (m ²)	Adjusted pairs	Photo count	Correction factor	Corrected pairs
Cattle Bay	2450	4900	1150	2300	1199	1.40	1679
Penguin Bay	8650	17300	3680	7360	1745	1.62	2827
Yvon Villarceau	72000	108000	7830	11745	5379	1.62	8714
Opposite Hook Keys		NA	?	?	0	NA	0
The Wedge	NA	NA	3670	5505	2832	1.62	4588
The Dragon	NA	NA	5250	7875	6138	1.17	7181
The Twins	NA	NA	1170	1755	1256	1.40	1758
Paris Coast (Total)	315000	472500	10090	15135	10226	NA	13477
Rocky Bay Boulder Beach	250	375	?	188	NA	NA	200
Rocky Bay Slump	2000	3000	0	0	0	0	0
Rocky Bay (Total)	2250	3375	?	188	NA	NA	200
Azimuth South	750	1500	750	1500	840	1.40	1176
Azimuth Point	550	1100	0	0	0	1.62	0
Azimuth North	5000	10000	2000	4000	3945	1.17	4616
Azimuth Coast (Total)	6300	12600	2750	5500	4785	NA	5758
Monument Harbour	?	250	?	250	NA	NA	200
Smoothwater Bay	?	1000	?	50	NA	NA	100
Davis Point	?	?	?	?	NA	NA	200
Overall	406650	619925	25500	42528	23334	NA	33239

Corrected 2012 photo-counts indicate that the number of breeding pairs of Rockhopper Penguins on Campbell Island may have declined by as much as 35.2% from 1984–2012, if one considers 1984 population estimates unadjusted for lower nest densities compared to corrected photo-counts (Table 2.4). All colonies except for Azimuth North and Smoothwater Bay were estimated to have declined by > 20% from 1984 (unadjusted pairs) to 2012 (Table 2.4). Our adjustment for lower nest densities from 2.0 to 1.5 nests/m² for the Yvon Villarceau, Paris Coast, and Rocky Bay colonies resulted in decreases in total population estimates from those of Cunningham and Moors (1994): from 814,550 to 619,925 (-23.9%) breeding pairs in 1942, and from 51,300 to 42,528 (-17.1%) breeding pairs in 1984. Using 1942 and 1984 population estimates adjusted for a lower nest density and the 2012 corrected photo-count estimate resulted in estimated declines from 1984–2012 of 21.8% (42,528 to 33,239 breeding pairs) and an overall decline from 1942–2012 of 94.6% (619,925 to 33,239 breeding pairs). In contrast, the change in relative area method suggested that colony area was similar between 1984 and 2012, declining just 0.7% (Table 2.4). However, within this period the overall change in relative area was -22.6% from 1984–1996, followed by an increase of 28.3% from 1996–2012. The relative area method produced a similar estimate of change for Penguin Bay and The Wedge compared to the photo-count vs. adjusted nests method, but a lesser decline for Yvon Villarceau and Azimuth South, greater for The Dragon, and exaggerated positive changes for Cattle Bay, The Twins, and Azimuth North. The intermediate estimate of an overall decline of 21.8% from 1984–2012 from the photo-count method corresponds to an annual rate of change (λ) of 0.991, a much slower rate of decline than from 1942 to 1984 ($\lambda = 0.940$; Table 2.4).

Table 2.4 Estimated % change in relative area between 1984, 1996, and 2012 of Eastern Rockhopper Penguin colonies on Campbell Island from photopoint photos, and % change of number of pairs (Area * 2.0 nests/m² across all colonies compared to corrected pairs from Table 2.3) and adjusted pairs compared to corrected pairs (Table 2.3). Also shown are population growth rates (λ) from adjusted pairs in 1942 and 1984 and corrected pairs in 2012 (Table 2.3).

Colony	% change										Growth rate (λ)		
	Relative area			Pairs			Adjusted pairs			Adjusted pairs			
	1984-1996	1996-2012	1984-2012	1984-2012	1984-2012	1942-1984	1984-2012	1942-1984	1984-2012	1942-1984	1984-2012	1942-1984	1984-2012
Cattle Bay	49.1%	31.7%	96.2%	-27.0%	-53.1%	-27.0%	-27.0%	0.982	0.989				
Penguin Bay	?	?	-70.5%	-61.6%	-57.5%	-61.6%	-61.6%	0.980	0.967				
Yvon Villarceau	-17.3%	15.7%	-4.6%	-44.4%	-89.1%	-25.8%	-25.8%	0.950	0.989				
Opposite Hook Keys	-100.0%	?	-100.0%	-100.0%	NA	-100.0%	-100.0%	NA	NA				
The Wedge	-27.5%	7.1%	-22.4%	-37.5%	NA	-16.7%	-16.7%	NA	0.994				
The Dragon	-25.2%	-0.4%	-25.5%	-31.6%	NA	-8.8%	-8.8%	NA	0.997				
The Twins	36.3%	9.3%	48.9%	-24.9%	NA	0.2%	0.2%	NA	1.000				
Paris Coast (Total)	-18.9%	3.9%	-15.7%	-33.2%	-96.8%	-11.0%	-11.0%	0.924	0.996				
Rocky Bay Boulder Beach	?	?	?	-20.0%	-50.0%	6.7%	6.7%	0.984	1.002				
Rocky Bay Slump	NA	?	NA	NA	-100.0%	NA	NA	NA	NA				
Rocky Bay (Total)	?	?	?	-20.0%	-94.4%	6.7%	6.7%	0.936	1.002				
Azimuth South	4.0%	-10.6%	-7.1%	-21.6%	0.0%	-21.6%	-21.6%	1.000	0.991				
Azimuth Point	NA	?	NA	NA	-100.0%	NA	NA	NA	NA				
Azimuth North	29.1%	105.9%	165.7%	15.4%	-60.0%	15.4%	15.4%	0.979	1.005				
Azimuth Coast (Total)	22.3%	78.8%	118.6%	4.7%	-56.3%	4.7%	4.7%	0.981	1.002				
Monument Harbour	?	?	?	-20.0%	0.0%	-20.0%	-20.0%	1.000	0.992				
Smoothwater Bay	?	?	?	100.0%	-95.0%	100.0%	100.0%	0.933	1.025				
Davis Point	?	?	?	NA	?	?	?	NA	NA				
Overall	-22.6%	28.3%	-0.7%	-35.2%	-93.1%	-21.8%	-21.8%	0.940	0.991				

ERSST anomalies from summer and winter 1913–2012 reveal three periods of contrasting trends: a cool period 1913–1950, a warm middle era 1951–1989 punctuated by cool years in the late 1960s, and a return to cooler temperatures 1990–2012, especially in summer, with a few warmer years in the early 2000s (Figure 2.3). The increase in ERSST between monthly values averaged over the 1913–1944 large Rockhopper Penguin population era and the 1945–1995 period of decline was 0.30 °C. The increase in annual mean ERSST around Campbell Island of 0.30 °C was driven more by temperature increases over winter (+0.35 °C) than in summer (+0.26 °C). The recent period of population growth from 1996–2012 corresponded to a slight decline in annual ERSST of 0.06 °C relative to the warm era, perhaps importantly driven more by lower temperatures over spring (-0.09 °C) and summer (-0.16 °C), than in fall (-0.03 °C) or winter (+0.03 °C). Around Campbell Island in the early cool period (1913–1944) only 3.1% of years had annual mean ERSST above the 90th percentile (0.4 °C above the 100-yr mean), whereas 17.6% of years in the middle warm period (1945–1995) of population decline were extremely warm, but none were as warm in the recent cool period (1996–2012). The frequency of anomalously warm years in the middle period was significantly greater than during the early cool period ($z = 1.978$, $p = 0.024$) and late cool period ($z = 1.857$, $p = 0.031$). In the early and late cool periods warm years occurred at similarly low rates ($z = 0.7334$, $p = 0.465$).

DISCUSSION

Our most plausible estimate, obtained from corrected photo-counts, of the 2012 Eastern Rockhopper Penguin population size on Campbell Island is 33,239 breeding pairs. This estimate represents a 21.8% decline from the adjusted estimate of 42,528 pairs in 1984 and is intermediate to estimated declines of 35.8% based on an unadjusted 1984 population estimate and a crude estimate of a 0.7% decline based on comparisons of relative colony area in photographs under the assumption of constant nest density. Our estimate of the overall decline over the 71-year period from 1942–2012 is 94.6%, representing a decrease from an adjusted estimate of 619,925 breeding pairs in 1942 to 33,329 pairs in 2012. We discuss below important biases associated with the change in relative colony area method. Nevertheless, this method, along with observations of recent colony expansion indicate that the recent decline occurred during the period 1984–1996 and was followed by overall population growth 1996–2012, concurrent with lower SSTs and an increased abundance of a key prey species.

Biases in methods

We found that the total numbers of nests and birds in the Penguin Bay sub-colonies increased from 2011–2012, leading us to conclude that 2012 was not a year in which an unusually large proportion of the population skipped breeding and is therefore a suitable year on which to make an island-wide population estimate. Assuming a constant nest density through time (Cunningham and Moors 1994), the % change in relative colony area method would be accurate on a flat colony viewed directly from above. However, our lack of nest density measurements, the complex topography of the Campbell Island colonies, and the oblique photo angles of the photopoints decrease the reliability of this method. For example, colony expansion in the foreground of the photos of the Cattle Bay and Azimuth North colonies produced unrealistically large positive changes in relative colony area from 1984–2012 (increases in colony area of 96% and 166%, respectively). Furthermore, we observed that nest density in areas of recent colony expansion appears lower than in long-established central areas of colonies because remaining vegetation and soil limit nest sites. If we substitute more realistic estimates of increases in area of 30% for both colonies, the overall change in relative area from 1984–2012 is -14.3%, much closer to the -21.8% estimated using photo-counts. Despite this caution on interpreting changes in relative colony area, our result that most colonies continued to decline rapidly during the period 1984–1996 before stabilizing or growing 1996–2012 is corroborated by a visual comparison of the relative positions of colony boundaries and the recent colonization of some sections of colonies into vegetated areas (see Figure 2.2). Cunningham and Moors (1994) described a satellite colony in Cattle Bay that formed between 1958 and 1975 as evidence of a period of population growth. This satellite colony had disappeared by 1984, remained absent in 1996, but was present again in 2010.

Food availability

The leading hypothesis to explain the dramatic Rockhopper Penguin population decline on Campbell Island and at other breeding sites has been a reduction in food availability related to changing oceanographic conditions linked to climate change (BirdLife International 2010). The slower rate of decline that we found for the much smaller population from 1984–2012 using the photo-count method, versus the rapid decline of the originally huge population from 1942–1984, conforms to a density-dependent response to a decrease in food availability, providing support for this hypothesis. It appears likely that Rockhopper Penguins experienced greater food availability and higher reproductive success and survival in the cooler period after

1990. Average year class strength of southern blue whiting (*Micromesistius australis*), the most common prey of Rockhopper chicks on Campbell Island in 1985 and 1986 (75.6% of prey by number, Marchant and Higgins 1990) was c. 3.8 times greater 1990–2009, than 1977–1989 (Dunn and Hanchet 2014). Furthermore, 40% of years in the later period had a year class strength exceeding the overall mean, but no years were above average in the earlier period. Campbell Island's populations of Campbell Albatross (*Thalassarche impavida*) and especially Grey-headed Albatross (*T. chrysostoma*) experienced declines during the same 1940s–1990s period and of a similar magnitude as the historical Rockhopper Penguin decline, but like Rockhopper Penguins, have stabilized or grown since the late 20th century (Waugh et al. 1999b; Moore 2004; Sagar 2014). Reduced bycatch mortality in long-line fisheries, but also improved reproductive success and juvenile survival are likely responsible for the improved trends of late, because 0+ age group southern blue whiting are important prey for both species, especially Campbell Albatross (Cherel et al. 1999b; Waugh et al. 1999a).

Sea surface temperature

Cunningham and Moors (1994) suggested that on Campbell Island the Rockhopper Penguin population growth rate was negatively related to locally measured SSTs and those the authors calculated from air temperatures 1944–1985. The longer 1913–2012 ERSST record in the region surrounding Campbell Island and recent 1984–2012 population trends largely support such a relationship (Figure 2.3). As predicted, ERSST was low, and had been low for the previous 30+ years when the Rockhopper Penguin population was large in 1942. However, although the initial period of rapid decline began in 1945, summer ERSST did not exceed the long-term average until 1950 (Figure 2.3) and annual ERSST not until 1955. It should be noted that ERSST data from the 1940s are more uncertain because of reduced sampling effort during WWII (Smith and Reynolds 2005). In addition, between 1944 and 1946 the Interdecadal Pacific Oscillation (IPO) shifted from its positive to negative phase, corresponding to positive SST anomalies and reduced south-west winds near New Zealand from 1946–1977 (Salinger et al. 2001). If the start of the decline did actually precede the warming, then local ERSST did not drive the initial rapid decline. We suggest that elevated adult mortality associated with poor food availability on pre-moult and/or over-winter foraging areas likely caused the initial rapid decline. This hypothesis is supported by large, between-year reductions in breeding population size and an observation of colony-wide abstention from laying in the mid-1940s (J.H. Sorensen in Cunningham and Moors 1994). Cunningham and Moors (1984) suggested the Rockhopper Penguin population increased during the period 1958–1975, perhaps only in the later years,

following cooler SSTs between 1957 and 1968. The ERSST record suggests this cooler period occurred slightly later, 1963–1970, but could still explain the apparent temporary population growth. We found that the population continued to decline rapidly from 1984–1996, but grew from 1996–2012. The latter period overlaps a period of generally lower-than-average ERSST from 1990–2012, especially during the summer chick-rearing period (Figure 2.3). A lagged response between lower ERSST and population growth is expected if growth occurs through higher reproductive success and/or juvenile survival, because Rockhopper Penguins delay breeding until 4–5 years old (Guinard et al. 1998; Dehnhard et al. 2014).

The increase in ERSST between monthly values averaged over the 1913–1944 large Rockhopper Penguin population era and the 1945–1995 period of decline was 0.30 °C. This increase is lower than increases in annual average SST of 1.4 °C and 0.5 °C measured over the second-half of the 20th Century at Marion and Gough islands respectively (Mélise et al. 2003). Rising SSTs at these sites were concurrent with large population declines of Eastern and Northern Rockhopper Penguins, respectively (Crawford et al. 2006; Cuthbert et al. 2009). Perhaps more important than the increase in average ERSST in the present study was the increase in the frequency of years of extremely warm ERSST around Campbell Island that may have greatly reduced adult Rockhopper survival. In the Falkland Current region annual adult survival of Southern Rockhopper Penguins decreased from 0.96 to 0.81 with a pre- to post-moult period temperature anomaly of +0.3 °C (Dehnhard et al. 2013). Around Campbell Island anomalously warm years (+0.4 °C) were more common during the middle period (1945–1995) of Rockhopper Penguin population decline than during the early (1913–1944) or later cool periods (1996–2012) of population growth. Southern Rockhopper Penguin survival also decreased when temperature anomalies were cooler than -0.8 °C (Dehnhard et al. 2013), but the coldest year in the Campbell Island ERSST record was only an anomaly of -0.57 °C and only ten percent of years had anomalies <-0.35 °C, so that relatively cool years seem only to have benefitted Rockhopper Penguins on Campbell Island.

It may be that seasonal rather than annual anomalies in temperature are most relevant to Rockhopper Penguin population trends. Exceptionally cool SSTs around Campbell Island April–June 2012, during and after moult, were linked to low diet quality and low body masses of adults and chicks in the subsequent breeding season (Chapter 3). The recent period of population growth from 1996–2012 corresponded to a slight decline in annual ERSST relative to the warm era, especially during spring and summer. This result agrees with the expectation of Cunningham and Moors (1994) that SSTs around Campbell Island during the summer chick-rearing period are important to Rockhopper Penguin population dynamics. However, the

mechanisms driving population change will only be fully understood by research on breeding and over-winter foraging habitat and long-term studies of demographics, diet, and prey availability.

Predation

Another potential contributing factor to Rockhopper Penguin population declines throughout their range is predation by pinniped populations growing after historical exploitation (BirdLife International 2010). The number of New Zealand fur seals (*Arctocephalus forsteri*) breeding on Campbell Island is unknown, but appears far below pre-exploitation size in the early 1800s and little changed from the 1940s (Bailey and Sorensen 1962). Sorensen recorded fur seals preying upon Rockhopper Penguins in the 1940s on Campbell Island (Bailey and Sorensen 1962), but this was never seen in the three years of this study (K.W.M. pers. obs.) In contrast, New Zealand sea lions (*Phocarctos hookeri*) regularly preyed upon adult and sub-adult Rockhopper Penguins on Campbell Island (Chapter 5). The breeding output of New Zealand sea lions on the island has grown from < 20 pups born in 1947 (Bailey and Sorensen 1962) to > 681 pups in 2009 (Maloney et al. 2012). The peak count in January 1943 at the most-used haul-out beach of non- and post-breeding sea lions at Sandy Bay, Northwest Bay, was 150 sea lions, mostly immature males (Bailey and Sorensen 1962). Some of these males would have been vagrants from the species' nearest and largest breeding site at the Auckland Islands 290 km away (Maloney et al. 2012). Sea lions were too few on Campbell Island in the mid-20th Century to have caused the dramatic Rockhopper decline.

Although perhaps not the principal driver of the recent decline, inter-colony differences in predation rates likely contribute to the large variation we found in colony-specific population changes. For example, the divergent population trends of the Penguin Bay and Cattle Bay colonies, located within 2 km of each other, are unlikely to be caused by differences in food availability between colonies because Rockhopper Penguins typically forage 180–380 km from colonies during incubation (Ludynia et al. 2013), and 5–50 km from colonies during chick-rearing (Sagar et al. 2005; Ludynia et al. 2012). Predation by Brown Skuas (*Catharacta antarctica lonnbergi*), Northern Giant Petrels (*Macronectes halli*), and New Zealand sea lions on all ages of Rockhopper Penguins from eggs to adults appear to be an important driver of the continuing rapid population decline at Penguin Bay (Chapter 5). This colony appears particularly vulnerable to predation because its location and topography seem better suited to the growing population of sea lions than other colonies. Additionally, avian predators are likely

more successful at Penguin Bay because its single large colony fragmented into four sub-colonies as it declined whereas all other colonies split into two or remained singular (Jackson et al. 2005). Inter-colony differences in topography and orientation may also influence the magnitude of negative effects on breeding success from exposure to wind, sea spray, rain, and mud, and safety from accidental injury and sea lion predation for penguins transiting through boulders in heavy swells at the shoreline (Demongin et al. 2010, Crofts et al. 2011, K.W.M. pers. obs.).

Two conservation management actions undertaken by New Zealand's Department of Conservation (DOC) may have contributed to the recent positive trend. In 1989 the last of the feral sheep introduced in 1895 were shot (Williams and Robertson 1996), and sheep may have disrupted Rockhopper colonies and reduced reproductive success. However, Moors (1986) suggested disturbance by sheep was not a major cause of the Rockhopper Penguin decline, as all colonies had declined regardless of accessibility to sheep. In 2001 Norway rats (*Rattus norvegicus*) were eradicated from the entire island. Rats were apparently unable to eat intact Rockhopper eggs (Taylor 1986), but hoarded large numbers of small chicks. It is unknown whether rats scavenged or killed these chicks (Cunningham and Moors 1994), but rats were known to attack Yellow-eyed Penguin (*Megadyptes antipodes*) chicks on Campbell Island (Amey and Moore 1995).

Recommendations for future monitoring

We recommend that the Rockhopper Penguin photopoint series be repeated at 5-yr intervals. Ideally the photopoints would be repeated in two consecutive years at each 5-yr interval in an attempt to account for the possibility of mass abstention of breeding. The magnitude of population change likely in a shorter time period for this species of delayed reproduction and high adult survival (Dehnhard et al. 2013) is presumably too small to be detected given our methods. Climatic oscillations such as the El Niño Southern Oscillation that may affect the population also occur on a similar time scale (Timmermann et al. 1999). Every effort should be made to take the full set of photos during the same late-November window during female-only incubation at the exact GPS positions used in this study (Appendix 2.1). Ideally, multiple overlapping high-resolution images will be taken at sufficiently high focal lengths to allow for photo-counting of individual penguins. Although photo-counting is more time-consuming than the relative colony area method, we had greater confidence in photo-counting because of the biases inherent in the latter method discussed above. Additionally, the complementary and

more vertical photo angles used for photo-counting in this study should be taken at the same time whenever possible (Appendix 2.1). Full census counts of birds and nests in Penguin Bay should be made in mid-November whenever possible and repeated in late-November during photopoint survey years to establish photo-count correction factors. Our method would be improved by establishing photo-count correction factors for additional colonies or sections of colonies. Aerial photos, whether taken by helicopter (Trathan 2004), remote-controlled aircraft (Watts et al. 2010), or kite (Fraser et al. 1999) would greatly improve count accuracy, and along with a high-resolution digital elevation model (DEM) would allow for accurate mapping of colony area. Advances in satellite technology may also prove an efficient and economic tool for monitoring sub-Antarctic penguins (Lynch et al. 2012b).

Global perspective

Range-wide, the outlook for the Southern sub-species of Rockhopper Penguin is cautiously optimistic. The world's largest population at the Falkland Islands has increased since 1995 during a period of cool SSTs and high reproductive success and adult survival, including a 51% population increase from 2005–2010 (Baylis et al. 2013; Dehnhard et al. 2013). Increases of 15% occurred at the largest Chilean populations at Isla Noir from 1980–2005 (Oehler et al. 2008) and Isla Diego Ramirez from 1981–2002 (Kirkwood et al. 2007). The Eastern sub-species considered here is of greater concern with Indian Ocean populations in decline or of uncertain status. At Marion Island the population declined by about 70% from 1994–2008, whereas the Prince Edward Island population declined 15% from 2001–2008 (Crawford et al. 2009). Recent trends at the important Kerguelen and Crozet islands are unknown. In the New Zealand region the small breeding population of Eastern Rockhopper Penguins on the Antipodes Islands 740 km north-east of Campbell Island continued a long-term decline in recent years, decreasing by 15% 1995–2011 to just c. 2,900 pairs (from values in Hiscock and Chilvers 2014). The similarly small Rockhopper Penguin population on the Auckland Islands 290 km northwest of Campbell Island was estimated to have declined by 28–64% from 1972–1989 (Cooper 1992). The 2007 estimate on Macquarie Island of 32,000 to 43,000 pairs is much lower than past estimates (BirdLife International 2010). The population total of the Southern subspecies (c. 900,000) now likely outnumbers the Eastern (c. 400,000) by 2.25 to one (Baylis et al. 2013; Pütz et al. 2013).

The recent cooling of ERSST around Campbell Island was concurrent with a 'warming hiatus' in global surface temperatures since 1998, related to an increase in sub-tropical Pacific subsurface heat uptake and increased stratospheric loadings of reflective volcanic particulates

(England et al. 2014; Santer et al. 2014). These transient cooling influences are likely to be overwhelmed within the next decade by warming caused by continually increasing concentrations of atmospheric greenhouse gases (England et al. 2014). This suggests that the brief respite from ocean warming that appears to have benefited Rockhopper Penguins on Campbell Island in recent years will soon end, and their population decline may resume.

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Appendix 2.1 Locations of Eastern Rockhopper Penguin photopoints (PP1-15, excluding 14) and complimentary photo positions on Campbell Island. The Rocky Bay co-ordinates mark only this colony's location under huge boulders. Locations use grid format Lat/Lon hddd°mm.mmm and datum WGS 84.

Name	Location
PP1	S52 32.261 E169 02.172
PP2	S52 32.230 E169 02.198
PP3	S52 32.233 E169 02.206
PP4	S52 32.203 E169 02.219
PP5	S52 32.208 E169 02.134
PP6	S52 32.214 E169 02.000
PP7	S52 32.254 E169 02.019
PP8	S52 32.513 E169 01.441
PP9	S52 32.873 E169 01.467
PP10	S52 33.298 E169 02.283
PP11	S52 30.772 E169 07.975
PP12	S52 32.431 E169 03.993
PP13	S52 29.642 E169 09.339
PP15	S52 32.287 E169 02.239
SW of PP8	S52 32.700 E169 01.187
SE of PP9	S52 33.042 E169 01.826
NW of PP10	S52 33.227 E169 02.169
SE of PP10	S52 33.363 E169 02.383
S of PP13	S52 29.694 E169 09.381
Above Big colony at Yvon v.1	S52 32.604 E169 01.371
Above Big colony at Yvon v.2	S52 32.623 E169 01.349
Above Big colony at Yvon v.3	S52 32.625 E169 01.351
Above Cattle Bay	S52 32.496 E169 03.910
Above Dragon	S52 33.191 E169 02.077
Above Wedge	S52 32.919 E169 01.668
Rocky Bay colony	S52 33.790 E169 04.728



MASSEY UNIVERSITY
GRADUATE RESEARCH SCHOOL

**STATEMENT OF CONTRIBUTION
TO DOCTORAL THESIS CONTAINING PUBLICATIONS**

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Kyle William Morrison

Name/Title of Principal Supervisor: Dr. Phil Battley

Name of Published Research Output and full reference:

Morrison KW, Bury SJ, Thompson DR (2014) Higher trophic level prey does not represent a higher quality diet in a threatened seabird: implications for relating population dynamics to diet shifts inferred from stable isotopes. *Marine Biology* 161 (10):2243-2255. doi: 10.1007/s00227-014-2502-y

In which Chapter is the Published Work: 3

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Kyle designed the study, collected and prepared the samples, analysed the data, and wrote the paper.

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Chapter 3

HIGHER TROPIC LEVEL PREY DO NOT REPRESENT A HIGHER QUALITY DIET IN A THREATENED SEABIRD: IMPLICATIONS FOR RELATING POPULATION DYNAMICS TO DIET SHIFTS INFERRED FROM STABLE ISOTOPES

Morrison KW, Bury SJ, Thompson DR (2014) *Marine Biology* 161 (10):2243-2255.



Figure 3.0 Top: Female Eastern Rockhopper Penguin feeds a chick of a few days old. Bottom: Penguins depart through the antenna of an automated PIT-tag data logger. Photos by Kyle Morrison.

ABSTRACT

Diet quality is a key determinant of population dynamics. If a higher trophic level, more fish-based diet is of higher quality for marine predators, then individuals with a higher trophic level diet should have a greater body mass than those feeding at a lower trophic level. We examined this hypothesis using stable isotope analysis to infer dietary trophic level and foraging habitat over three years in Eastern Rockhopper Penguins *Eudyptes chrysocome filholi* on sub-Antarctic Campbell Island, New Zealand. Rockhopper Penguins are 'Vulnerable' to extinction because of widespread and dramatic population declines, perhaps related to nutritional stress caused by a climate-induced shift to a lower trophic level, lower quality diet. We related the stable nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotope values of blood from 70 chicks, 55 adult females, and 55 adult males to their body masses in the 2010, 2011, and 2012 breeding seasons and examined year, stage, age, and sex differences. Opposite to predictions, heavier males consumed a lower trophic level diet during incubation in 2011, and average chick mass was heavier in 2011 when chicks were fed a more zooplankton-based, pelagic/offshore diet than in 2012. Contrary to the suggested importance of a fish-based diet, our results support the alternative hypothesis that Rockhopper Penguin populations are likely to be most successful when abundant zooplankton prey are available. We caution that historic shifts to lower trophic level prey should not be assumed to reflect nutritional stress and a cause of population declines.

INTRODUCTION

Living organisms must balance their energy intake and expenditure to grow, survive, and reproduce. Diet quality describes prey characteristics in terms of their suitability as an energy source. An optimal quality diet maximizes net energy gain per unit time (Emlen 1966; MacArthur and Pianka 1966). This holistic definition of diet quality integrates the abundance of prey in the environment and the quantity and nutritional quality of prey obtained, in that a high quality diet is composed of prey that are energy dense, contain essential components for growth and reproduction, are readily available, and relatively easy to capture, subdue, and digest (Emlen 1966; MacArthur and Pianka 1966; Jodice et al. 2006). When diet quality decreases, e.g., through a reduced prey population size, the greater foraging effort required from predators may result in the predator population declining in health, having lower reproductive success, and decreased juvenile and adult survival, culminating in a population

decrease. For example, over-exploitation of seals, whales, and finfish in the Southern Ocean caused major changes in the strength of predator-prey relationships across trophic levels through changes in food availability (Laws 1985; Emslie and Patterson 2007; Ainley and Blight 2009). Diet quality is likely to decrease for many marine species in the future as marine ecosystems continue to be heavily modified by climate change and fisheries (Worm et al. 2006; Cury et al. 2011).

The potential negative effects of decreases in diet quality appear especially significant for penguins. Penguins feed on varying proportions of zooplankton (especially macrozooplanktonic crustaceans like krill), cephalopods, and fish (Cherel et al. 2010; Masello et al. 2010) that are increasingly targeted by commercial fisheries (Pauly et al. 1998; Alonzo et al. 2003). Breeding penguins are central-place foragers susceptible to localized prey depletion (Birt et al. 1987), exacerbated because swimming is energetically demanding relative to flight (Elliott et al. 2013). Penguins must have sufficient energy reserves to allow for long periods of fasting during breeding and moult (Green et al. 2007). Consequently, body mass of adult or chick penguins is commonly positively correlated with reproductive success, chick survival to fledging, and post-fledging survival (Olsson 1997; Moreno et al. 1999; McClung et al. 2004; Crawford et al. 2008). Additionally, adult survival is linked to adult body condition, as demonstrated by a mass starvation event of adult penguins at the Falkland Islands in 1986 (Keymer et al. 2001).

During the 37 year period 1970–2007 the global populations of Southern Rockhopper Penguins (*Eudyptes chrysocome*) and Northern Rockhopper Penguins (*E. moseleyi*) declined by 34 and 57%, respectively (BirdLife International 2010), resulting in IUCN Red List rankings of ‘Vulnerable’ and ‘Endangered’ (BirdLife International 2014; but see Robson et al. 2011; Baylis et al. 2013). At the few breeding sites where the population record extends back further to the mid-20th century, declines of c. 90% representing millions of birds have been documented (Cunningham and Moors 1994; Pütz et al. 2003; Cuthbert et al. 2009). The largely synchronous declines of Rockhopper Penguin populations throughout their circumpolar sub-Antarctic (Southern Rockhopper Penguin) and sub-tropical Atlantic and Indian Ocean (Northern Rockhopper Penguins) ranges might signal a single shared cause. The leading hypothesis is well described by the “Nutritional Stress Hypothesis” (NSH; Trites and Donnelly 2003) which posits that a decrease in diet quality causes lower body mass, reduced reproductive success, and lower juvenile and adult survival, with a subsequent population decline of a predator population. In the case of Rockhopper Penguins, the decrease in diet quality is suggested to have been caused by climate change producing either warmer (Cunningham and Moors 1994),

cooler (Guinard et al. 1998; Pütz et al. 2006b), or sub-optimal (Dehnhard et al. 2013) sea-surface temperatures (SST).

Evaluating support for the NSH as the cause of Rockhopper Penguin population declines requires assessment of what constitutes a high quality diet for Rockhopper Penguins. Fish generally have a higher lipid and energy density than zooplankton or cephalopods (Clarke and Prince 1980; Cherel and Ridoux 1992; Meynier et al. 2008). Additionally, fish are more rapidly digested by seabirds, including Southern Rockhopper Penguins (Jackson 1992), than are crustaceans or cephalopods (Wilson et al. 1985; Jackson et al. 1987). The prediction follows that penguins with a higher $\delta^{15}\text{N}$ value – those feeding on a higher proportion of fish – should be in better body condition. In support of fish being higher quality prey for penguins the body condition of Magellanic Penguin (*Spheniscus magellanicus*) chicks has been shown to be positively correlated with the proportion of fish in their diet, as inferred from higher $\delta^{15}\text{N}$ values (Forero et al. 2002). Following from this result, researchers considering the NSH for Rockhopper Penguins (Hilton et al. 2006) and dietary effects on their breeding success (Booth and McQuaid 2013) have assumed that a higher trophic level, more fish-based diet is of higher quality. However, no study has tested this assumption in any penguin species other than Magellanic Penguins by examining whether adults or chicks feeding on higher trophic level prey are actually heavier at a given stage or age.

Stable isotope analysis (SIA) is increasingly used in studies of marine predators, where nitrogen isotopes can evaluate dietary trophic levels and carbon isotopes can infer prey habitats. The heavier nitrogen isotope (^{15}N) is enriched at increasing trophic levels (Deniro and Epstein 1981), so that fish and cephalopods have a higher $^{15}\text{N}:^{14}\text{N}$ ratio (i.e., higher $\delta^{15}\text{N}$ value) compared to zooplankton prey (Hobson et al. 1994). In contrast, ^{13}C shows little enrichment with increasing trophic level (Deniro and Epstein 1978), but carbon isotopes can provide useful insights into dietary sources. Benthic and inshore plankton at the base of the food chain are enriched in ^{13}C relative to pelagic and offshore plankton (higher $^{13}\text{C}:^{12}\text{C}$ ratio, i.e., higher $\delta^{13}\text{C}$ value), allowing interpretation of predator foraging habitat (Hobson et al. 1994). Values of $\delta^{15}\text{N}$ and particularly $\delta^{13}\text{C}$ are lower at higher latitudes (Jaeger et al. 2010), providing additional insight into likely foraging areas. Stable isotope values of whole blood are useful for assessing how the diet of individuals relates to their body condition because whole blood integrates information on diet over the previous 3–4 weeks (Hobson and Clark 1992; Bearhop et al. 2002).

Campbell Island, in New Zealand's sub-Antarctic, formerly held the world's largest population of the eastern sub-species of Southern Rockhopper Penguins (Eastern Rockhopper

Penguin, *E. c. filholi*), but a dramatic decline between 1942 and 1984 shrank the population by an estimated 94%, from c. 800,000 to just 51,500 breeding pairs (Moors 1986; Cunningham and Moors 1994). The population continued to decline at a slower rate 1984–1996, but grew 1996–2012 (Chapter 2). Contrary to the hypothesis of a fish-based diet being of higher quality, adult and chick stomach contents during chick rearing in 1985–1986 and 1986–1987 found a higher proportion of fish relative to other, more stable populations (Cooper et al. 1990; Marchant and Higgins 1990). Cunningham and Moors (1994) suggested the population decline on Campbell Island was being caused by a climate-driven reliance on fish, as opposed to the zooplankton-dominated diet documented elsewhere (Cooper et al. 1990). These contradictory interpretations of what constitutes a high quality diet for Rockhopper Penguins indicate that additional studies of diet quality are urgently required at Campbell Island and other key breeding sites.

We examined blood samples of Eastern Rockhopper Penguin chicks and adults on Campbell Island over three years to determine whether a higher quality diet is composed of prey of higher trophic level, in that body mass is positively correlated with $\delta^{15}\text{N}$ values. What relationship to expect between body mass and $\delta^{13}\text{C}$ values is less obvious because $\delta^{13}\text{C}$ values reflect differences in foraging habitat in multiple dimensions (benthic or pelagic, inshore or offshore, latitudinally). We predicted that individuals feeding on more benthic/inshore prey would be heavier, because Tremblay and Cherel (2000) found that female Eastern Rockhopper Penguins that made a greater proportion of benthic dives brought a greater mass of food ashore, and because intuitively, inshore-feeding individuals may expend less energy in travel to and from foraging areas. Eastern Rockhopper Penguins lay a two-egg clutch but their c. 40% smaller first-laid “A-egg” often fails to hatch, or if both the A- and B-eggs hatch then usually the later-hatching, smaller A-chick starves to death at a young age (St. Clair and St. Clair 1996). We predicted no differences in mass or isotope values of independently raised chicks of either chick-type at 24 days (d) of age. We addressed four specific questions:

1. Were chicks heavier when fed higher trophic level or more benthic/inshore prey?
2. Did adults that fed at a higher trophic level or on more benthic/inshore prey prior to colony arrival or during their incubation foraging trip return with greater body mass?
3. Were there year, breeding stage, age, chick-type, or sex related differences in diet and body mass?
4. Were the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of Rockhopper Penguins on Campbell Island different from those of other populations?

MATERIALS AND METHODS

Sample collection

Eastern Rockhopper Penguins were sampled at Penguin Bay, Campbell Island (52° 32' 12" S, 169° 2' 10" E), between October and January over three seasons, 2010–2011, 2011–2012, and 2012–2013. Hereafter breeding seasons will be referred to by the year in which they began. Breeding chronology was very similar between years and to sporadic records made since the 1940s (Bailey and Sorensen 1962; Marchant and Higgins 1990; Table 3.1). Following breeding and moult Eastern Rockhopper Penguins have a c. 5-month over-winter period at sea. Males arrive first by about a week, but females have a longer initial fast at their nests because males make the first incubation foraging trip of about two weeks duration. After males return females make an incubation foraging trip of about one week, returning near hatching. Only females feed chicks during the guard period while males continue their second long fast, guarding their chick until chicks form crèches at around 24 d of age. Males may make an extended trip to recover body condition before joining the female in chick provisioning until chicks fledge at c. 65 d of age (Marchant and Higgins 1990).

Table 3.1 Mean dates and durations (in days, \pm SD) of Eastern Rockhopper Penguin breeding stages in 2011 and 2012 of males at nests with a chick at the end of the guard phase and of females at nests that hatched an egg. Samples sizes are given in brackets.

	2011	2012
♂ courtship/incubation fast	14-Oct \pm 1.9 d to 19-Nov \pm 1.7 d 36.1 \pm 2.3 d, (35)	11-Oct \pm 2.2 d to 17-Nov \pm 1.5 d 36.8 \pm 2.6 d, (26)
♀ courtship/incubation fast	20-Oct \pm 2.0 d to 4-Dec \pm 1.6 d 44.5 \pm 2.4 d, (41)	19-Oct \pm 1.6 d to 4-Dec \pm 1.8 d 46.0 \pm 2.5 d, (46)
♂ incubation foraging trip	19-Nov \pm 1.7 d to 2-Dec \pm 1.2 d 13.1 \pm 1.4 d, (35)	17-Nov \pm 1.5 d to 3-Dec \pm 1.6 d 15.8 \pm 1.4 d, (26)
♀ incubation foraging trip	4-Dec \pm 1.6 d to 11-Dec \pm 2.3 d 7.4 \pm 3.4 d, (41)	4-Dec \pm 1.8 d to 13-Dec \pm 2.5 d 8.7 \pm 2.0 d, (46)
Incubation period A-eggs	5-Nov \pm 2.3 d to 14-Dec \pm 3.1 d 38.8 \pm 1.5 d, (28)	4-Nov \pm 2.2 d to 13-Dec \pm 1.9 d 39.1 \pm 1.9 d, (14)
Incubation period B-eggs	10-Nov \pm 2.4 d to 13-Dec \pm 2.5 d 33.3 \pm 1.0 d, (55)	8-Nov \pm 2.2 d to 12-Dec \pm 2.1 d 33.9 \pm 1.0 d, (48)
♂ incubation/guard fast	2-Dec \pm 1.2 d to 6-Jan \pm 3.3 d 34.5 \pm 3.4 d, (35)	3-Dec \pm 1.6 d to 4-Jan \pm 3.0 d 32.0 \pm 3.4 d, (26)

In 2010 adults were sampled in late October, likely about one week after arrival for females and two weeks for males because of our field team's timing of arrival on the island (Table 3.1, Table 3.2). In 2011 and 2012 we arrived before penguins returned and recorded the date of arrival of adults previously implanted with a PIT tag (ISO FDX-B 11 × 2.1 mm glass-encased transponder; Allflex Australia Pty). PIT tag codes, time, and date data were recorded by hand at nest sites using an RS320 Stick Reader (Allflex Australia Pty), or automatically using two radio frequency identification (RFID) data loggers and antennae set up along the penguin's travel pathway into the study colonies (S. Cockburn, Department of Conservation, Wellington). In 2011 and 2012 adults were sampled within two days of their arrival and return from incubation foraging trips. Mean sampling dates in 2011 and 2012 were similar to the breeding chronology of a larger sample of PIT-tagged adults we monitored (Table 3.1, Table 3.2). Different individuals were sampled at each stage and in each year. Adults were sexed based on their breeding schedule and bill depth (Warham 1972). In 2011 and 2012 chicks were PIT-tagged at 18 d and marked with blue water-soluble paint to enable their identification as they gained mobility prior to crèching. Chicks were sampled at 20–30 d of age in 2010 when hatch dates were uncertain, and at 24 d of age in 2011 and 2012 when hatch dates and chick-type (A-chicks from first-laid A-eggs, or B-chicks from second-laid B-eggs) were known through daily nest checks. We deliberately sampled chicks whose sibling egg had failed to hatch so that each chick's measurements reflected total parental investment in chick provisioning. Chicks typically receive one feed per day in the evening from their mothers during the guard stage (Marchant and Higgins 1990). We measured chicks in the afternoon while females were away foraging to limit the effect of time-since-feeding on chick mass. We measured body mass at the time of blood sampling using a 1 kg (± 10 g), 2.5 kg (± 20 g), or 5 kg (± 50 g) spring scale. We examined body mass rather than a body condition index, because indices not validated against measured values of fat and protein may decrease predictability relative to using body mass alone (Schamber et al. 2009).

Table 3.2 Mean sampling dates, stable carbon ($\delta^{13}\text{C}$, ‰) and nitrogen ($\delta^{15}\text{N}$, ‰) isotope values, body masses (g), and C/N mass ratios of Eastern Rockhopper Penguin chicks and adult females and males (\pm SD). Chicks were sampled from 20–30 days old (d) in 2010 and at 24 d in 2011 and 2012. A- and B-chicks are sub-groups of the 30 chicks in 2012 based on laying order within each two-egg clutch. In 2010 adult “Arrival” samples were taken partway through their courtship/incubation fast, but in 2011 and 2012 adults were sampled within two days of colony arrival and upon return from their incubation foraging trip. Isotope and body mass values that are significantly different (Tukey HSD test, $\alpha < 0.05$) between sex/age groups (compared at the same stage and year for adults) are indicated with different superscript letters, significant differences between stage/year groups (compared within the same sex/age group) are indicated with different superscript numbers. Sample sizes are given by “n”, with a total $n = 180$.

Stage	Year	n	Date	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Body mass	C/N mass ratio
Chicks	2010	15	9-Jan \pm 0.9	9.82 \pm 0.47 ^{A,1}	-19.61 \pm 0.33 ^{A,1}	----	3.39 \pm 0.20
Chicks	2011	25	5-Jan \pm 0.9	8.97 \pm 0.16 ^{A,2}	-20.86 \pm 0.22 ^{A,2}	1147 \pm 96 ^{A,1}	3.37 \pm 0.09
Chicks	2012	30	4-Jan \pm 1.8	9.83 \pm 0.22 ^{A,1}	-19.08 \pm 0.51 ^{A,3}	857 \pm 224 ^{A,2}	3.43 \pm 0.07
A-chicks	2012	6	5-Jan \pm 1.0	9.72 \pm 0.13 ^{A,1}	-18.68 \pm 0.42 ^{A,4}	701 \pm 139 ^{A,3}	3.44 \pm 0.09
B-chicks	2012	24	4-Jan \pm 2.0	9.86 \pm 0.24 ^{A,1}	-19.18 \pm 0.49 ^{A,3}	895 \pm 227 ^{A,2}	3.43 \pm 0.07
Female	2010	10	28-Oct \pm 1.2	7.67 \pm 0.21 ^{B,1}	-23.42 \pm 0.34 ^{B,1}	----	3.61 \pm 0.09
Female	2011	10	19-Oct \pm 2.1	7.27 \pm 0.31 ^{B,2}	-22.84 \pm 0.52 ^{B,2}	3615 \pm 219 ^{B,1}	3.32 \pm 0.04
Female	2012	10	18-Oct \pm 2.4	7.06 \pm 0.28 ^{B,2}	-23.09 \pm 0.37 ^{B,2}	3549 \pm 196 ^{B,1}	3.43 \pm 0.10
Female	Incubation	2011	10-Dec \pm 1.2	7.96 \pm 0.31 ^{B,1}	-22.45 \pm 0.28 ^{B,3}	2675 \pm 178 ^{B,2}	3.34 \pm 0.04
Female	Incubation	2012	11-Dec \pm 2.2	8.52 \pm 0.24 ^{B,3}	-22.53 \pm 0.29 ^{B,3}	2387 \pm 158 ^{B,3}	3.28 \pm 0.02
Male	2010	10	27-Oct \pm 0.7	8.08 \pm 0.38 ^{C,1}	-22.68 \pm 0.43 ^{C,1}	----	3.46 \pm 0.05
Male	2011	10	14-Oct \pm 0.5	7.44 \pm 0.23 ^{B,1}	-22.38 \pm 0.43 ^{B,1}	3505 \pm 148 ^{B,1}	3.28 \pm 0.05
Male	2012	10	14-Oct \pm 0.5	6.86 \pm 0.42 ^{B,2}	-22.71 \pm 0.29 ^{B,1}	3421 \pm 230 ^{B,1}	3.35 \pm 0.05
Male	Incubation	2011	2-Dec \pm 0.5	7.85 \pm 0.26 ^{B,3}	-22.47 \pm 0.21 ^{B,1}	3730 \pm 207 ^{C,2}	3.35 \pm 0.03
Male	Incubation	2012	5-Dec \pm 0.6	7.72 \pm 0.23 ^{C,3}	-22.68 \pm 0.24 ^{B,1}	3400 \pm 259 ^{C,1}	3.29 \pm 0.02

Stable isotope analysis

All individuals were sampled using a 25 gauge needle and 1.0 mL syringe to collect < 1.0 mL of blood from the brachial vein. Samples were placed in 2.0 mL Eppendorf tubes and preserved with 75% ethanol in 2010 and with 95% ethanol in 2011 and 2012 from the same batch in the latter two years. Preservation of blood in ethanol may enrich $\delta^{13}\text{C}$ values to a different degree between batches of ethanol (Bugoni et al. 2008). This potential effect should be considered in our comparisons of $\delta^{13}\text{C}$ values from 2010 to those from 2011 and 2012. Samples from each year were stored in ethanol for *c.* 2.5, 1.5, and 0.5 years prior to being simultaneously dried and analysed. Storage in ethanol for periods of up to 12 weeks may increase sample $\delta^{13}\text{C}$ values (Kaehler and Pakhomov 2001), but any effect of longer term storage is unknown. Lipid extraction was unnecessary because of the low lipid content of whole blood (Cherel et al. 2005a), as demonstrated by the low C/N mass ratios of our samples (Table 3.2). Whole blood samples were dried for two days in an oven at 60 °C before being ground with a mortar and pestle. An electronic balance was used to weigh out 0.7–0.8 mg of each sample into a tin boat. SIA were conducted at the National Institute of Water and Atmospheric Research (NIWA) stable isotope laboratory in Wellington, New Zealand, following Butler et al. (2014). Additionally, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were corrected against NIST standards (NIST 8573 USGS40 L-glutamic acid, NIST 8548 IAEA-N2 ammonium sulphate, and NIST 8542 IAEA-CH-6 Sucrose) using a three-point normalisation process. A laboratory standard DL-Leucine (DL-2-Amino-4-methylpentanoic acid, $\text{C}_6\text{H}_{13}\text{NO}_2$, Lot 127H1084, Sigma, Australia) was calibrated routinely against a suite of international NIST standards. Repeat analysis of NIST and internal DL Leucine laboratory standards during the batch analyses produced data accurate to within 0.19‰ for $\delta^{15}\text{N}$ and 0.36‰ for $\delta^{13}\text{C}$ and a precision of better than 0.19‰ for $\delta^{15}\text{N}$ and 0.31‰ for $\delta^{13}\text{C}$.

Statistical analysis

We used separate simple linear regression analyses for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values versus body mass for chicks and adults at each stage in 2011 and 2012. For regressions between body mass and isotope values, we pooled data within a sex for stages/years when data were not significantly different. We did not include adult or chick body masses from 2010 in any analysis because adults were measured partway through their courtship/incubation fast and chick age was unknown. Chick $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, and body mass raw values had bimodal distributions, so we used separate Kruskal-Wallis tests to evaluate whether chick $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, and body masses differed between 2011 and 2012, followed by Dwass-Steel-Critchlow-Fligner tests

for all pairwise comparisons. In 2012 chick data was normally distributed and independent variables had equal variances between A- and B-chicks, so we used Unpaired t tests to test for differences between A- and B-chicks. Mann-Whitney U tests were used to compare chick and adult $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. We used 2-way ANOVAs to compare $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values at arrival between the sexes and between all three years, followed by post-hoc Tukey's Honestly-Significant-Difference (HSD) tests for pairwise comparisons. A 3-way MANOVA was used to compare $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between the sexes at arrival and incubation return in 2011 and 2012, because $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were correlated ($r^2 = 0.158$, $n = 90$, $P < 0.001$). We present MANOVA results using F statistics derived from Wilk's lambda. We again used post-hoc Tukey's HSD tests for pairwise comparisons. Adult body masses were compared between the sexes, years, and stages in 2011 and 2012 using Mann-Whitney U tests because of the bimodal distribution of body mass. All means are presented \pm SD. Statistical tests were performed using Systat 13 (Systat Software Inc.) and Statistica 12 (StatSoft Inc.).

RESULTS

We collected blood samples for SIA from 70 chicks, 55 adult females, and 55 adult males over the 2011, 2012, and 2013 breeding seasons (Table 3.2). Sample sizes of A-chicks versus B-chicks were unknown in 2010, but were $n = 1$ A and $n = 24$ B in 2011 and $n = 6$ A and $n = 24$ B in 2012. Male and female mean arrival, laying, and incubation departure dates were similar between years, being on average 0–3 days earlier in 2012 relative to 2011 (Table 3.1). The incubation foraging trips of males and females were three and two days longer, respectively, in 2012 compared to 2011. Males' incubation/guard period fast was three days shorter in 2012 than in 2011 (Table 3.1). In no sex/age group did mean $\delta^{13}\text{C}$ values show a pattern of decrease from 2010 to 2012, therefore mean $\delta^{13}\text{C}$ values were not larger after longer storage time in ethanol (Table 3.2).

Chick $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values and body masses

We found no support for the prediction that higher trophic level prey is of higher quality, i.e., produces chicks of greater body mass. Chick $\delta^{15}\text{N}$ values were not related to chick body masses in 2011 or 2012 (2011: $r^2 = 0.020$, $n = 25$, $p = 0.503$; 2012: $r^2 = 0.026$, $n = 30$, $p = 0.393$).

Likewise, chick $\delta^{13}\text{C}$ values were not related to chick body masses in either year (2011: $r^2 = 0.020$, $n = 25$, $p = 0.497$; 2012: $r^2 = 0.041$, $n = 30$, $p = 0.285$). Neither $\delta^{15}\text{N}$ nor $\delta^{13}\text{C}$ values were related to body masses of A- or B-chicks in 2012 when chick types were also considered separately. In 2012 the body masses of B-chicks were greater than A-chicks ($t_{12.67} = -2.654$, $p = 0.020$). A-chicks had higher $\delta^{13}\text{C}$ values than B-chicks ($t_{8.80} = 2.531$, $p = 0.033$), but similar $\delta^{15}\text{N}$ values ($t_{14.55} = -1.972$, $p = 0.068$).

Contrary to the hypothesis that higher trophic level prey is of higher quality, at 24 d of age chicks were heavier in 2011 when fed lower trophic level prey than in 2012 (Figure 3.1A, Table 3.2). Chick $\delta^{15}\text{N}$ values (Kruskal-Wallis, $H_2 = 46.9$, $P < 0.001$), $\delta^{13}\text{C}$ values ($H_2 = 52.3$, $P < 0.001$), and body masses ($H_2 = 36.2$, $P < 0.001$) all differed between years (Table 3.2). Chick $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were lower in 2011 than in 2010 ($P < 0.001$) and 2012 ($P < 0.001$), when they were similar (both $P > 0.80$). Chick body masses were higher in 2011 than in 2012 ($p = 0.022$). When comparing only B-chicks, body masses were also higher in 2011 than in 2012 ($t_{29.85} = 5.236$, $P < 0.001$). Chick $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were both consistently higher than those of adults (Figure 3.1, Table 3.2).

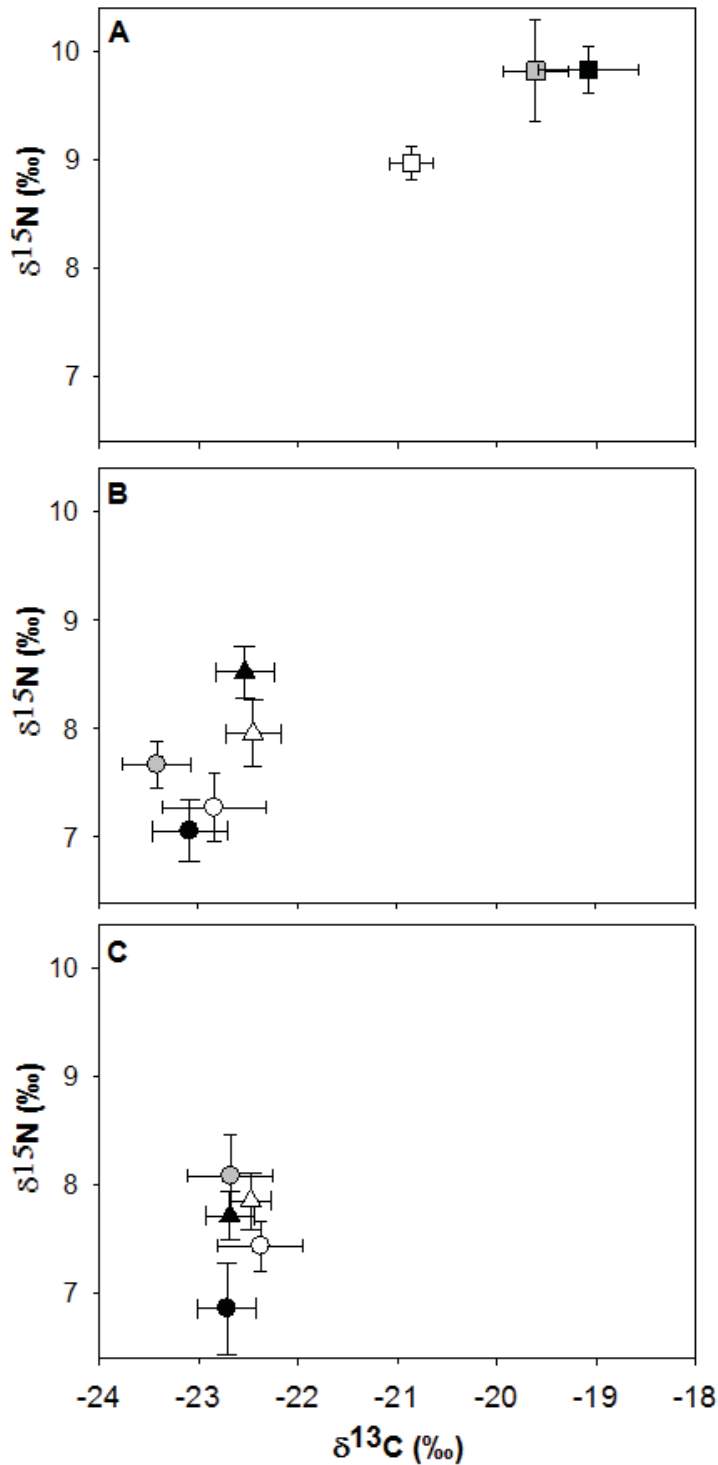


Figure 3.1 Stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values of Eastern Rockhopper Penguin chicks (A), and adult females (B) and males (C). Penguins were sampled in 2010 (grey), 2011 (white), 2012 (black). Chicks (squares) were sampled from 20–30 days old in 2010 and 24 days old in 2011 and 2012. In 2010 adult “arrival” samples were taken partway through their courtship/incubation fast, but in 2011 and 2012 adults were sampled within two days of colony arrival (circles) and upon return from their incubation foraging trip (triangles).

Adult $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values and body masses

In regressing adult body masses at arrival against $\delta^{15}\text{N}$ values we again found no support for the prediction that higher trophic level prey is of higher quality. Adult body masses at arrival were not significantly related to $\delta^{15}\text{N}$ values in either sex in 2011 or 2012 (Figure 3.2). In both males and females $\delta^{13}\text{C}$ values and body masses at arrival were similar between 2011 and 2012. Pooled female $\delta^{13}\text{C}$ values at arrival were positively correlated with body masses ($r^2 = 0.325$, $n = 20$, $p = 0.009$; Figure 3.3A).

Contrary to expectations, males with a lower $\delta^{15}\text{N}$ value at incubation return in 2011 were heavier ($r^2 = 0.477$, $n = 10$, $p = 0.027$, Figure 3.2B). There was also a trend for males with lower $\delta^{13}\text{C}$ values at incubation return in 2011 to be heavier ($r^2 = 0.398$, $n = 10$, $p = 0.051$). Male $\delta^{13}\text{C}$ values at arrival and incubation return in 2011 were similar (1-way ANOVA, $F_{1,18} = 0.415$, $p = 0.527$). When male 2011 data was pooled, males with lower $\delta^{13}\text{C}$ values in 2011 were significantly heavier ($r^2 = 0.258$, $n = 20$, $p = 0.022$), in contrast to the positive correlation found in females at arrival in 2011 and 2012 combined (Figure 3.3).

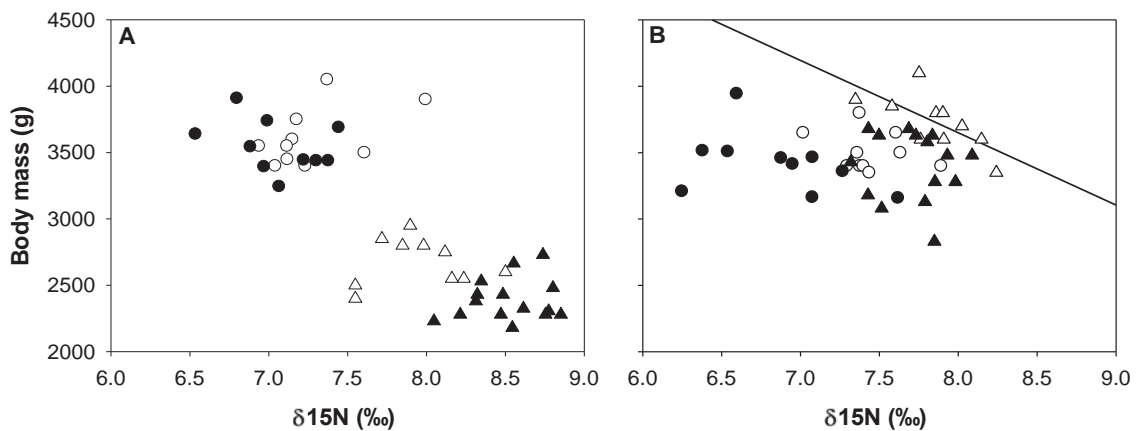


Figure 3.2 Body masses of adult female (A) and male (B) Eastern Rockhopper Penguins in relation to $\delta^{15}\text{N}$ values. Penguins were sampled in 2011 (white) and 2012 (black) at colony arrival (circles) and upon return from incubation foraging trips (triangles). The linear regression line in panel B shows that males with lower $\delta^{15}\text{N}$ values were heavier at incubation return in 2011 ($r^2 = 0.477$, $n = 10$, $P = 0.027$).

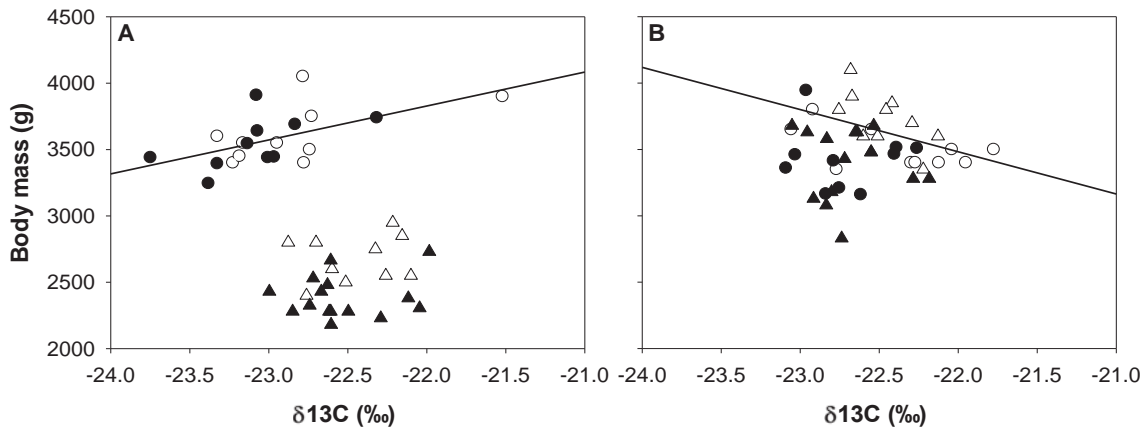


Figure 3.3 Body masses of adult female (A) and male (B) Eastern Rockhopper Penguins in relation to $\delta^{13}\text{C}$ values. Penguins were sampled in 2011 (white) and 2012 (black) at colony arrival (circles) and upon return from incubation foraging trips (triangles). The linear regression line in panel A shows that females with higher $\delta^{13}\text{C}$ values were heavier at arrival when 2011 and 2012 data were pooled ($r^2 = 0.325$, $P = 0.009$). In contrast, the linear regression line in panel B shows that males with lower $\delta^{13}\text{C}$ values were heavier in 2011 when arrival and incubation return data were pooled ($r^2 = 0.258$, $n = 20$, $P = 0.022$).

In 2011 and 2012 adult $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were positively correlated ($r^2 = 0.158$, $n = 90$, $P < 0.001$) and tended to follow similar patterns between years, stages, and sexes (Table 3.2). Generally, both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were lower at arrival than at incubation return (3-way MANOVA, $F_{1,88} = 96.6$, $P < 0.001$), except for male $\delta^{13}\text{C}$ values which were similar between stages ($F_{1,43} = 9.63$, $P < 0.001$). Post hoc Tukey's HSD tests indicated that female $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were lower at arrival than at incubation return in both 2011 and 2012 (Table 3.2). As in females, male $\delta^{15}\text{N}$ values were lower at arrival than at incubation return in 2011 and 2012. However, male $\delta^{13}\text{C}$ values were similar at both stages in both years. Female $\delta^{15}\text{N}$ values at arrival were similar in 2011 and 2012. In contrast, female $\delta^{15}\text{N}$ values were lower in 2011 than in 2012 at incubation return, as found for chicks in 2011 versus 2012. Male $\delta^{15}\text{N}$ values were higher at arrival in 2011 than in 2012, but were similar at incubation return in both years. Female and male $\delta^{15}\text{N}$ values were similar at each stage within years, except that females had higher $\delta^{15}\text{N}$ values than males at incubation return in 2012. Likewise, both sexes had similar $\delta^{13}\text{C}$ values at each stage in both years, but females tended to have lower $\delta^{13}\text{C}$ values than males at arrival in 2011 ($p = 0.050$).

Overall, adults were heavier in 2011 than 2012 (Table 3.2), heavier at arrival than at incubation return, and males were heavier than females. Females were heavier at incubation return in 2011 than in 2012. Likewise, males were heavier at incubation return in 2011 than in 2012. Females were heavier at arrival than at incubation return in both 2011 and 2012. In contrast, males weighed less at arrival than at incubation return in 2011. Both sexes arrived at a similar mass in 2011 and 2012, however females were lighter than males at incubation return in both 2011 and 2012.

DISCUSSION

We found no support for the hypothesis that a high quality penguin diet contains a greater proportion of upper trophic level prey than a low quality diet. Contrary to predictions, Eastern Rockhopper Penguin (*Eudyptes chrysocome filholi*) chick and adult $\delta^{15}\text{N}$ values were not positively correlated with body masses in 2011 or 2012. Instead, we found the reverse relationship: adult males were heavier in 2011 when their diet was biased towards lower trophic level prey on their incubation foraging trip. Similarly, mean chick mass at 24 d of age was significantly higher in 2011 when average chick $\delta^{15}\text{N}$ values were lower than in 2012. Other differences in diet and body mass between years, breeding stages, age, chick-type, and sex are discussed below.

Chick $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values

The lower $\delta^{15}\text{N}$ values of chicks in 2011 indicate they were fed a greater proportion of lower trophic level prey (zooplankton) than in 2010 and 2012 when chicks consumed a greater proportion of higher trophic level prey (fish and cephalopods; Hobson et al. 1994). The lower $\delta^{13}\text{C}$ values of chicks in 2011 suggest their zooplankton prey came from more pelagic/offshore waters than the fish and cephalopods sourced from more benthic/inshore waters in 2010 and 2012 (Hobson et al. 1994). Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of chicks in 2011 were higher than in 2012 by 0.96‰ and 1.78‰ respectively, but both differences were likely underestimated because of the high likelihood of $\delta^{13}\text{C}$, and especially $\delta^{15}\text{N}$ depletion in the food-limited chicks of 2012 (Williams et al. 2007; Sears et al. 2009). Adult $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values at incubation return showed little variation and had very similar means between the sexes in 2011 when chick $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values also contained little variation. In 2011 both males and females made shorter incubation foraging trips but returned at heavier masses than in 2012. Females also made chick-provisioning trips of shorter duration and provisioned chicks more frequently in

2011 compared to 2012 (Chapter 4). Consequently, chicks were heavier in 2011 than in 2012. These results suggest foraging specialization on abundant pelagic zooplankton in 2011. In contrast, in 2012 penguins broadened their diet and foraging habitat to include more fish and/or cephalopods, but ended up returning at lower masses from longer trips and rearing smaller chicks. Likewise, for Macaroni Penguins (*Eudyptes chrysolophus*) and Gentoo Penguins (*Pygoscelis papua*) at South Georgia years of a fish-based, rather than krill-based diet are associated with small meal masses, and low provisioning rates, fledging masses, and fledging success (Croxall et al. 1999; Waluda et al. 2012).

In 2012 females on incubation foraging trips fed on a greater proportion of higher trophic level prey than in 2011. Likewise, females fed chicks higher trophic level prey in 2012 versus 2011. This suggests prey selection by females for both self-feeding and chick-provisioning is not fixed, but demonstrates behavioural plasticity that likely reflects inter-annual differences in prey availability. Tremblay and Cherel (2003; 2005) suggested Rockhopper Penguins exhibited much plasticity between individuals and populations with respect to foraging behaviour and diet. Cunningham and Moors (1994) hypothesized that warm SST around Campbell Island led to decreased Eastern Rockhopper Penguin diet quality and lower chick fledging weights. In partial support of this hypothesis monthly SST values were 0.36 °C higher in 2012 than in 2011 when averaged over the three months prior to laying (Aug, Sept, Oct), but were similar during incubation and the guard period (Nov, Dec, Jan) in a rectangular region surrounding Campbell Island, 52–53 °S, 168.25–169.75 °E (111 km latitudinally by 102 km longitudinally) that encompasses the expected foraging radius of < 50 km for chick-rearing Eastern Rockhopper Penguins (Sagar et al. 2005; MODIS-Aqua 4 micron night 4 km data from http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_month). In contrast, average SST in April–June during and after moult and prior to breeding in 2012 was lower than in any other year 2002–2014 and was 1.85 °C lower than in 2011. The potential negative effects of warm pre-laying SST and exceptionally low over-winter SST on subsequent Eastern Rockhopper Penguin diet quality suggests a quadratic relationship between SST and diet quality. Similarly, Dehnhard et al. (2013) found a quadratic relationship between adult survival of Southern Rockhopper Penguins in the southwest Atlantic and SST in a three month period overlapping moult.

Décima et al. (2013) found that an inter-annual increase in SST of c. 3 °C was associated with an increase of c. 2 ‰ in the baseline $\delta^{15}\text{N}$ values of zooplankton in the California Current Ecosystem. It is possible that SST being 0.36 °C higher in the three months prior to laying in 2012 versus 2011 caused a slight increase in the isotopic baseline of the prey

base around Campbell Island. However, we suggest that the increase in chick $\delta^{15}\text{N}$ values by 0.96‰ we observed between 2011 and 2012 was caused by a shift in diet to higher trophic level prey rather than an increase in the isotopic baseline, given the modest temperature increase and physical diet observations described later. Likewise, the increase in chick $\delta^{13}\text{C}$ values between 2011 and 2012 could be associated with an increase in isotopic baseline values because of an increased rate of primary productivity (Hilton et al. 2006). Again our results favour the default explanation of a shift to more benthic/inshore prey in 2012 rather than a shift in isotopic baseline, because we would expect chick mass to have been greater instead of much less in 2012 if primary productivity was higher in 2012 than 2011.

In 2012 when enough samples were collected from A-chicks to allow a novel dietary comparison with B-chicks, we found that at 24 d of age A-chicks had both a lower body mass and had been fed more benthic/inshore prey than B-chicks. The lower body mass of A-chicks could be related to their lower hatching mass and egg hormone concentrations (Poisbleau et al. 2008; 2009; 2011), but these differences were no longer apparent in 18 d old Southern Rockhopper Penguins raised independently in assigned treatment groups (Poisbleau et al. 2008; Dehnhard et al. 2011a). Instead, the differences we found in both chick body mass and diet suggest A-chicks were fed a lower quality diet by parents of lower quality or that had decreased their reproductive investment after failing to hatch their larger, typically favoured and more successful B-egg (St. Clair and St. Clair 1996).

Eastern Rockhopper Penguin chicks in the present study had higher $\delta^{15}\text{N}$ values ($8.97 \pm 0.16\text{‰}$ to $9.83 \pm 0.22\text{‰}$) than those from the Crozet Islands (6.82 ± 0.28 ; Cherel et al. 2007) or Kerguelen Islands ($8.16 \pm 0.3\text{‰}$; Cherel et al. 2010). The higher values at Campbell Island likely reflect a greater reliance on fish and cephalopods during chick-rearing than at the Indian Ocean sites where the pelagic crustacean *Euphausia vallentini* is the dominant prey species (>82% of the number of prey at both sites; Tremblay and Cherel 2003). For example, in 1985–1986 Campbell Island chick diet samples were dominated by a single fish species, southern blue whiting (*Micromesistius australis*; 75.6% by number of prey; Marchant and Higgins 1990).

Adult $\delta^{15}\text{N}$ values

Contrary to our prediction, males with lower $\delta^{15}\text{N}$ values were heavier at incubation return in 2011, indicating that a more zooplankton-based diet was a higher quality diet. An alternative interpretation is that males with lower body mass had higher $\delta^{15}\text{N}$ values because of greater $\delta^{15}\text{N}$ enrichment from protein catabolism, which may have occurred during their

courtship/early-incubation period of fasting (Cherel et al. 2005b). Multiple lines of evidence suggest the latter interpretation is less likely. There was no relationship between body mass and $\delta^{15}\text{N}$ values of females at incubation return, although females underwent a longer courtship/incubation fast (Table 3.1), lost a greater proportion of their arrival body mass (K.W.M. unpub. data), and had shorter incubation foraging trips than males (Table 3.1). There were also trends for heavier males to have lower $\delta^{15}\text{N}$ values at arrival in both 2011 and 2012 that can only be attributed to differences in diet quality (Figure 3.2). Additionally $\delta^{15}\text{N}$ enrichment in whole blood of King Penguins (*Aptenodytes patagonicus*) fasting for 25 and c. 40 days averaged only 0.30 and 0.17‰ (Cherel et al. 2005b). In the present study male $\delta^{15}\text{N}$ values at incubation return in 2011 had a range of 0.89‰, far too large to be accounted for solely by individual variation in protein catabolism during fasting. That said, $\delta^{15}\text{N}$ enrichment from protein catabolism may have contributed to “arrival” $\delta^{15}\text{N}$ values being highest in 2010 when adults were sampled after c. 1–2 weeks of fasting.

The $\delta^{15}\text{N}$ values of both males and females were higher at incubation return than at arrival. As our other results support a lower trophic level diet as being of higher quality, we must ask why both sexes transitioned to a higher trophic level diet between their pre-breeding and incubation periods and why chicks were fed a still more fish- and cephalopod-based diet? We suggest this is because of changes in prey availability with proximity to the breeding colony or else through time because of local depletion or seasonal trends, rather than a change of deliberate choice. In contrast, adult Southern Rockhopper Penguin diet decreased in trophic level between pre-breeding and breeding stages at the Falkland Islands in one year of study (Dehnhard et al. 2011b), but was similar between stages in another two years (Ludynia et al. 2013). The $\delta^{15}\text{N}$ values of adults at arrival and during chick-rearing, and those of chicks were all similar in one year for Eastern Rockhopper Penguins at the Crozet Islands (Cherel et al. 2007).

Female and male $\delta^{15}\text{N}$ values were similar at each stage within years, except that females had higher $\delta^{15}\text{N}$ values than males at incubation return in 2012. This finding contrasts with that of Dehnhard et al. (2011b) who found that males consumed a higher trophic level diet than females prior to arrival. The slightly larger body size and consequently greater theoretical diving depth and duration of males common to a number of seabird species (Burger 1991) is generally associated with consumption of more fish by male than female seabirds (Bearhop et al. 2006). However, male and female Southern Rockhopper Penguins had very similar dive characteristics on incubation trips on Staten Island (Pütz et al. 2006a).

It is noteworthy that the $\delta^{15}\text{N}$ values of Eastern Rockhopper Penguins in the current study are comparable, albeit slightly higher, than those from Crozet (Cherel et al. 2007) and

Kerguelen (Cherel et al. 2010) islands in the Indian Ocean ($\delta^{15}\text{N}$ average values 6.8–9.8‰), whereas at the Falklands Islands in the southwest Atlantic $\delta^{15}\text{N}$ values range from 13.3‰ to 15.8‰ (Masello et al. 2010; Dehnhard et al. 2011b; Ludynia et al. 2013). The higher $\delta^{15}\text{N}$ values of Southern Rockhopper Penguins at the Falklands Islands reflect differences in baseline $\delta^{15}\text{N}$ values between regions, rather than penguins feeding at hugely different trophic levels (Dehnhard et al. 2011b).

Adult $\delta^{13}\text{C}$ values

Female $\delta^{13}\text{C}$ values were lower at arrival than at incubation return in 2012, although male arrival and incubation $\delta^{13}\text{C}$ signatures were similar between stages in both years. Males' consistent maintenance of similar $\delta^{13}\text{C}$ values at arrival and incubation return may result if the longer duration of male incubation foraging trips allows males to return to their further offshore, higher latitude pre-breeding foraging area. However, females are constrained from foraging further offshore on their shorter incubation foraging trips, as found for Southern Rockhopper Penguins at the Falkland Islands (Ludynia et al. 2013).

At arrival females had lower $\delta^{13}\text{C}$ values than males across years. Likewise, the pre-breeding diet of females suggested a tendency towards a more pelagic/offshore or higher latitude diet compared to male Southern Rockhopper Penguins at the Falkland Islands prior to colony arrival (Ludynia et al. 2013). No sex differences were found between the over-winter distribution or $\delta^{13}\text{C}$ values at arrival of Eastern Rockhopper Penguins from Crozet and Kerguelen islands and Northern Rockhopper Penguins at Amsterdam Island, although again females had slightly lower $\delta^{13}\text{C}$ values at arrival (Thiebot et al. 2012). Males have a shorter over-winter period at sea (Thiebot et al. 2012) and earlier initiation of return migration than females (Thiebot et al. 2013), differences that may be reflected in the tendency for females to have lower pre-breeding $\delta^{13}\text{C}$ values than males.

Females with higher $\delta^{13}\text{C}$ values at arrival were heavier. Higher $\delta^{13}\text{C}$ values might reflect more time spent foraging at lower latitudes closer to Campbell Island in the weeks preceding breeding which could decrease mass loss in the final days of females' return migration. Another nonexclusive explanation is that females that made more benthic dives prior to breeding were more successful at obtaining prey, as found for chick-rearing females at the Kerguelen Islands (Tremblay and Cherel 2000). Interestingly, the opposite pattern was found in males being heavier with lower $\delta^{13}\text{C}$ values in 2011 with pooled arrival and incubation return data. Males that foraged at higher latitudes and further offshore may have encountered

greater prey availability in 2011. Additional years of study are required to confirm a consistent sex-difference in the effect of foraging habitat as inferred from $\delta^{13}\text{C}$ values on adult body mass.

Conclusions on diet quality

Why were Magellanic Penguin chicks fed a higher trophic level diet in better body condition (Forero et al. 2002), but Eastern Rockhopper Penguin chicks with higher $\delta^{15}\text{N}$ values were not of greater body mass in the current study? The primary fish prey of Magellanic Penguins in the Argentine study region of Forero et al. (2002) is Argentine anchovy (*Engraulis anchoita*) which is an energy-rich pelagic species likely to have a much greater energy density than the largely demersal fish species found in the diet of Eastern Rockhopper Penguins on Campbell Island (Vlieg 1984; Heath and Randall 1985; Marchant and Higgins 1990). For example, Argentine anchovy of unstated length have an energy density of 8.4 kJ g^{-1} wet mass (Drago et al. 2010), whereas blue whiting (*Micromesistius poutasou*) of 80–120 mm length, of the same size class and congeneric to the southern blue whiting common in the diet of Eastern Rockhopper Penguins on Campbell Island (Marchant and Higgins 1990), has an energy density of just 4.2 kJ g^{-1} wet mass (Velasco and Olaso 2000). Generally having only fish prey of relatively low energy density available to Eastern Rockhopper Penguins at Campbell Island may be a function of the low productivity of the surrounding marine environment compared to the high productivity habitat of Magellanic Penguins (Bradford-Grieve et al. 2003; Boersma et al. 2009). Furthermore, the smaller body size of Eastern Rockhopper Penguins relative to Magellanic Penguins (bill length 21% shorter, Marchant and Higgins 1990; Yorio et al. 2001) may limit the ability of Eastern Rockhopper Penguins to capture larger, reproductively mature fish which are typically of higher energy density (Anthony et al. 2000). Additionally, the higher chick $\delta^{15}\text{N}$ values in 2012 relative to 2011 likely also reflect a higher proportion of low-lipid cephalopod prey fed to chicks in 2012 (Cherel and Ridoux 1992; Meynier et al. 2008). Small cephalopod beaks ($n = 2$ to > 50) were found in the stomach contents of five chicks killed by Brown Skuas (*Catharacta antarctica lonnbergi*) in 2012, but no beaks were present in five skua-killed chicks in 2011 (K.W.M. unpub. data). Furthermore, pieces of cephalopod regurgitated by adult Eastern Rockhopper Penguins, but too large for chicks to swallow were commonly found spilled around nests in 2012, but not in 2011 (K.W.M. pers obs).

In other marine predators the assumed positive relationship between $\delta^{15}\text{N}$ values and diet quality as measured by body mass or condition is no more certain. The nutritional condition of striped dolphins (*Stenella coeruleoalba*) was unrelated to $\delta^{15}\text{N}$ values (Gomez-

Campos et al. 2011). In Cassin's Auklets (*Ptychoramphus aleuticus*) pre-breeding $\delta^{15}\text{N}$ values were not related to body condition of adult females measured 1–2 days after laying (Sorensen et al. 2009). Instead, female Cassin's Auklets with a less fish-based diet laid earlier and laid larger eggs (Sorensen et al. 2009). In three Arctic-breeding seabirds, two showed a positive effect of $\delta^{15}\text{N}$ values on body mass, but only in one of two tissue types sampled (Moody et al. 2012). Similarly to our findings, Cruz et al. (2012) found that Blue-footed Booby (*Sula nebouxi*) chicks with higher $\delta^{15}\text{N}$ values had poorer body condition. Likewise, a higher trophic level diet was associated with lower body condition in adult female Marbled Murrelets (*Brachyramphus marmoratus*; Janssen et al. 2009), and a slower growth rate in South American sea lion (*Otaria flavescens*) pups (Drago et al. 2010). The lack of a consistent positive relationship (and more often a negative relationship) between $\delta^{15}\text{N}$ values and diet quality challenges the conclusions of retrospective isotopic studies of threatened seabirds which assume a positive relationship exists (Hilton et al. 2006; Norris et al. 2007; Wiley et al. 2013). We suggest that population declines of marine predators should not be attributed to a historic shift to a lower trophic level, lower quality diet without first demonstrating that a lower trophic level diet is actually of lower quality over multiple years in the species of interest. A shift to lower trophic level prey, if accompanied by an increase in abundance or availability, can instead reflect an improvement in diet quality, as demonstrated by population increases in Antarctic penguin species that shifted from a fish-based diet to exploit the 'krill surplus' (Croxford et al. 1992; Emslie and Patterson 2007).

Hilton et al. (2006) hypothesized that Rockhopper Penguins formerly had a more fish-based diet, and that this higher quality diet supported the much larger populations that existed prior to widespread population decreases in the 20th century (Cunningham and Moors 1994; Pütz et al. 2003; Cuthbert et al. 2009). However, Hilton et al. (2006) did not find a consistent shift to lower trophic level prey in the isotopic signatures of Rockhopper Penguin feathers dating back into the 19th century from seven breeding sites. They instead showed that the primary productivity of the Southern Ocean had declined as SST increased. A similar study in the southern Indian Ocean of seven penguin species also suggested a constant dietary trophic level through the 20th century, but a decrease in primary productivity coincident with a climate regime shift in the 1970s and penguin population declines in sub-Antarctic and subtropical regions (Jaeger and Cherel 2011). These results agree with the current study in identifying abundant, low trophic level zooplankton prey as the main component of a high quality diet important to the maintenance of stable Rockhopper Penguin populations.

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Chapter 4

CANALIZED PARENTAL ROLES CONSTRAIN THE ABILITY OF EASTERN ROCKHOPPER PENGUINS TO COPE WITH NUTRITIONAL STRESS

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Figure 4.0 Top: Near arrival, courting pairs of Eastern Rockhopper Penguins (males with larger bills than females) are of similar body mass. Bottom: Fat male relieves thin female during incubation. Photos by Kyle Morrison.

ABSTRACT

Behavioural plasticity may allow organisms to respond adaptively to environmental variability caused by climate change, facilitating population persistence. Sexes may divide parental roles, and there may or may not be plasticity in this division. Poor food availability or quality can induce nutritional stress that increases costs of parental care. However, the effect of nutritional stress on sex-specific parental investment and offspring fitness have rarely been investigated in species that divide parental roles. We examined chick-provisioning rates of transponder-tagged female and male Eastern Rockhopper Penguins (*Eudyptes chrysocome filholi*) using an automated gateway on Campbell Island, New Zealand in a year of good diet quality and a poor year of nutritional stress. All seven species of *Eudyptes* penguins are unique among penguins in exhibiting canalized parental roles during the first 3–4 weeks of chick-rearing; males fast while guarding chicks provisioned exclusively by females. Each species is also ‘Vulnerable’ or ‘Endangered’, generally because of long-term population declines linked to climate-induced nutritional stress. We found that chick growth was strongly positively correlated with total provisioning rate. Both sexes made longer foraging trips and provisioned less often under nutritional stress, but males decreased their investment in chick-provisioning much more than females by making extra-long self-feeding trips early in the crèche period. We show that *Eudyptes* chicks would be fed more often if the sexes shared all chick-provisioning, especially under nutritional stress. We conclude that the canalized division of labour strategy of *Eudyptes* penguins may limit chick growth and survival to recruitment under nutritional stress. Our identification of this previously unappreciated consequence of the breeding ecology of *Eudyptes* penguins is important for predicting future population dynamics in a changing marine environment.

INTRODUCTION

The consequences of ongoing climate change, including warmer temperatures, increased climate variability, and more frequent extreme events, are challenging organisms the world over to respond adaptively (Timmermann et al. 1999; Walther et al. 2002; Parmesan 2006). The behavioural, physiological, and life-history responses that will maintain the fitness of individuals and result in population persistence require phenotypic plasticity: the expression of different phenotypes under varying environmental conditions (Stearns 1989; Nussey et al. 2007). Much recent research has considered plasticity of phenology in relation to climate change, especially whether species are advancing their timing of breeding to match earlier

peaks in food availability (Edwards and Richardson 2004; Both et al. 2009; Dunn and Moller 2014). Less studied is behavioural plasticity in reproductive investment in response to adverse environmental conditions, especially in species in which sex-specific parental roles may constrain plasticity.

Division of labour (DOL) in parental care occurs in species in which one or more parental task (e.g., feeding, brooding, or defence) is not equally shared between males and females. DOL evolves when it results in synergistic (non-additive) fitness benefits of biparental care to offspring, or when the fitness benefit of providing a particular care type is unequal between the sexes (Barta et al. 2014). For example, male-biased sexual size dimorphism may favour males specialising in offspring defence if males are more successful at defence than females or stand more to gain through benefits such as nest site retention (Paredes and Insley 2010). Thus, DOL may represent a trade-off between offspring provisioning and defence. More equitable parental care may result in higher chick growth than in a DOL scenario, but lower chick survival (Ashbrook et al. 2008).

In long-lived top predators, much of the variation in reproductive success among years is driven by prey availability or quality (Hedd et al. 2006; Tierney et al. 2009; Wolf et al. 2009). In 'poor' food years, parents may be unable to obtain sufficient food energy to meet the needs of their offspring and for their own self-maintenance, resulting in adults in poor body condition, low offspring survival, or low juvenile survival of offspring in poor condition at independence (Reilly and Cullen 1982; Horswill et al. 2014). Individuals obtaining inadequate food to meet their energetic requirements for breeding and self-maintenance are experiencing nutritional stress (Kitaysky et al. 2010; Franci et al. 2015). We did not measure individuals' stress hormone levels to quantify nutritional stress in a physiological sense, but had previously defined a year of nutritional stress as having lower reproductive success, and lower chick and adult body masses (Chapter 3). Years of nutritional stress are further characterized by parents buffering their own survival probability by increasing time spent self-feeding, shortening time spent brood guarding, lowering provisioning rates, and delivering smaller meals (Trites and Donnelly 2003; Busser et al. 2004). Life-history theory predicts that long-lived species should be the most prudent parents – most reluctant to invest heavily in current reproduction because of their potential to have a long, productive future (Drent and Daan 1980). Nevertheless, seabirds that experience severe nutritional stress during breeding can have a lower probability of surviving (Kitaysky et al. 2010). Therefore, nutritional stress can reduce seabird population growth rates through both low reproductive success and low adult survival (Kitaysky et al. 2007; 2010). Improving our poor understanding of the behavioural plasticity of

long-lived, prudent parents with sex-specific roles requires detailed investigations into reproductive investment and output in years with and without nutritional stress.

Eudyptes penguins are excellent subjects to examine behavioural plasticity in response to nutritional stress. They are relatively small-bodied, but long-lived and have an especially slow life-history strategy relative to other 2-egg clutch penguin species, including a late age at first breeding and low annual fecundity (Stein and Williams 2013), traits suggesting selection for prudence in reproductive investment. Long generation times also slow microevolution, hindering the ability of long-lived species to adapt to rapid environmental change (Visser 2008; Forcada and Trathan 2009). *Eudyptes* penguins are unique among penguins in their canalized DOL during the guard phase that occurs over the first third of the chick-rearing period: males fast at nest sites while guarding chicks and females are solely responsible for chick-provisioning and make near-daily foraging trips. These dichotomous parental care phenotypes are called “canalized” because they do not vary with environmental conditions (Waddington 1942; Debat and David 2001). Opportunities for additional matings select for DOL in many species. For example, in many shorebird species females abandon brood care to males not long after hatching, often to seek a second mate (Jonsson and Alerstam 1990; Jamieson 2012). In contrast, *Eudyptes* penguins lay synchronously, and do not relay or double-clutch, so that any opportunity for additional parentage is restricted to males early in the incubation stage (Warham 1975). Hypotheses surrounding the evolution of the unique DOL of *Eudyptes* penguins, and investigations of its consequences for parental investment and reproductive fitness are notably lacking, despite the remarkable demands these inflexible roles place on each sex.

The breeding strategy of *Eudyptes* penguins is also exceptional in its extreme fasts, notwithstanding the lengthy periods ashore of the much larger-bodied *Aptenodytes* penguins. Typical courtship/incubation fasts of penguins outside of *Eudyptes* and *Aptenodytes* are one or a few days, 20–35 days in Chinstrap (*Pygoscelis antarctica*) and Adélie (*P. adeliae*) penguins, but 35–49 days in *Eudyptes* (Williams 1995; Croxall and Davis 1999; Hull et al. 2004; Chapter 3). Male *Eudyptes* penguins also make an incubation/guard fast of 23–35 days, whereas all other penguin species avoid a long male guard stage fast by alternating brooding and chick-provisioning duties between the sexes about daily or at 4–12 day intervals in *Aptenodytes* penguins (Williams 1995; Descamps et al. 2002). Often male *Eudyptes* penguins do not begin chick-provisioning at the start of the crèche stage, but make an extended multi-day trip to regain body mass. Female *Eudyptes* penguins may also make long trips in the crèche stage, apparently to recover mass lost while regularly provisioning chicks through the guard phase

(Tremblay and Cherel 2005). Hence, DOL appears to limit the provisioning rates *Eudyptes* penguins provide chicks, particularly from males, hypothetically reducing potential reproductive fitness.

Eudyptes penguins are the largest penguin genus by number of species, have the largest geographic range, and may be the largest by number of individuals (BirdLife International 2014). *Eudyptes* is also the only multi-species penguin genus in which all species are threatened by extinction (IUCN threat statuses of 'Vulnerable' or 'Endangered'; BirdLife International 2014). The leading hypothesis explaining widespread dramatic population declines in recent decades in most species of *Eudyptes* is a climate-induced reduction in prey availability/quality causing nutritional stress and low demographic rates (Crawford et al. 2006; BirdLife International 2010; Hiscock and Chilvers 2014; Morrison et al. 2015 – hereafter 'Chapter 2'; Trathan et al. 2014), although competition with pinnipeds and predation by introduced mammals and growing pinniped populations may be important at some sites (Trathan et al. 2012; Chapter 5; Mattern 2013b). Penguins require sufficient body reserves to endure and recover from prolonged stages of fasting (Green et al. 2007). If penguins reach a minimum threshold body condition they will reduce parental investment or abandon breeding (Robin et al. 2001). Thus, nutritional stress is likely to lower reproductive success and the subsequent survival of chicks fledging in poor condition (Dann et al. 2000; Horswill et al. 2014). Investigating how the DOL of *Eudyptes* penguins is affected by nutritional stress may explain the genus' apparent susceptibility to environmental variability. Furthermore, a better understanding of how *Eudyptes*' breeding strategy interacts with prey abundance/availability and demographic performance may improve predictability of future population trends in a changing marine environment.

We examined the effects of nutritional stress on the chick-provisioning behaviour of female and male Eastern Rockhopper Penguins and their chick's growth in contrasting breeding seasons of high (2011) and low (2012) diet quality (Chapter 3). In the year of low diet quality both sexes made longer incubation foraging trips, but returned at lower masses, and a higher trophic level diet resulted in chicks of lower body mass at the end of the guard phase (Chapter 3), suggesting that in 2012 nutritional stress is likely to have altered parents' reproductive investment. We addressed the following questions:

- 1) Were there inter-annual or sex-differences in the timing or duration of chick-provisioning trips, or the proportion of individuals that made a long trip (≥ 4 nights at sea)?
- 2) Is female, male, or total provisioning frequency related to chick mass at 30–31 d old?

- 3) Are female provisioning rates correlated with arrival mass, arrival date, or their mate's provisioning rate? – i.e., do females compensate for males that make a long trip?
- 4) Under a hypothetical scenario without DOL, would chicks receive a greater total number of feeds throughout chick-rearing?

MATERIALS AND METHODS

Study site

We studied Eastern Rockhopper Penguin adult provisioning rates and chick size in the East and West sub-colonies in Penguin Bay, Campbell Island (52° 32' 12" S, 169° 2' 10" E) in two seasons, 2011–2012 and 2012–2013 (hereafter referred to by the year in which the seasons began). Breeding chronology for 2011 and 2012 is reported in Chapter 3. The East sub-colony contained 24 and 19 breeding pairs, whereas the West sub-colony consisted of 460 and 452 breeding pairs in 2011 and 2012, respectively (Chapter 2). The Eastern Rockhopper Penguin population on Campbell Island was estimated at 33,239 breeding pairs in 2012, after undergoing a dramatic decline of 94.6% since 1942. Periods of decline in the past 70 years were associated with warmer mean sea-surface temperatures (SSTs) and an increased frequency of anomalously warm years that are expected to have led to nutritional stress and low demographic rates (Cunningham and Moors 1994; Chapter 2). While cooler and less variable SSTs appear to have paused the overall decline since 1996, the Penguin Bay population has continued to decline, apparently because of high pinniped and avian predation rates (Chapters 2 and 5). We studied penguins within the East and West sub-colonies because their reliable use of a narrow travel pathway of c. 200 m length from the sea was conducive to recording transit times with an automated system.

Data collection

Adult foraging trip durations, provisioning rates, and chick sizes were measured from hatching in the second and third weeks of December, until our departure from the island when chicks were c. 36 d old in the third week of January in 2011 and 2012. Trip durations and provisioning rates were only considered for adults with a chick alive at our departure. We documented hatching success (nests that hatched an egg / nests that contained an egg), chick success (chicks alive at our departure / nests that hatched an egg), and overall reproductive success

(chicks alive at our departure / nests that contained an egg) using daily nest checks using binoculars or the naked eye, or at nests where visual checks were insufficient to confirm nest contents, through c. weekly physical checks involving carefully lifting an incubating bird's tail. During courtship or incubation in 2010, 2011, and 2012 almost all adults breeding within study plots with mapped nest site numbers were individually marked with PIT tags (ISO FDX-B 11 × 2.1 mm glass-encased transponder; Allflex Australia Pty). Adults were sexed based on their breeding schedule and bill depth (Warham 1972). PIT tag codes, date, and time (to the minute) data were recorded by hand at nest sites using an RS320 Stick Reader (Allflex Australia Pty), or automatically using radio frequency identification (RFID) data loggers and antennae set up along the penguins' travel pathway into the study colonies (S. Cockburn, Department of Conservation, Wellington). In 2011 penguins' direction of travel was determined by the order they were recorded by two data loggers spaced apart by > 1 min travel time along the pathway. In 2012 we again used two data loggers, but one was a dual logger that used two antennae to independently record direction of travel. When direction of travel was not recorded (a bird was logged by only one antenna), all morning records (00:00–12:00) were assumed to be departures, and evening records (12:00–24:00) were assumed to be returns, because morning returns were very rare.

We categorized trips as 'day trips', where a bird departed and returned on the same day, and multi-day trips as 'short trips' of one to three nights at sea, or 'long trips' of ≥ 4 nights at sea, after Tremblay and Cherel (2005). On the odd occasion where a penguin departed and returned from two trips on the same day, these trips were considered as independent day trips. We discounted intervals between departures and returns of < 1 h duration, as these were unlikely to represent foraging trips. Short trips were only recorded when either the departing or return direction of travel was known in order to reduce assignment of multi-day trips to birds making day trips but being logged poorly. We did not subtract "travel time" ashore before passing through an antennae from the length of provisioning trips, because travel time appeared to vary greatly from c. 5 min to c. 2 h depending on the presence of Northern Giant Petrels (*Macronectes halli*) waiting to ambush penguins along the pathway and to scavenge penguins skilled by New Zealand sea lions (*Phocarctos hookeri*) just off-shore (K.W.M. pers. obs., Chapter 5). Similarly, time at sea was sometimes extended by 1–2 h as rafts of penguins were delayed from landing by sea lions hunting along the shoreline. Although we lack the data to account for these delays, predation rates by sea lions were not higher in the year of nutritional stress for penguins (Chapter 5), so that delays were unlikely to have influenced our results.

To determine provisioning rates adults were recorded as having made a provisioning trip on every date they were logged between their chick's hatch date and up to and including the day before their chick's measurement date, while accounting for multiple trips in a day and the departure date of trips lasting multiple days. Individual behaviour at the gateway or PIT-tag orientation meant that some adults had low logging rates. Logging rate was the total number of times a bird was recorded by an antennae (minus records beyond the expected two per transit in 2011 and three per transit in 2012) divided by the bird's number of trips. Nests in which either parent had a logging rate < 2.1 logs/trip were excluded from analyses involving provisioning rate. This was the minimum logging rate at which logs/trip was no longer significantly positively related to trips/day within each sex and year, giving us confidence that a low trips/day reflected a low provisioning rate rather than being an artefact of a low logging rate.

The PIT-tag gateway recorded the date of colony arrival of PIT-tagged females in 2011 and 2012. In 2012 the arrival body mass of females was measured < 24 h after arrival. We monitored the reproductive success of 116 and 125 nests where eggs were laid in 2011 and 2012, respectively. One or both parents were PIT-tagged at all nests. Nests were checked daily in 2011 and 2012 to establish hatch dates. In both years chicks were PIT-tagged at 18 d and marked with blue water-soluble paint to enable their identification as they gained mobility prior to crèching around 24 d. Chick mass, bill length, and flipper length were measured at 30 or 31 d old in 2011 and 2012. We considered only solo-raised chicks by excluding nests with two chicks beyond six day old. We measured chicks in the afternoon while adults were usually away foraging to limit the effect of time-since-feeding on chick mass. We measured body mass using a 1 kg (± 10 g), 2.5 kg (± 20 g), or 5.0 kg (± 50 g) spring scale, flipper length with a ruler (± 1 mm), and bill length with Vernier calipers (± 0.05 mm).

Data analysis

Transit times and trip durations are derived in 2011 from: 1284 day trips and 65 short trips by 69 females, seven long trips by 61 females, 312 day trips and 13 short trips by 60 males, and 37 long trips by 58 males; 2012: 371 day trips, and 189 short trips, and eight long trips by 41 females, 42 day trips and 10 short trips by 23 males, and 35 long trips by 40 males. Differences in sample sizes between and within sex-year groups resulted from the exclusion of some individuals with poor logging rates (< 2.1 logs/trip), and because some individuals were not recorded making a short or day trip, but did make a long trip. Nests with chick size

measurements at 30 or 31 d old and both parents with logging rates ≥ 2.1 logs/trip included seven chicks in 2011 and 17 chicks in 2012.

We examined relationships between chick morphometric measurements and between male and female provisioning rates using linear regression. We related chick mass to provisioning rates using general linear models (GLMs). Measurements and rates were compared between years and sexes using 2-sample t-tests (t-values) for normally distributed variables, and with Kruskal-Wallis (H-values) for non-normally distributed variables. Statistical analyses were performed in Systat 13 (Systat Software Inc.).

RESULTS

Reproductive success

Nest monitoring demonstrated that reproductive success was much higher in 2011 than in 2012. In 2011 and 2012 respectively, hatching success was 0.69 and 0.58, chick success was 0.88 and 0.61, and overall reproductive success was 0.60 and 0.35. The most important causes of egg and chick loss resulting in reproductive failure were predation by Brown Skuas (*Catharacta antarctica lonnbergi*), disappearance (unknown cause, but probable skua predation), egg displacement, trampling, and in 2012 female abandonment of eggs. In 2012 at least 7.5% of nest failures during incubation resulted from females abandoning eggs and departing on their incubation foraging trip before their mate returned. The four females that abandoned eggs departed around the mean departure date of relieved females, and had their mate return within 3 d. The actual rate of abandonment was likely higher because rapid predation of unattended eggs made it difficult to differentiate skua predation followed by female departure from abandonment followed by skua predation. One nest was observed failing during incubation in 2011 because prolonged aggression by a non-breeding pair drove off a solo-incubating female. Where two chicks hatched, starvation of the smaller, second-hatched A-chick was common in both years, but starvation of solo chicks did not appear to be an important cause of mortality before our departure in either year. In 2011, five pairs of sibling chicks survived until our departure (4.3% of nests with eggs), but no 2-chick nests survived in 2012.

Transit times and trip durations

Females departed before males, and returned after males on chick-provisioning trips in both 2011 and 2012 (Table 4.1, Figure 4.1). The average departure time of females was slightly

earlier in 2012 than in 2011, but was 3 h later in 2012 than in 2011. Similarly, males departed at the same time in both years on average, but returned 2.72 h later in 2012. The average durations of day trips made by females were longer than those of males by 2.56 h in 2011 and by 3.08 h in 2012 (Figure 4.2). Females made short trips of shorter duration than males by 8.56 h in 2011, but female short trip lengths were significantly longer in 2012 relative to 2011, so that both sexes had short trips of similar duration in 2012 (Table 4.1, Figure 4.3). The percentage of trips that occurred over multiple days were similarly low in both sexes in 2011, but increased to 33.8% of female trips and 19.2% of male trips in 2012 (Table 4.1).

Table 4.1 Transit times and durations of day (0 nights at sea), short (1–3 nights at sea), and long (≥ 4 nights at sea) trips during chick rearing of females and males that successfully reared a chick until 20-Jan 2012 (2011 season) or 18-Jan 2013 (2012 season). Significant differences between parameters (Mann-Whitney *U*-test, $\alpha < 0.05$) between the sexes within a year are indicated by different superscript letters, significant differences between years within a sex are indicated by different superscript numbers. Transit times and trip durations are means \pm SD. See Materials and Methods for sample sizes.

	2011		2012	
	Female	Male	Female	Male
Departure time	5:10 \pm 2.57 ^{A,1}	7:11 \pm 3.22 ^{B,1}	5:03 \pm 1.65 ^{A,2}	6:56 \pm 2.62 ^{B,1}
Return time	16:30 \pm 2.13 ^{A,1}	16:03 \pm 2.63 ^{B,1}	19:29 \pm 2.58 ^{A,2}	18:46 \pm 1.95 ^{B,2}
Day trip duration (h)	11.62 \pm 2.46 ^{A,1}	9.06 \pm 3.63 ^{B,1}	14.68 \pm 2.76 ^{A,2}	11.60 \pm 3.03 ^{B,2}
Short trip duration (h)	32.47 \pm 11.88 ^{A,1}	41.03 \pm 15.41 ^{B,1}	44.06 \pm 13.48 ^{A,2}	36.75 \pm 4.52 ^{A,1}
% trips multi-day	4.8	4.0	33.8	19.2
Long trip duration (d)	5.7 \pm 0.8 ^{A,1}	7.3 \pm 2.6 ^{A,1}	6.8 \pm 2.9 ^{A,1}	11.1 \pm 2.5 ^{B,2}
% made a long trip	11.5	63.8	19.5	87.5

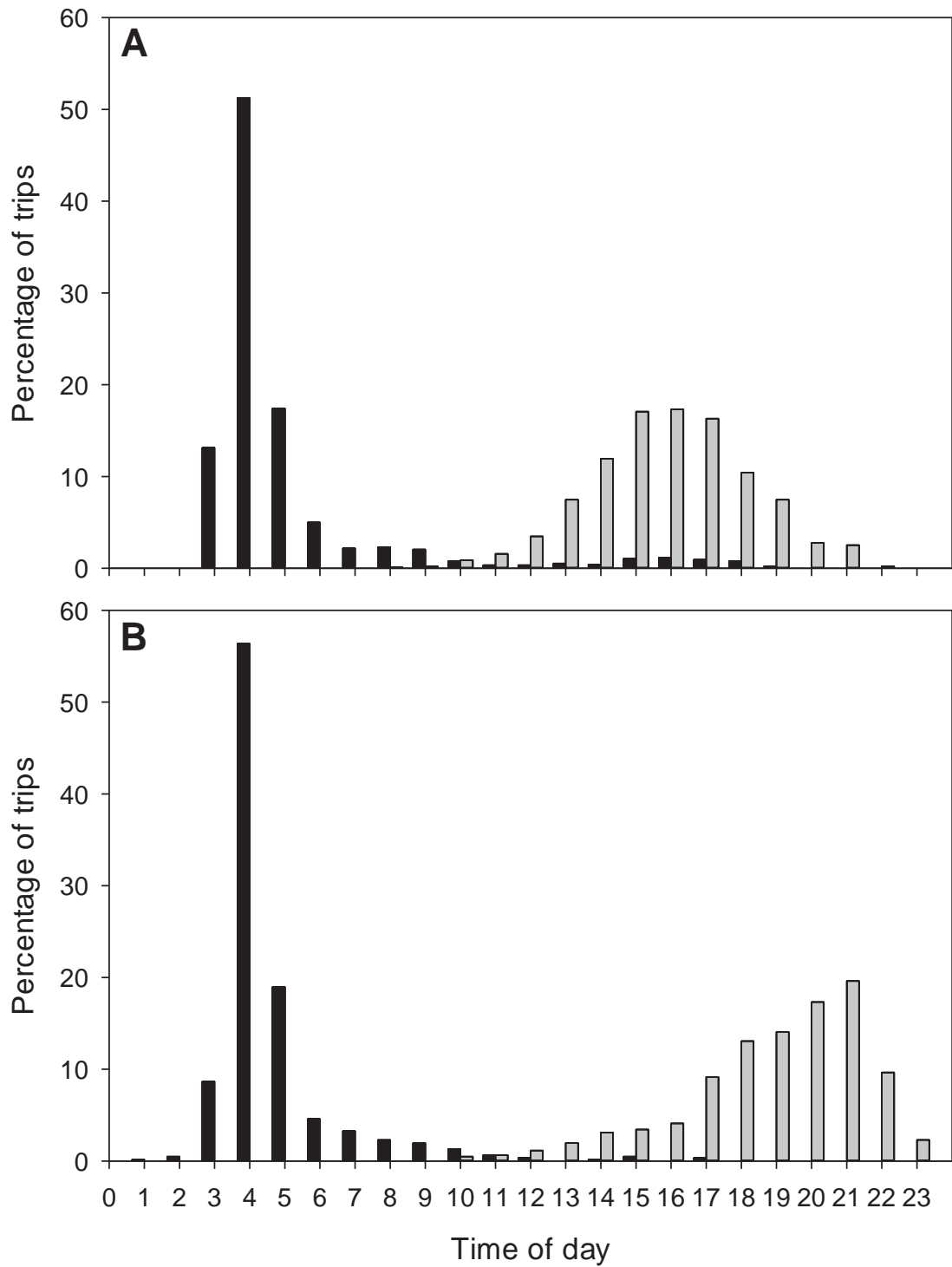


Figure 4.1 Frequency distribution of the timing of colony departures (black bars) and returns (grey bars) of chick-rearing Eastern Rockhopper Penguins in 2011 (A) and 2012 (B). See Materials and Methods for sample sizes.

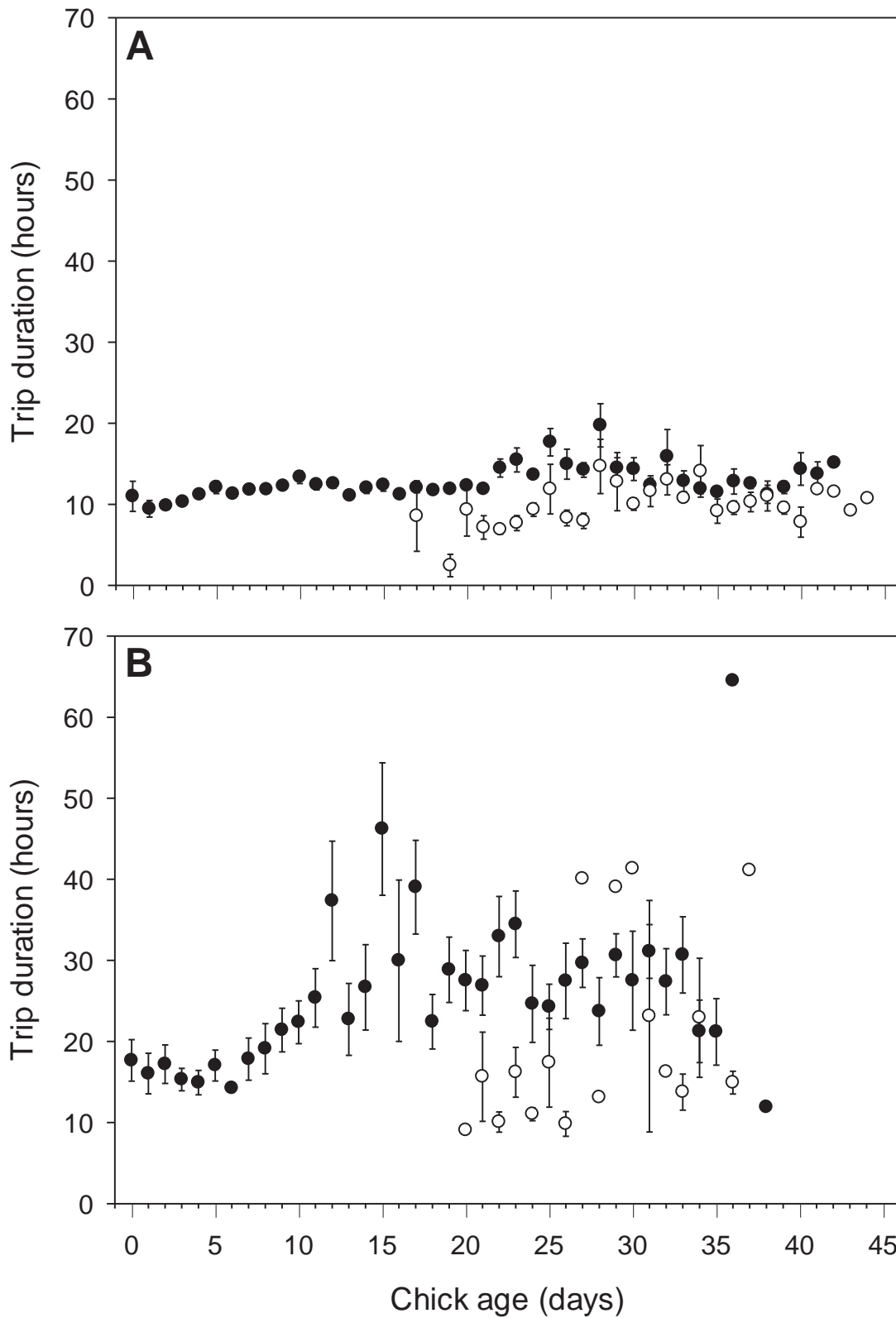


Figure 4.2 Mean (\pm SD) provisioning trip durations of female (filled circles) and male (hollow circles) Eastern Rockhopper Penguins in 2011 (A), 2012 (B). Data exclude long trips (≥ 4 nights at sea). See Materials and Methods for sample sizes.

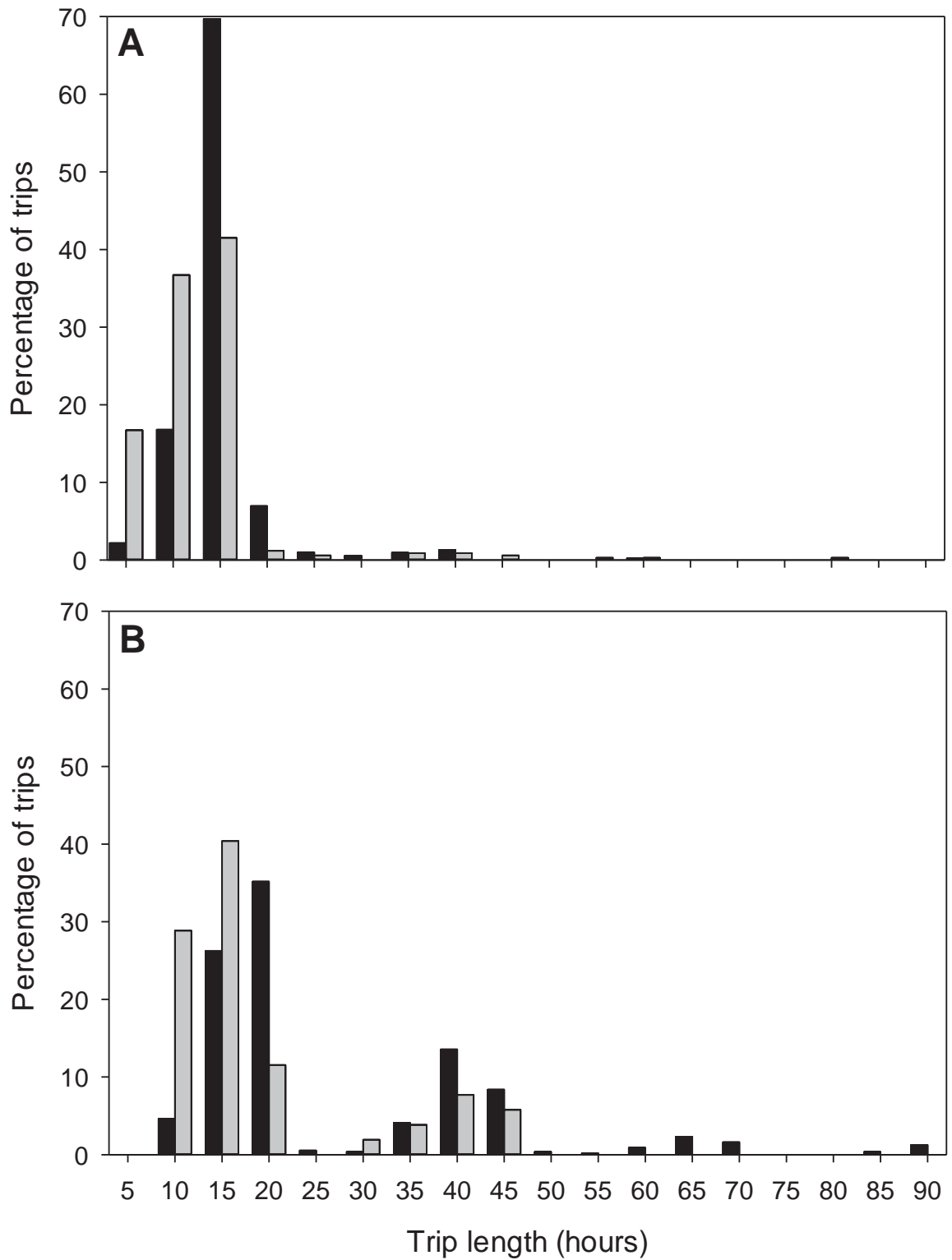


Figure 4.3 Frequency distribution of the duration of provisioning trips of female (black bars) and male (grey bars) Eastern Rockhopper Penguins in 2011 (A) and 2012 (B). Data exclude long trips (≥ 4 nights at sea). See Materials and Methods for sample sizes.

Females making day trips of longer duration than males did not correspond to females having a lower provisioning rate than males in either year (Table 4.1, Table 4.2). Instead, females had much higher provisioning rates than males because of the much larger percentage of males (63.8 and 87.5%, in 2011 and 2012, respectively) than females (11.5 and 19.5%) that made a long trip (Table 4.1, Figure 4.4). The average duration of long trips was similar between the sexes in 2011, but male long trips were longer than female long trips by 4.3 d in 2012. The average durations of long trips are underestimated, especially for males in 2012, because of individuals that had yet to return from a long trip before our departure from the island, including three females and four males in 2011, and three females and 25 males in 2012.

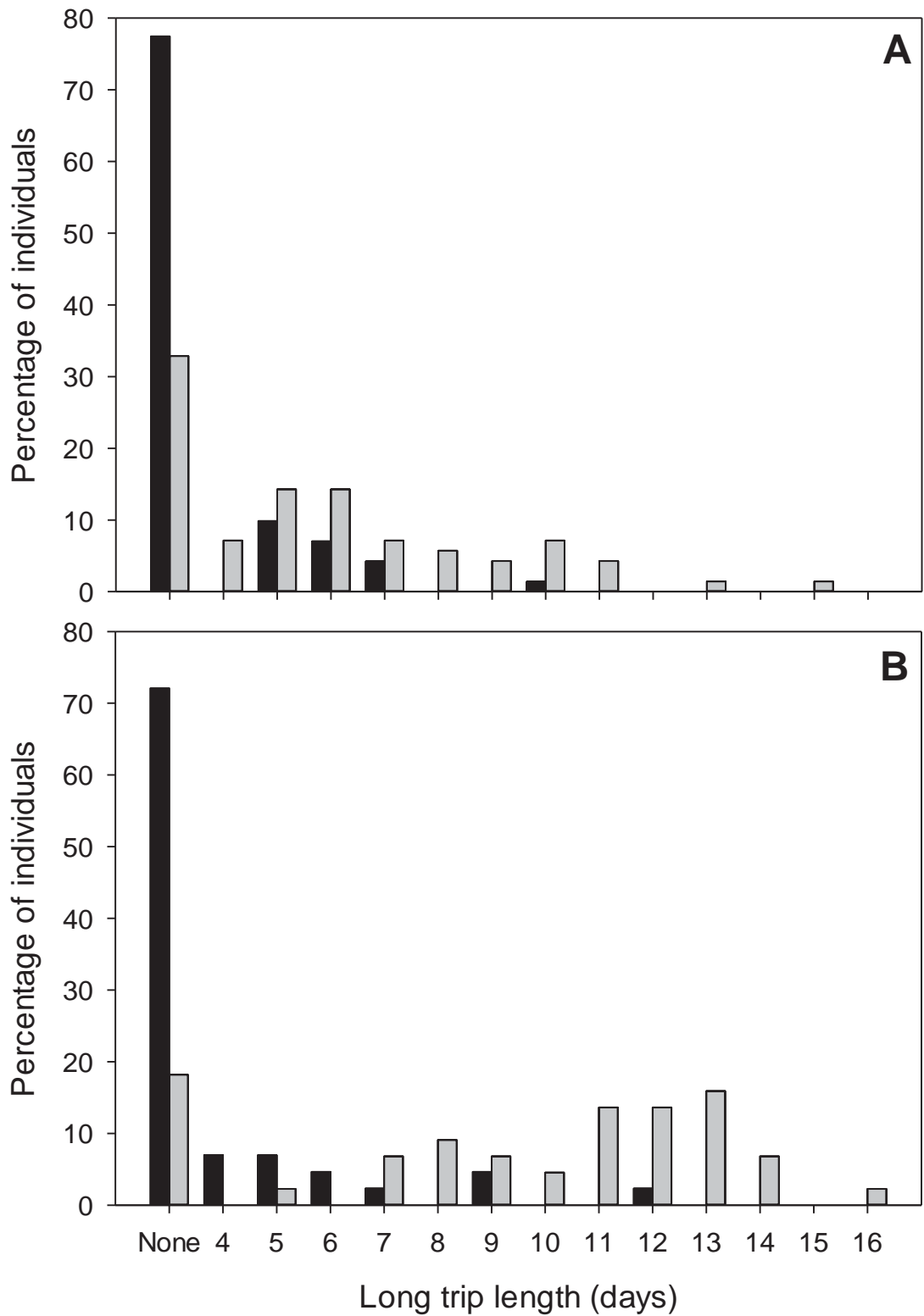


Figure 4.4 Frequency distribution of the duration of long trips (≥ 4 nights at sea) of female (black bars) and male (grey bars) Eastern Rockhopper Penguins in 2011 (A) and 2012 (B). See Materials and Methods for sample sizes.

Chick size and provisioning rates at 30–31 d old

Heavier chicks had longer bills ($r^2 = 0.721$, $F_{1,22} = 56.783$, $p < 0.0001$), and longer flippers ($r^2 = 0.791$, $F_{1,22} = 83.020$, $p < 0.001$). Longer billed chicks also had longer flippers ($r^2 = 0.746$, $F_{1,22} = 64.550$, $p < 0.001$), so we considered only chick mass in relation to provisioning rates. Total provisioning rate was strongly positively linearly related to female ($r^2 = 0.945$, $F_{1,22} = 185.082$, $p < 0.001$) and male ($r^2 = 0.773$, $F_{1,22} = 75.015$, $p < 0.001$) provisioning rates. To avoid multicollinearity we related chick mass to female, male, and total provisioning rates in separate GLMs.

The average hatch date of measured chicks was 13 December in both 2011 and 2012 (Table 4.2). Mean chick morphometric measurements at 30–31 d old were all significantly greater in 2011 than in 2012, although the proportional differences between annual means varied between measures. Chick bill length was 2.4 mm (9.0%) longer, flipper length was 20 mm (15.4%) longer, and chick mass was 441 g (43.0%) greater in 2011 than 2012 (Table 4.2).

Table 4.2 Chronological and morphometric data of Eastern Rockhopper Penguin chicks and the provisioning rates provided by their parents in 2011 (N = 7) and 2012 (N = 17). Chick masses (g), bill lengths (mm) and flipper lengths (mm) were measured at 30–31 d old. Provisioning rates (feeds/d) were calculated from chick hatching until crèching (guard stage) and from crèching until we stopped recording 20-Jan 2012 and 18-Jan 2013. Differences between years in each parameter are shown with *H*-values (*df* = 1), except hatch dates, chick masses, chick bill lengths, and female crèche provisioning rates are compared with *t*-values (*df* = 54). Data are means ± SD.

	2011	2012	<i>t</i> or <i>H</i>	<i>p</i>
Hatch date (± d)	13-Dec ± 1.2	13-Dec ± 1.4	1.536	0.139
Chick age at crèche (d)	23.4 ± 3.0	22.3 ± 1.6	3.673	0.055
Chick age at last trip recorded (d)	37.6 ± 2.6	35.9 ± 1.4	6.206	0.013
Chick mass (g)	1466 ± 201	1025 ± 233	4.370	0.0002
Chick bill length(mm)	29.2 ± 1.8	26.8 ± 2.1	2.702	0.018
Chick flipper length (mm)	153 ± 7	133 ± 16	10.332	0.001
Female guard provisioning rate	0.95 ± 0.06	0.71 ± 0.12	37.084	< 0.0001
Female crèche provisioning rate	0.88 ± 0.13	0.54 ± 0.19	7.675	< 0.0001
Male crèche provisioning rate	0.55 ± 0.23	0.17 ± 0.18	26.207	< 0.0001
Total crèche provisioning rate	1.43 ± 0.24	0.71 ± 0.23	38.448	< 0.0001

Chicks were heavier when provisioning rates (PR) were higher, from females, males, or both sexes combined (chick mass and female PR: GLM, $F_{1,20} = 5.034$, $p = 0.036$; male PR: GLM, $F_{1,20} = 4.497$, $p = 0.047$; total PR: GLM, $F_{1,20} = 9.730$, $p = 0.005$; Figure 4.5). Provisioning rate * year interaction effects were not significant in each GLM. Chick mass was explained slightly better by total provisioning rate than by provisioning rates of either parent singly (though both were still significant: chick mass and total PR: $r^2 = 0.713$, $F_{1,22} = 54.687$, $p < 0.001$; female PR: $r^2 = 0.678$, $F_{1,22} = 46.415$, $p < 0.001$); male PR: $r^2 = 0.498$, $F_{1,22} = 21.810$, $p < 0.001$).

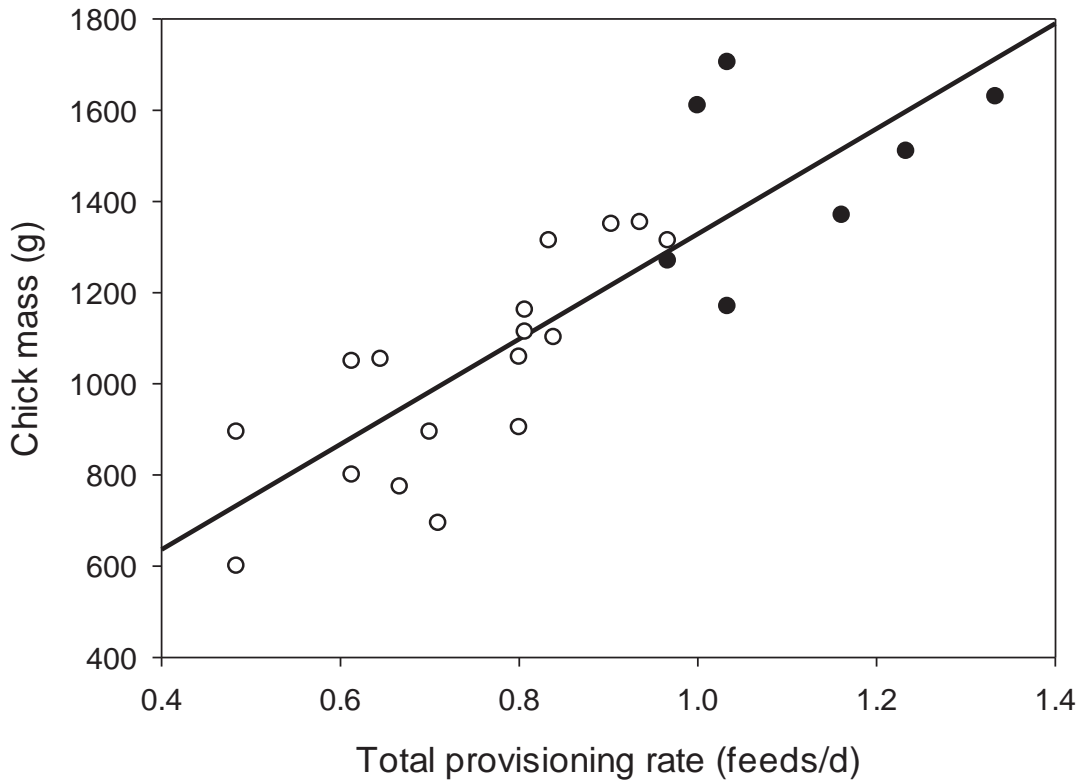


Figure 4.5 Eastern Rockhopper Penguin chick mass at 30–31 d old in relation to total provisioning rate in 2011 (filled circles, $N = 7$) and 2012 (hollow circles, $N = 17$). Chicks that were fed more frequently were heavier ($r^2 = 0.713$, $F_{1,22} = 54.687$, $p < 0.001$).

Crèche stage provisioning rates

Males went to sea at the start of the crèche stage when mean chick age was 1.1 d younger in 2012 than 2011, although this difference was non-significant (Table 4.2). We stopped recording 2 d earlier in 2012, so that chicks reached an older age by an average of 1.7 d in 2011 during the crèche stage of provisioning rate recording. Both females and males provisioned more frequently in 2011 than 2012 (Table 4.2). Female provisioning rate was significantly greater than male provisioning rate in 2011 ($t_{52} = 6.368$, $p < 0.001$) and 2012 ($H_1 = 28.662$, $p < 0.001$). Mean crèche female provisioning rate was lower by 0.34 trips/d (39%) in 2011 than 2012, whereas male crèche provisioning rate decreased by 0.38 trips/d (69%). In total, chicks were only fed half as often in the crèche stage in 2012 as in 2011 (Table 4.2). The crèche provisioning rates of mates were unrelated to one another in both 2011 ($r^2 = 0.041$, $F_{1,25} = 1.078$, $p = 0.309$) and 2012 ($r^2 = 0.061$, $F_{1,22} = 1.739$, $p = 0.198$).

Correlates of female provisioning rate

In 2011 female arrival date was not correlated with provisioning rate during the guard phase ($r^2 = 0.004$, $F_{1,27} = 0.094$, $p = 0.761$). In contrast, in 2012 females that arrived at the colony at an earlier date provisioned their chicks more frequently ($r^2 = 0.407$, $F_{1,12} = 8.220$, $p = 0.014$).

Female arrival mass was not correlated with provisioning rate in 2012 ($r^2 = 0.001$, $F_{1,12} = 0.004$, $p = 0.952$).

DISCUSSION

The chick-provisioning behaviour of Eastern Rockhopper Penguins changed dramatically between years of high diet quality and low diet quality. As predicted for a long-lived species, both females and males exhibited a shift from offspring- to self-investment in the year of low diet quality when their lower body masses, longer incubation and chick-provisioning trips, and lower chick-provisioning rates suggest they were under nutritional stress (Chapter 3; this study). The decrease in chick-provisioning rate was greater for males than females because in the year of nutritional stress most males made an especially long self-feeding trip after their incubation/guard stage fast. The total provisioning rate that chicks received to 30–31 d old explained a large proportion (71%) of variation in chick body mass, demonstrating the importance of investment by both sexes in chick-provisioning. We found that in the year of nutritional stress females that were heavier at arrival did not provision their chicks more often, but earlier-arriving females did deliver meals more frequently. We discuss below how the provisioning behaviour documented in our study compares to that of other *Eudyptes* penguins, possible evolutionary pressures leading to the genus' unique division of labour (DOL) strategy, and potential consequences for these species' demographic rates and population dynamics in an increasingly variable marine environment.

Day and short trip durations

A shift from offspring- to self-investment in years of good (2011) and poor (2012) quality diet is evident in the trip lengths undertaken by females on Campbell Island. Their foraging day trips during the guard phase in 2011 (11.62 ± 2.46 h) were similar to those of chick-provisioning female Eastern Rockhopper Penguins at Kerguelen and Crozet Islands and Northern Rockhopper Penguins (*E. moseleyi*) at Amsterdam Island (ranging from 11.2 ± 3.6 h to 13.59 ± 3.5 h; Cherel et al. 1999a; Tremblay and Cherel 2003; Tremblay and Cherel 2005) and

to the average duration of all trips by female PIT-tagged Southern Rockhopper Penguins (*E. c. chrysocome*) over three years at the Falkland Islands (11.3 ± 0.6 h, 12.3 ± 0.8 h, 11.2 ± 0.8 h; Ludynia et al. 2012). Over-night trips were also similarly infrequent at Kerguelen, Crozet and Amsterdam Islands (≤ 11 % of all trips recorded) during the guard phase to at Campbell Island in 2011 (4.8%). In contrast, females on Campbell Island in 2012 made longer day trips (14.68 ± 2.76 h), and more frequent multi-day trips (33.8%).

Long trip durations

A key consequence of DOL in *Eudyptes* penguins is that the long incubation/guard fast males make tends to necessitate a long self-feeding trip early in the crèche period. A higher proportion of males made a long trip (≥ 4 nights at sea) in the poor year (87.5%) than in the good year (63.8%). Consequently male provisioning rates were lower in 2012 than in 2011 (0.17 ± 0.18 versus 0.55 ± 0.23 feeds/d). Moreover, the minimum duration of long trips of males in 2012 were longer on average, by 3.8 d. It appears that males' long incubation/guard fast and associated extended recovery trips result in males provisioning chicks less often than females during the crèche period (Barlow and Croxall 2002; this study). In addition, female *Eudyptes* penguins lose mass during the guard stage when they are making near daily provisioning trips (Tremblay and Cherel 2003), seemingly causing some females to require a long recovery trip during the crèche stage and lowering their potential provisioning rate. As in males, the proportion of females making a long trip was higher in the poor year (19.5% versus 11.5%). Females at Kerguelen and Crozet Islands displayed considerable inter-individual variation by making 0–3 long trips of 5–29 d duration during chick-rearing (Tremblay and Cherel 2005).

Among other populations of *Eudyptes* penguins the proportion of either sex making one or more long trips likely also varies between years and sites, depending on food availability. Male Southern Rockhopper Penguins at Staten Island tended to make a post-guard trip averaging 8 ± 3 d in two years of study (Raya Rey et al. 2007). Male Eastern Rockhopper and Macaroni Penguins (*E. chrysolophus*) at Marion Island were reported to make post-guard trips of 10–15 d duration (Williams 1982), but these values may be over-estimates as they relied upon nest checks rather than an automated system to record departure and return times. At South Georgia few Macaroni Penguins of either sex made trips > 48 h; such trips were performed by < 30 % of males and females in three years of study (Barlow and Croxall 2002). There was no difference between the sexes in the number of trips > 48 h in duration.

However, one male Macaroni Penguin made no provisioning trips, two made a single trip, and a fourth provisioned its chick only twice, demonstrating that females can successfully raise a chick with little or no male contribution to chick-provisioning – at least in years and at sites of sufficient food availability. The relatively abundant food supply near South Georgia, close to the Antarctic Polar Front, is evident in the shorter chick-rearing period of Macaroni Penguins breeding there (60 d versus 70 d at the Crozet Islands) and their short pre-moult foraging period at sea (12–14 d) in comparison to 20–70 days for other populations of Macaroni Penguins and other *Eudyptids* breeding at less productive, lower latitude sites (Williams and Croxall 1991). In the other species of *Eudyptes* penguins the frequency of occurrence and length of extended foraging trips has not been studied in detail, although, as in Rockhopper Penguins, long post-guard trips and low provisioning rates by males early in the crèche period seem typical (Warham 1974b; Mattern 2013a).

Provisioning rates

Increases in trip durations, particularly by males, resulted in lower provisioning rates in the poor year. In the good year females fed chicks almost daily during the guard stage (0.95 ± 0.06 feeds per day), as found at Kerguelen and Crozet Islands (0.999 ± 0.14 and 0.99 ± 0.08 feeds per day, respectively; Tremblay and Cherel 2005). We found that the female provisioning rate remained high early in the crèche stage (0.88 ± 0.13 feeds per day, recorded from c. 23–37 d of age), but may have decreased later, as at the Kerguelen and Crozet Islands (0.76 ± 0.21 and 0.41 ± 0.08 feeds per day, respectively, recorded from 30–60 d of age). The long foraging trip durations of Southern Rockhopper Penguins at Staten Island corresponded to low provisioning rates by females and males during crèche over two years (0.48 ± 0.05 to 0.57 ± 0.09) of low breeding success (Raya Rey et al. 2007). In the present study female provisioning rates were lower during the poor year (0.71 ± 0.12 feeds per day during guard, and 0.54 ± 0.19 feeds per day during crèche). The decrease in provisioning rate between the good and poor years was even greater for males, from 0.55 ± 0.23 to 0.17 ± 0.18 feeds per day. Females did not adjust their provisioning rate with respect to that of their mate, as the crèche provisioning rates of mates were unrelated in both years. Although Macaroni Penguin chicks received a smaller number of total feeds in a year of low chick growth rates and asymptotic masses, males provided a similar proportion of feeds as in two other years (Barlow and Croxall 2002). Although we did not record provisioning rates through the entire chick rearing period, our estimated total number of feeds were similar to those estimated from monitoring throughout

chick-rearing elsewhere (Barlow and Croxall 2002; Tremblay and Cherel 2005; Raya Rey et al. 2007).

Chick growth

Chicks that were fed less often weighed less at 30–31 d of age in both years of study. When chicks were provisioned frequently in 2011 their average bill length, flipper length, and body mass were very similar to those of 30 d old Southern Rockhopper Penguin chicks at New Island during two years of high breeding success and population growth (Poisbleau et al. 2008; Poisbleau et al. 2010; Dehnhard et al. 2014). However in 2012 when chicks received far fewer feeds, especially from males, they were of smaller size, especially in flipper length and body mass. We expect that a large proportion of chicks in 2012 subsequently starved to death before fledging, or experienced high mortality rates as juveniles because of insufficient body reserves at fledging (Reilly and Cullen 1982; Horswill et al. 2014).

Evolutionary ecology of parental division of labour

Our results suggest Eastern Rockhopper Penguin chicks are fed less often and grow more slowly because of their parents' fixed role division, especially under nutritional stress. We estimated that by sharing chick brooding and foraging duties throughout chick rearing, as do all other penguin species, *Eudyptes* penguins would hypothetically be able to deliver 17.2–34.5% more total feeds to their chick (Table 4.3). The strong, positive relationship we found between provisioning rate and chick mass suggests that a greater food intake would result in larger chicks at fledging, with a greater likelihood of surviving to recruit into the population (Reilly and Cullen 1982; Horswill et al. 2014). The ability to provision chicks at a higher rate without DOL could also shorten the chick-rearing period or allow adults to maintain a higher a body mass, presumably increasing adult survival and population growth rates. *Eudyptes* penguins show sex differences in foraging behaviour and diet (Pütz et al. 2006; Ludynia et al. 2013; Chapter 3), so that if the sexes equitably shared chick-provisioning duties, then competition for prey would be relaxed. A further negative consequence of DOL is the long incubation foraging trips males make in preparation for their incubation/guard period fast. This long trip of 15.8 ± 1.4 d duration at our study site in 2012 extended females' courtship/incubation fast to a mean of 46.0 ± 2.5 d (Chapter 3), causing some nests to fail through female abandonment of eggs. Female Royal Penguins (*E. schlegeli*) have also been observed to abandon eggs (Carrick 1972).

Table 4.3 Male and female Eastern Rockhopper Penguin average chick-provisioning rates (feeds/d) as measured in the “good year” 2011 and “poor year” 2012 (in terms of diet quality) and estimated total number of feeds delivered to a chick with parental division of labour (DOL), and hypothetical provisioning rates and total feeds without DOL. Total feeds based on a guard stage of 23 d, and crèche stage of 45 d.

	2011			2012		
	Guard	Crèche	Total feeds	Guard	Crèche	Total feeds
With DOL						
Female rate	0.95	0.88	61.5	0.71	0.54	40.6
Male rate	0.00	0.55	24.7	0.00	0.17	7.7
Total rate	0.95	1.43	86.2	0.71	0.71	48.3
Without DOL^a						
Female rate	0.47	0.88	50.5	0.35	0.54	32.4
Male rate	0.47	0.88	50.5	0.35	0.54	32.4
Total rate	0.95	1.76	101.1	0.71	1.08	64.9
% change in total feeds			+17.2%			+34.5%

^aWe assume that the total provisioning rate during the guard stage remains the same in the hypothetical scenario without DOL, but is shared equally between the sexes. During the crèche stage we assume that without DOL both males and females would have the same provisioning rate as we measured for females during the crèche stage (with DOL).

Within penguins, *Eudyptes* penguins are unique in having canalized parental roles. If DOL reduces breeding success under nutritional stress then why has it evolved, and why only in *Eudyptes* penguins? We hypothesize that DOL is an inherited trait from the ancestral Eudyptid species that experienced two necessary ecological conditions. Firstly, the marine environment was formerly less variable and breeding seasons of nutritional stress were rare, so that negative effects of DOL were less severe and infrequent. This scenario is supported by the climatological record which demonstrates an increase in the frequency of extreme climate events and higher and more variable sea-surface temperatures since the mid-20th century (Easterling 2000; Mélice et al. 2003; Chapter 2). Other characteristics of the breeding strategy

of *Eudyptes* penguins also support a historically stable environment. These traits include a relatively fixed, synchronous timing of breeding that is initiated on return migration to colonies, apparently based on photoperiod rather than on the abundance or timing of prey availability near colonies. The long courtship/incubation fasts of both sexes and the prolonged incubation/guard fast of males can only have evolved under reliably high food availability near breeding colonies to allow rapid recovery from mass loss. *Eudyptes* penguins lay a single 2-egg clutch in which the second-laid egg receives preferential investment and is typically the only egg to hatch or chick to survive if both eggs hatch (St. Clair and St. Clair 1996; St. Clair 1998). Preferential investment in a single egg, including the systematic and perhaps deliberate loss of the first-laid egg soon after laying in Macaroni, Royal, and Erect-crested (*E. sclateri*) Penguins, along with the genus' inability to lay additional eggs, further demonstrate the genus' inability to adapt reproductive output to environmental variation. In contrast, Galapagos Penguins (*Spheniscus mendiculus*) are highly adapted to a variable marine environment, including flexible timing of breeding, no long breeding fasts, the ability to relay and lay multiple clutches within a year, and a brood reduction strategy in which two chicks are raised under favourable conditions (Boersma et al. 1990). Other authors have ascribed the interspecific variation in penguin breeding biology to the degree of seasonality in prey availability or inshore versus offshore foraging (Boersma et al. 1990; Croxall and Davis 1999; Davis and Renner 2003), but we emphasize here the importance of predictability in prey availability for the evolution of DOL in *Eudyptes* penguins.

The second key ecological condition selecting for DOL in *Eudyptes* penguins is likely to have been a male-biased capacity for nest defence from nest predators and conspecifics, owing to males' larger size and more aggressive nature. We hypothesize that male *Eudyptes* penguins have a greater capacity for nest defence relative to their mate than in other penguin genera because male-biased sexual size dimorphism tends to be larger in *Eudyptes* penguins than in the *Pygoscelis* penguins that are the only other species that typically have fixed surface nests in dense colonies (male *Eudyptes* bill length 11–13% and bill depth 15–20% larger than females' (range of species means), male *Pygoscelis* bill length 9% and bill depth 8–10% larger than females' (Williams 1995; Poisbleau et al. 2010; Borboroglu and Boersma 2013; Gorman et al. 2014). The fitness consequences of insufficient nest defence may also be greatest in *Eudyptes* penguins, owing to their surface nesting habit and smaller body size relative to their avian nest predators (Chapter 5). Nest defence from conspecifics appears especially important because of greater variation in nest-site quality within Eudyptid colonies than for other penguins. Large variation in nest site quality of *Eudyptes* penguins is suggested by the complex

topography of many Eudyptid colonies, where nests are more successful if sheltered by rocks than exposed (Chapter 5) and are more vulnerable to predation if located on the colony periphery (Chapter 5 and references therein). The importance of obtaining a high quality nest and competition to do so is also suggested by males arriving to claim nest sites before females by about a week, and both sexes having a long pre-laying fast ashore (Chapter 3) and a late age at first breeding (Stein and Williams 2013). Female *Eudyptes* penguins incubating without their male partner present may be subject to prolonged periods of forceful biting and flipper-slapping from female, but especially male conspecifics, including both non-breeders and other breeders, sometimes resulting in egg loss (Warham 1963; Strange 1982; Davis and Renner 2003; K.W.M. pers. obs). Solo-incubating males always react aggressively to intrusions by conspecifics, usually driving them off quickly, whereas solo-incubating females adopt a submissive posture when attacked and do not fight back (Warham 1963). Likewise disruption by conspecifics of chick-provisioning Rockhopper Penguins is targeted at females, but not males (Warham 1963; Poisbleau et al. 2013b). Females whose mate leaves on its incubation foraging trip earlier than other males receive the most abuse because of the abundance of off-duty (not incubating) birds in the colony (K.W.M. pers. obs.). The risk of egg- (and perhaps nest site- and mate-) loss for early-departing males has likely selected for the extended (7-10 d) period of shared incubation following clutch completion where both sexes remain at the nest site followed by highly synchronous male departure on their incubation foraging trip, seen only in *Eudyptes* penguins (Davis and Renner 2003). We suggest that the greater vulnerability of female Eudyptids to nest predators (Chapter 5), but perhaps more importantly to attacks from conspecifics, would result in increased rates of chick loss if the sexes alternated brood care and provisioning roles during the guard stage. As we hypothesize here for the evolution of DOL in *Eudyptes* penguins, the male-biased chick brooding found in the Alcidae family of seabirds is thought to have evolved because of a greater capacity for males, which are larger and more aggressive than females, to better defend the chick and nest site from predators, congeners, and conspecifics (Creelman and Storey 1991; Fraser et al. 2002; Paredes and Insley 2010; Wojczulanis-Jakubas and Jakubas 2012).

Implications

We have demonstrated that the unique DOL of *Eudyptes* penguins is an important factor in the genus' well-documented sensitivity to climate variability and associated nutritional stress (Dehnhard et al. 2013; Horswill et al. 2014; Chapter 2). We suggest that Eudyptid penguins are also poorly adapted to shift their breeding phenology to match changes in the timing of peak food availability resulting from climate change, given their long-distance migrations and synchronous breeding. Migratory species lack information on local environmental conditions in breeding areas before their return, constraining their phenological response to climate change (Rubolini et al. 2010; Hinke et al. 2012; Lynch et al. 2012a). In addition, in colonial seabirds benefits of synchronous breeding including reduced conspecific disturbance and predation risk, may result in stabilizing selection that limits individual responses and the potential for directional selection to match a new optimal breeding phenology (Reed et al. 2006). Similarly, pairs that alter their breeding strategy to reduce DOL are likely to have low breeding success through conspecific- and predator-induced nest failure (Ashbrook et al. 2008). We conclude that *Eudyptes* penguins, ostensibly anchored in a reproductive strategy poorly adapted to a marine environment where food availability is less predictable, will continue to be highly threatened from climate change.

ACKNOWLEDGEMENTS

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Chapter 5

NEW ZEALAND SEA LION AND BROWN SKUA PREDATION IS CAUSING THE CONTINUED DECLINE OF AN EASTERN ROCKHOPPER PENGUIN COLONY ON CAMPBELL ISLAND

Co-authors: D.P. Armstrong, P.F. Battley, S.E. Jamieson, D.R. Thompson

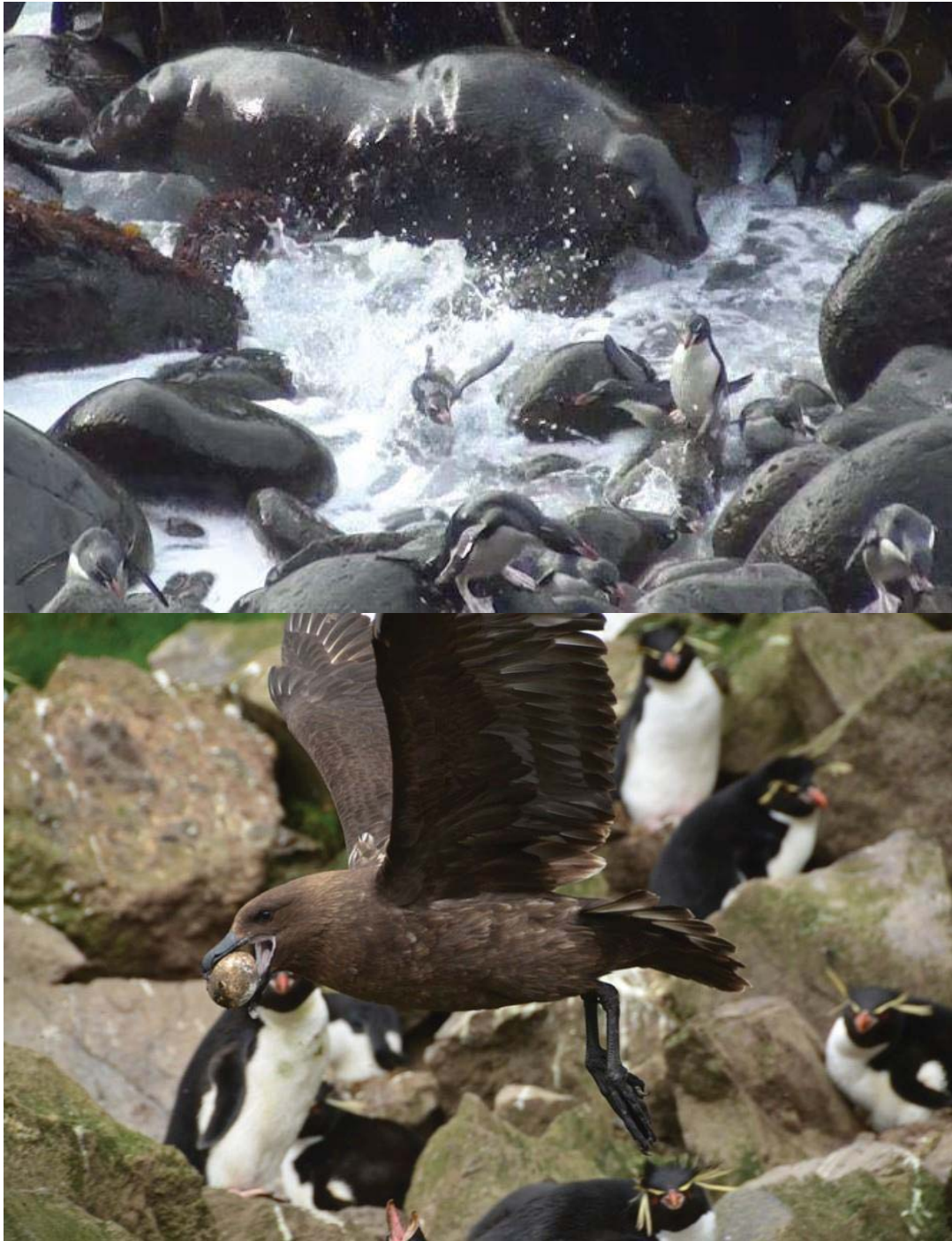


Figure 5.0 Top: New Zealand sea lion pursues landing Eastern Rockhopper Penguins. Bottom: Brown Skua with penguin egg. Top: image from a video by Ray Buchheit. Bottom: photo by Kyle Morrison.

ABSTRACT

Identification of factors causing population declines is a critical prerequisite for conserving threatened species. The most likely cause of dramatic decreases in numbers of the ‘Vulnerable’ Southern Rockhopper Penguin (*Eudyptes chrysocome*) in the 20th century is oceanographic change reducing food availability; the massive decline of the Eastern sub-species (*E. c. filholi*) on Campbell Island, New Zealand (94.6%, 1942–2012) has been attributed to climate change. This decline was paused in the mid-1990s by a shift to favourable conditions, but a localized decline continued at a small, fragmented population (Penguin Bay; one of five sub-colonies extinct in 2010, 3,012 pairs in 2012, down from 7,360 in 1984). Emerging concerns for *Eudyptes* penguins are the effects of increased predation from native predators (Brown Skuas (*Catharacta antarctica lonnbergi*) and New Zealand sea lions (*Phocarctos hookeri*) at Campbell Island). We found that penguin eggs and chicks in exposed, peripheral nests in small sub-colonies were most vulnerable to predation by skuas, so that average reproductive success was 25% lower at the smallest sub-colony than at the largest. Sea lions were estimated to depredate 6% of the adult penguin population each year, which modelling identified as the most important driver of the population’s negative growth rate ($\lambda = 0.905$, $-0.095\%/yr$). We conclude that although occasional years of very poor food availability may exert a larger ‘bottom-up’ effect on penguin demographic rates, the ‘top-down’ effects of high avian and pinniped predation rates can be sufficient to drive the decline of small penguin populations.

INTRODUCTION

Seabirds typically breed colonially on islands free of terrestrial mammalian predators, and exhibit delayed recruitment, high adult survival rates, and low fecundity. Generally, seabird population dynamics are under ‘bottom-up’ control in which food availability or quality, determined by oceanographic conditions and competition, regulates seabird population sizes, trends, and distributions (Ashmole 1963; Sandvik et al. 2005; Frederiksen et al. 2006). However, the ‘top-down’ effect of predation can be the most important determinant of seabird population dynamics when seabird populations 1) face introduced alien predators (Hilton and Cuthbert 2010); 2) have grown ‘unnaturally’ large or predator naïve following predator release and predator populations recover (Hipfner et al. 2012); or 2) have been reduced to a small size through bottom-up processes or anthropogenic effects so that a higher

predator/prey ratio means that the group defense and predator swamping benefits of colonial breeding are less effective (Gilchrist 1999; Pichegru 2013).

The slow life history strategy of seabirds means that their population growth rate is most sensitive to changes in adult survival rate (Sæther and Bakke 2000). However, if breeding seabirds prioritise their own survival rate over reproduction under poor environmental conditions or predation danger, then adult survival rates may be high and relatively constant relative to reproductive success (Forcada et al. 2008; Jenouvrier et al. 2009a). Additionally, predators may target seabirds at higher rates in years when predators' alternative food sources are at low availability (Spear 1993; Regehr and Montevecchi 1997). Therefore, in order to ascertain the relative importance of top-down and bottom-up effects, studies of seabird population dynamics should ideally assess predation effects on reproductive success, sub-adult (pre-breeder) survival, and adult survival in years of contrasting environmental conditions (Votier et al. 2008).

Predation can be either compensatory, in that it replaces density-dependent mortality (e.g., bottom-up control or disease) or additive (in addition to other causes of death; Burnham and Anderson 1984). Ecological constraints and breeding behaviour may tip the balance towards additive predation. For example, *Eudyptes* penguins are obligate brood reducers; they typically only hatch one of two eggs laid (usually the larger, second-laid 'B-egg') or are unable to provide sufficient food to raise two chicks until fledging (Warham 1975; Lamey 1990). Thus, every nest could be viewed as having one insurance egg or chick, making nest predation more likely to be compensatory than additive. However, if eggs or chicks are lost for reasons unrelated to predation soon after laying or hatching (e.g., they are displaced from the nest), then the insurance value of those eggs/chicks is lost and predation is more likely to be additive.

In this paper we examine the top-down effects of predation on sub-colonies of Eastern Rockhopper Penguins (*E. chrysocome filholi*) nesting at Penguin Bay, Campbell Island, New Zealand. The population on Campbell Island was estimated at 33,239 breeding pairs in 2012, 94.6% lower than in 1942 (Cunningham and Moors 1994; Chapter 2). Periods of decline in the past 70 years were associated with warmer mean sea-surface temperatures (SSTs) and an increased frequency of anomalously warm years that are expected to have led to nutritional stress and low demographic rates (i.e., bottom-up effects). While cooler and less variable SSTs appear to have paused the overall decline on Campbell Island since 1996, the Penguin Bay population has continued to decline. Here, we examine the hypothesis outlined in Chapter 2, that the recent, localized decline in Penguin Bay is the result of high pinniped and avian

predation rates, i.e., predation is additive rather than compensatory. Predator populations on Campbell Island are currently high. Numbers of New Zealand sea lion *Phocarctos hookeri* are larger than at any time since the end of the sealing era in the early 1900s (Maloney et al. 2012), while Northern Giant Petrels *Macronectes halli* are known to have increased in number elsewhere as pinniped populations grew (Bonner and Hunter 1982; Hunter 1984; Wiltshire and Scofield 2000; Patterson et al. 2008) so may be commoner than previously. Furthermore, bottom-up processes have led to colony fragmentation and a dramatic reduction in the penguin population size on Campbell Island (Chapter 2). Smaller and more fragmented penguin colonies are known to be more vulnerable to predation of eggs and small chicks by avian predators such as Brown Skuas (*Catharacta antarctica lonnbergi*), because a greater proportion of nests are on the peripheries of colonies, where they are more readily depredated (Jackson et al. 2005). Our 2010–2013 study period included seasons of starkly different oceanographic conditions and penguin diet quality (Chapter 3), allowing an assessment of the relative importance of top-down and bottom-up effects on demographic rates.

Opportunistic observations suggest pinnipeds may be important predators of *Eudyptes* penguins (Bailey and Sorensen 1962; Bonner and Hunter 1982; Strange 1982; Raya Rey et al. 2011), but no previous study has quantified the pinniped predation rate in relation to the size or growth rate of a *Eudyptes* penguin population. In this study we assess the likely effects of pinniped predation of adults, and skua predation on eggs and chicks of Rockhopper Penguins at Penguin Bay, Campbell Island. We measured breeding success (egg and chick survival) in relation to nest location and shelter, sub-colony size, lay date, laying synchrony, and stage of the breeding season. We predicted that more synchronously-laid eggs at more sheltered or interior nests sites in larger sub-colonies would have higher hatching success, as shown for penguins elsewhere (Tenaza 1971; Emslie et al. 1995; St. Clair and St. Clair 1996). We expected that earlier laid eggs would be more successful because higher quality or more experienced seabirds tend to lay earlier (De Forest and Gaston 1996; Hipfner et al. 2010). We expected that most breeding failure would occur during incubation rather than chick-rearing as a result of high egg predation and displacement rates seen in Rockhopper Penguins elsewhere (St. Clair and St. Clair 1996; Hull 2004). We also evaluated whether daily egg survival rates differed between shared, female-only, and male-only incubation stages under the hypothesis that both parents would provide the best nest defense and the more aggressive, heavier, and larger-bodied males better defense than females (Chapter 4).

We estimated adult and first-year penguin survival rates, and predation rates of skuas on eggs and New Zealand sea lions on adults. Using this information and values from the literature we modelled the population growth rate in Penguin Bay and at a growing conspecific population. We addressed our focal question, is predation the primary cause of the localized population decline in Penguin Bay?, by evaluating whether a 'predation-free' population (with demographic rates unaffected by predation), would have a stable or increasing population growth rate.

MATERIALS AND METHODS

Study site

Eastern Rockhopper Penguins were studied in the East and West sub-colonies of Penguin Bay (Figure 5.1), Campbell Island (52° 32' 12" S, 169° 2' 10" E) over the 2010–2011, 2011–2012 and 2012–2013 breeding seasons (hereafter we refer to these breeding seasons by the year in which they began). Our research effort was limited in 2010, but we were present in Penguin Bay almost continuously from early Oct to c. 20 Jan in 2011 and 2012. The birds' reliable use of a narrow travel pathway between the sea and the East and West sub-colonies made it possible to record passive integrated transponder (PIT) tag codes with an automated system. Nests, skua-eaten penguin eggshells, and chicks were counted at these and the nearby Foreshore and Ravine sub-colonies in each year. First-year survival rates were estimated for two cohorts of chicks from all four sub-colonies. Unless stated otherwise, all descriptions refer to Campbell Island.

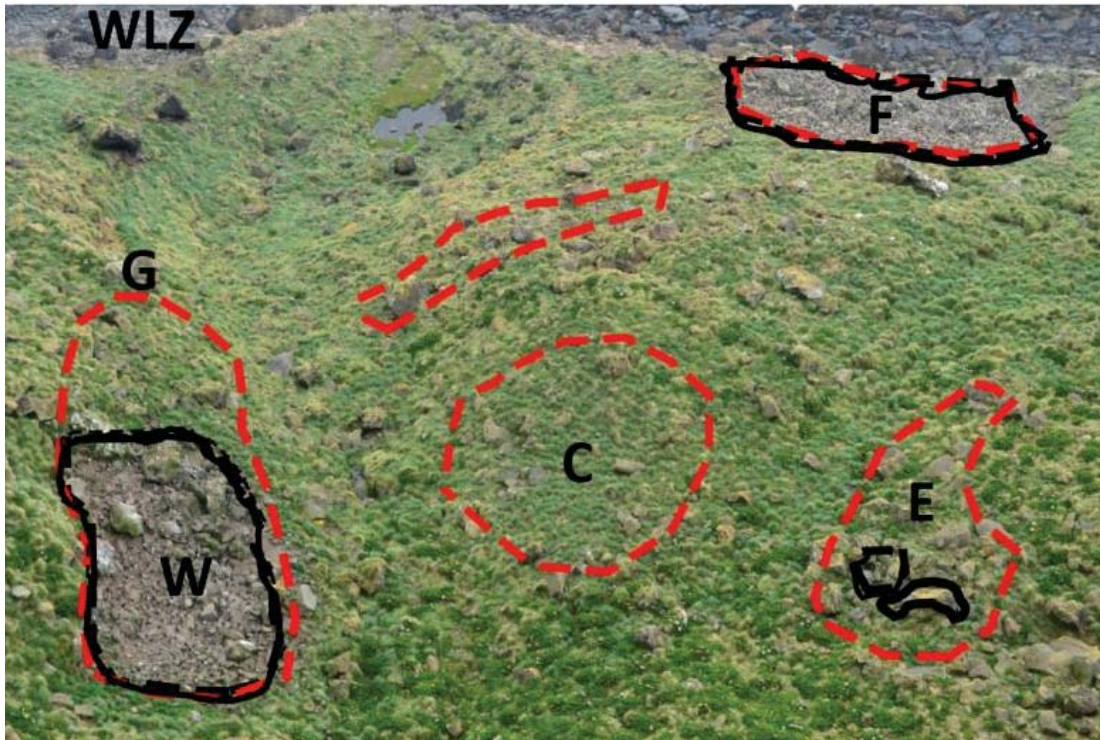


Figure 5.1 Oblique photograph of the Penguin Bay Eastern Rockhopper Penguin sub-colonies, excluding the Ravine sub-colony. Sub-colony boundaries in 1984 are outlined in red broken lines, in 2012 with solid black lines. Sites identified include 'W' (West sub-colony), 'C' (Central), 'E' (East), 'F' (Foreshore), 'G' (automated PIT gateway), and 'WLZ' (West Landing Zone, where West and East sub-colony penguins typically arrived and departed the sea and where many sea lion attacks occurred).

Study Species

Eastern Rockhopper Penguins are among the world's smallest penguin species (45–55 cm long, 2.2–4.3 kg; Marchant and Higgins 1990). The sexes are reliably separated by bill measurements (Warham 1972; Hull 1996), with larger-billed males readily distinguishable in breeding pairs. They are socially monogamous and appear to form long-lasting pair bonds through high nest site fidelity (Warham 1975). The nest site is a scrape lined with pebbles and vegetation if available. Colonies occur on rock terraces, on scree slopes, among boulders, and occasionally among vegetation or in caves, sometimes 400 m from shore (Marchant and Higgins 1990).

Rockhopper Penguins breed over the austral spring-summer, with four main stages – (1) arrival and courtship, (2) incubation, (3) guard, and (4) crèche stages – followed in autumn by the pre-moult exodus, the moult on land, and an over-winter period at sea. Breeding

chronology for 2011 and 2012 is reported in Chapter 3; key aspects of breeding biology are given here. Males typically arrive in the second week of October, females 6–8 d later. Both sexes then remain ashore and fast at their nest site until after egg laying (2 eggs in the first two weeks of November, *c.* two weeks after arrival). Eggs are always dimorphic in size: first-laid ‘A-eggs’ are *c.* 72% of the mass of B-eggs’ that are laid 4–5 d later (Demongin et al. 2010; Chapter 6). Proper incubation occurs only once B-eggs are laid, and A-eggs usually hatch 1–2 d after the B-egg hatches at 32–35 d after it was laid. Thus, A-eggs hatch 37–42 d after laying (Figure 5.2). Females do not relay lost eggs. Few pairs fledge two chicks, and it is usually the B-chick that survives.

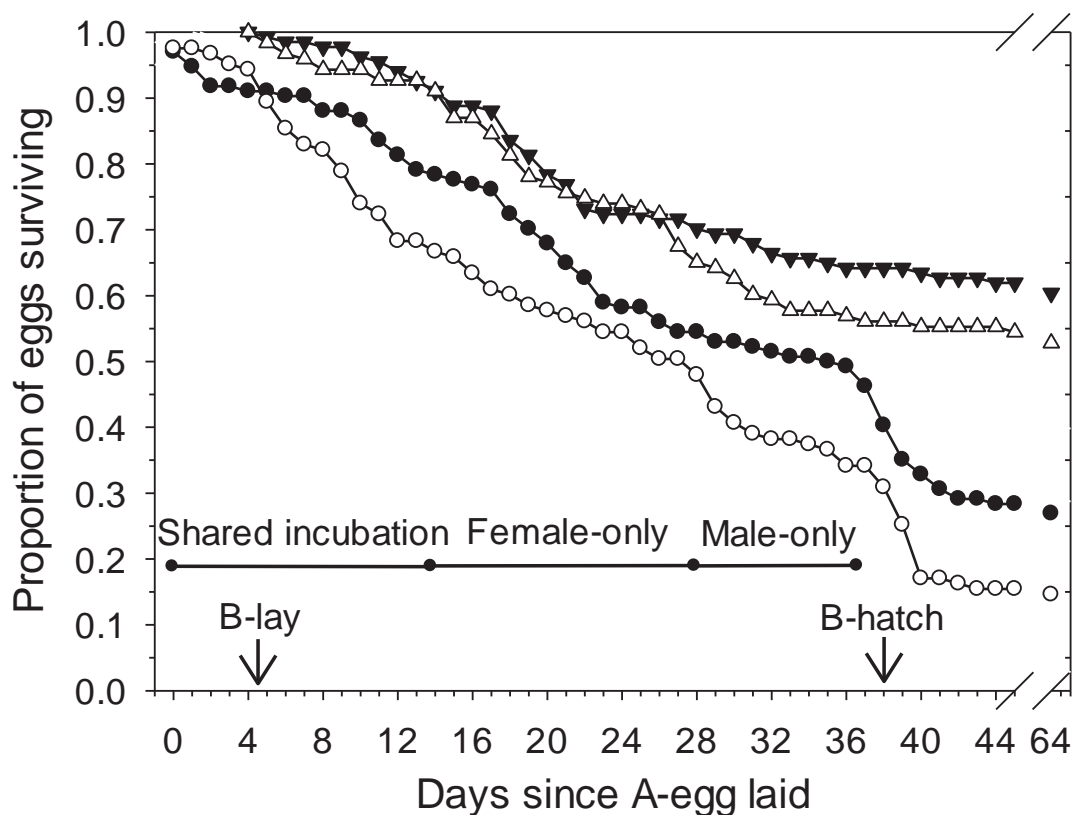


Figure 5.2 Proportion of Eastern Rockhopper Penguin first-laid A-eggs (circles) and second-laid B-eggs (triangles) surviving in relation to A-egg lay date in 2011 (filled symbols, $n = 134$ nests) and 2012 (hollow symbols, $n = 123$). Also indicated are median dates of B-egg laying and hatching, and shared, female-only, and male-only incubation shifts. Median A-egg hatch was one day after B-egg hatch. Eggs incubated beyond Day 44 were inviable.

Males depart fairly synchronously c. 9 d after clutch completion for a 13–16 d long foraging trip, while females incubate. When males return, females go to sea for 7–9 d, returning near hatching in the second week of December. During the guard period of c. 23 d, females (only) provision their chick(s) approximately daily while males brood the chick(s; Chapter 4). Chicks crèche then, at which point males may go back to sea for 7–11 d before returning to join females in chick provisioning until chicks fledge at 65–70 d old (Marchant and Higgins 1990; Chapter 4). Sub-adult penguins visit breeding colonies in late November and December, and come ashore to moult in January. Chicks fledge in mid-February and adults spend the next c. six weeks at sea during the pre-moult exodus to regain body condition prior to moulting during a 3–4 week fast ashore in April. All individuals spend the following 5–5.5 months over-wintering at sea.

Brown Skuas (c. 64 cm long, 1.5–2.2 kg; Hemmings 2013) nested in pairs, often near colonies of penguins or Campbell (*Thalassarche impavida*) and Grey-headed (*T. chrysostoma*) Albatrosses (K.W.M. pers. obs.). In Penguin Bay they showed stable territory locations between years, and likely had high mate and territory fidelity. The population was estimated at c. 100 pairs in 1984–1986 (Higgins and Davies 1996). The Penguin Bay skua population remained stable at c. six skua nests between 1984–1986 and 2010–2012 (G.A. Taylor pers. comm., K.W.M. unpub. data).

A second avian predator was the Northern Giant Petrel (80–95 cm long, 3.8–5.0 kg; Szabo 2013). Of an estimated 234 breeding pairs in 1996, 40 nests were within 3 km of Penguin Bay (Wiltshire and Scofield 2000). In 1996 and 2006 there was a small colony between Ramp Point and Penguin Bay (< 10 nests), but the closest colony (c. 5–10 nests) in 2010–2012 was above Cattle Bay (< 2 km from Penguin Bay, see Chapter 2 for locations). We observed at least one white-morph Southern Giant Petrel (*M. giganteus*) in Penguin Bay, but this species does not breed on Campbell Island. Up to 22 Giant Petrels were counted attending a sea lion eating a penguin offshore from Penguin Bay.

New Zealand fur seals (*Arctocephalus forsteri*) were recorded killing Eastern Rockhopper Penguins in the 1940s, but were not recorded doing so in 2010–2012. Their local population trend is unknown, but they appear to have remained at low levels since the sealing era (Bailey and Sorensen 1962). Up to 20 were seen ashore in Penguin Bay, and at least one pup was born below the Foreshore penguin sub-colony. Larger numbers breed in Cattle Bay, Rocky Bay, and southeast of Rocky Bay.

The population of New Zealand sea lions (*Phocarctos hookeri*) has grown rapidly, from minimum estimates of 51 pups in 1987 to 681 in 2009 (Moore and Moffat 1990; Maloney et al. 2012). In Penguin Bay pup production increased from one pup born over 1984–1986 (G.A. Taylor pers. comm.) to 6–7 pups/yr in 2010–2012. Up to 20 sub-adult and adult sea lions were recorded ashore in weekly counts in Penguin Bay from 24 Dec to 18 Jan in 2011 and 2012, including maximum counts of nine sub-adult males, seven bulls, and nine cows. Penguin Bay appears to attract more sea lions than the larger penguin colonies further west where we saw only zero to three individuals on six occasions 2010–2012.

Data collection

Nest and chick counts

Nest and chick counts at the Penguin Bay sub-colonies follow the methods reported in Chapter 1. Chicks/nest is used as a measure of (maximum) reproductive success from these two sets of counts, as chicks were counted at c. 26–37 d old.

Nest fates and skua predation

Egg fates and chick survival to crèching were determined for 134 nests in 2011 and 123 in 2012 (all 2011 nests active in 2012 were included in that sample: N = 104). Monitored nests included all nests within the small East sub-colony, and those within an irregularly-shaped plot encompassing 23–24% of the nests in the neighbouring West sub-colony. The shape of the West sub-colony plot was dictated by colony topography and visibility of nests from the colony edge, but included central as well as peripheral nests. Nest contents were recorded at 1–3 d intervals, but mostly daily, from the date the first egg was laid until chicks crèched at the end of the guard phase. Using binoculars or the naked eye we recorded the presence or absence and fate of A- and B-eggs and which parent(s) was attending the nest. Dates for laying, hatching, or failure were recorded as the day the egg or chick's status changed (if also monitored on the previous day) or on the median date between then and the previous check if not consecutive. Lay dates are expressed as days since the first egg of each type was laid in either year: Day 1 = 31 Oct for A-eggs and 3 Nov for B-eggs. Laying synchrony is calculated as the number of days between an egg's lay date and the median lay date of that egg type in each year. Nests were checked daily around hatching, and chicks were marked on their breasts with a small spot of blue (B-chicks) or purple (A-chicks) water-soluble paint. If two chicks had hatched at the same time, the larger was assumed to be the B-chick. If seven to 10 consecutive

nest checks could not confirm nest contents, the nest was physically examined. If eggs disappeared, the area around the nest was inspected to classify whether the egg had been ejected (egg outside the nest cup), trampled in the nest, buried in the nest, or was of unknown fate. The fates of individual eggs at 69 monitored nests in 2011 and 89 nests in 2012 were known with greater certainty because they were labelled with indelible black marker with a unique code shortly after laying. Just prior to laying in 2011 and 2012 we classified the degree to which a nest was sheltered: 'cavity' (sheltered on three of five sides by rock), 'lee' (in the lee of a rock providing shelter on one or two sides), or 'exposed' (no nearby rocks large enough to provide shelter). At the same time we recorded nest position as the number of nests between each monitored nests and the colony's edge. For example, a peripheral, outer-most nest scored '0', and an interior nest with four nests between itself and the colony's edge scored '4'.

In 2011 and 2012 almost all penguins breeding at monitored nests were individually marked with subcutaneous PIT tags. In order to assign egg failure dates obtained by nest checks to either the shared, female-only, or male-only incubation shifts we obtained the dates of incubation shift changes at each monitored nest from an automated gateway on the penguin's travel pathway between the sub-colonies and the sea that recorded PIT code, date, and time (see Chapter 3). When we lacked transit data we used parental attendance data from nest checks to obtain shift dates. If these too were uncertain we used the population-level median dates obtained from the automated gateway.

Skuas removed penguin eggs from the sub-colonies and ate them in adjacent areas specific to each colony. They tended to ingest the egg contents, leaving behind the shell. We only observed 1, non-resident skua swallow eggs whole on a single day, and we rarely saw eggshell fragments in skua faeces. In all years we collected eggshells found around the East, West, and Foreshore sub-colonies at intervals of 6–17 d throughout the incubation period, counted them, and measured their length and width where they were not too broken to do so. In 2011 and 2012 we measured the length and width of A- and B-eggs on their lay date at 340 nests at the East, West, and Foreshore sub-colonies. We calculated egg volume (cm^3) as $\text{length} * \text{width}^2 * 0.512$ (Stonehouse 1966). Separate discriminate analyses using cut-offs of ≤ 67.82 mm (length), ≤ 51.37 mm (width), and ≤ 99.74 cm^3 (volume) for A-eggs determined that each measurement correctly classified A- and B-eggs 92.9/92.4%, 95.3/93.5%, and 97.1/96.5% of the time, respectively. We assigned egg-type to skua-eaten eggshells based on volume, or on length or width if only one could be measured using those cut-offs. Eggshells that were too broken to make either measure were classified as 'Unknown' type, except in 2010 where we

only collected and counted eggshells for which both length and width could be measured, thereby under-recording the actual number of skua-eaten eggs.

First-year survival

First-year penguins were counted in and around each sub-colony at about weekly intervals from their first appearance in early December until our departure from the island c. 20 Jan. Penguins were regarded as being in their first year up until they had completed their first moult in late January, so that first-year penguins were 13–14 months old. All first-years along or just above the shoreline in the main part of Penguin Bay were counted in the Foreshore group, whereas any in the Ravine, including the Ravine shoreline were counted in the Ravine group. First-years were identified by their very short yellow crest feathers and mottled-grey throats and were the first age-class to initiate moult in January (Strange 1982). Although a few first-year birds had shed all of their old feathers before our departure, c. 20 Jan, it appeared as though few had gone back to sea. We assume that all first-year penguins hatched from Penguin Bay moulted in Penguin Bay, and that our maximum count represents all first-year penguins ashore simultaneously. The latter assumption appears justified in that Rockhopper Penguins appear to moult fairly synchronously by age class (moult takes c. four weeks and most individuals in a given age class moult over five to six weeks, Strange 1982; Williams 1995). We calculated first-year survival rates 2010 to 2011 and 2011 to 2012 as the overall maximum count of first-year penguins in Penguin Bay in the later year, divided by the overall number of chicks counted mid-crèche in the earlier year.

Adult survival

We PIT-tagged adult penguins in Oct–Dec in all years, and scanned penguins from Oct–Jan via an automated gateway on the penguin’s pathway into the East and West sub-colonies in 2011 and 2012, and a hand-held scanner (RS320 Stick Reader, Allflex Australia Pty) on other occasions at their nest sites. Additional automated gateways were used for short periods in 2011 at the Foreshore sub-colony to confirm that ‘missing’ tagged individuals had not emigrated there. In Apr 2013 our ‘recapture’ effort was limited to using the stick reader to find 45 tagged individuals on 14–15 Apr in the East and West sub-colonies for geo-location sensor (GLS) tag deployment. Recapture effort for GLS retrieval in spring Oct 2013 was restricted to stick-reading as many individuals as possible in the East and West sub-colonies over 23–25 Oct and 9–10 Nov 2013. For survival analysis, recaptures were grouped into Oct–Jan (3 months:

early breeding), Jan–Apr (3 months: late breeding/pre-moult), and Apr–Oct (6 months: overwinter) intervals.

Sea lion predation

Observations of New Zealand sea lions killing sub-adult and adult penguins along the shoreline and offshore from Penguin Bay were recorded in 2011 and 2012. We used binoculars to classify sea lion kills as “confirmed” if a sea lion was observed killing or eating what appeared to be a penguin (black and white colour pattern, correct size and shape, a prolonged handling time lasting multiple minutes that involved tearing off chunks of flesh through vigorous head-shaking and the conspicuous attendance of many avian scavengers; this was often seen immediately after a raft of penguins had returned to or, less often, departed from the shoreline). “Unconfirmed” kills were either observations of a dead penguin on the water not associated with a sea lion, or a sea lion eating an item at sea that may have been prey other than a penguin (e.g., octopus or large fish). We recorded all sea lion kills observed opportunistically while we were in Penguin Bay from the penguins’ arrival in mid-Oct to our departure c. 20 Jan, and during sea lion-focussed ‘all-day’ predation watches through most of the daylight period (05:00 to 21:00) when two observers alternated 4-h shifts. Many chick-rearing penguins departed the colony at 04:00–05:00 when it was still too dark to see offshore, but most had come ashore by 21:00 in both years (Chapter 4). We recorded the timing of the predation observation, general location, and the age-class (sub-adult or adult) and sex of the sea lion when possible.

Data analysis

Egg fates

We used an information-theoretic approach to model selection to evaluate factors that influenced the fate (hatch or fail) of A- and B-eggs (separately). It was common that an A-egg failed in the 1–2 d after its sibling B-egg hatched, so we conducted a third analysis to consider A-egg survival until B-egg hatching. This enabled us to differentiate between factors affecting A-eggs before and after B-egg hatching. To assess our expectations that eggs would be more vulnerable to predation if laid in smaller sub-colonies, in less sheltered sites, on the periphery, or out of synchrony, we considered six explanatory variables in these models: year, colony, nest shelter, nest position, lay date, and laying synchrony. We used an all-subsets approach to model comparison, plus a null model, but excluded interactions because all possible additive

combinations of variables were equally biologically plausible. The candidate model set included 64 models.

Following the methods of Burnham and Anderson (2002), we calculated Akaike's information criterion for small sample sizes (AIC_c) for all models, along with associated parameters. We began by comparing the AIC_c values of the global model (including all six variables) with and without a random effect of nest ID in order to determine whether such an effect was needed to account for correlated fates between eggs laid at the same nest site in both years. In both the A- and B-egg analyses the global model without the random effect of nest ID had a lower AIC_c value, so we did not consider nest ID further. We used parameter estimates and their standard errors from the most parsimonious and global models to assess the size of the effect and thus biological significance of each parameter. All analyses used a binomial distribution and the logit link function and were conducted using the arm package in R Studio (Gelman et al. 2012; R Core Team 2012).

Daily egg and chick survival rates

Daily A- and B- egg and chick survival rates (S) were calculated based on the number of eggs or chicks alive at the start (N_1) and end (N_2) of an incubation shift or the guard phase of duration in days (t), while assuming an exponential rate of decay, from the formula:

$$S = e^{(\ln(N_2-N_1)/t)} \quad [1]$$

Where e is the base of the natural logarithm. We did not account for inviable eggs in daily egg survival rates. This approach to estimating egg and chick survival rates is similar to that of nest survival by Mayfield (1961; 1975), with the exception that all of our nests were followed from their initiation (A-egg lay) date. Our method would be improved by incorporating measures of uncertainty in failure dates (Stanley 2000).

Modelling adult survival and recapture probabilities

Standard methods were used to estimate adult monthly survival (φ) and recapture (p , PIT tag recording) rates (Lebreton et al. 1992; Cooch and White 2014) using program MARK (White and Burnham 1999). Rates were estimated for six intervals between seven capture/recapture occasions from Oct 2010 to Oct 2013. A longer time period and recording throughout the breeding season and during each moult period would have allowed a better assessment of

whether survival rates were lower during the breeding season than at other times (as expected if sea lion predation is important). Given the limitations of our dataset the primary objective of the analysis was to provide an adult survival estimate for population modelling. First, a global model was defined that allowed survival and recapture rates to vary between intervals and to differ between the sexes. Second, reduced parameter models were constructed and evaluated to examine support for the hypotheses that survival differed between intervals and the sexes, and that survival was higher during all other periods (the ‘background’ rate) than during the late breeding/pre-moult period of the 2012 breeding season (Jan–Apr 2013) when low adult body masses, poor reproductive success, and low provisioning rates, especially of males, suggested penguins were nutritionally stressed (Chapters 3 and 4). To reduce the number of models compared, we used the method of Lebreton et al. (1992) by first finding the best-supported parameterization of recapture rate and then keeping it unchanged while find the best-supported parameterization of survival rate.

Goodness-of-fit was evaluated with the median \hat{c} procedure (Cooch and White 2014), and the estimated variance inflation factor \hat{c} was used to adjust standard errors and calculate QAIC_c, Akaike’s information criterion adjusted for lack of fit and small sample bias (Burnham and Anderson 2002). Models were ranked according to Δ_i , the difference in QAIC_c value from that of the top-ranked (most parsimonious) model. Adjusting for \hat{c} did not change model rankings. We also calculated QAIC_c weights (w_i). We used the sin link function and second-part variance estimation. Survival and recapture rates are from the best-supported models and are reported \pm 95% confidence intervals. The survival analysis included 483 individuals (245 males and 238 females; totals ‘tagged’ in Appendices 5.1 and 5.2). Most individuals were recaptured on at least one subsequent occasion (86% for both sexes). The effective sample size was 1705 (859 males and 846 females). See Appendices 5.1 and 5.2 for recapture matrices.

Sea lion predation rates

We estimated the proportion of the penguin breeding population in Penguin Bay killed by sea lions during the chick-rearing period in 2011 and 2012 as:

$$(p*d) / (n*2) \quad [2]$$

where p = the average daily predation rate (kills/d) from the all-day watches, d = the duration of the chick-rearing period (from the first hatch date to the expected median fledging date 68 d after the median hatch), and n = the total number of nests in Penguin Bay (Table 5.1). We used the first hatch date instead of the median hatch date (a difference of 7 d in 2011 and 6 d

in 2012) because females tend to return from their incubation foraging trip and begin making daily trips to sea 1–3 d before hatching (K.W.M. unpub. data). This extension of the chick-rearing period is also justifiable in that about half the actively breeding population would still be in danger after the median fledge date. This calculation assumes incorrectly that only breeding penguins are killed by sea lions (no first-year and pre-breeders), but neglects those breeding penguins killed outside of the chick-rearing period.

Table 5.1 Early incubation counts of nests, mid-crèche counts of chicks, reproductive success (chicks per nest), and % eggs skua-eaten in the Penguin Bay sub-colonies 2010–2012.

	East	West	Ravine	Foreshore	Overall
Nest count					
14-16 Nov 2010	34	541	1074	1546	3195
12-13 Nov 2011	24	460	1045	1408	2937
12-13 Nov 2012	19	452	1068	1473	3012
mean	26	484	1062	1476	3048
Chick count					
8-9 Jan 2011	6	195	434	682	1317
20-Jan 2012	11	238	478	647	1374
18-Jan 2013	5	124	260	458	847
mean	7	186	391	596	1179
Reproductive Success (chicks/ nest)					
2010	0.18	0.36	0.40	0.44	0.41
2011	0.46	0.52	0.46	0.46	0.47
2012	0.26	0.27	0.24	0.31	0.28
mean	0.30	0.38	0.37	0.40	0.39
% eggs eaten by skua*					
2010	35.3	11.0	NA	3.6	6.0
2011	60.4	14.0	NA	6.9	9.8
2012	36.8	29.1	NA	10.6	16.7
mean	44.2	18.0	NA	7.0	10.8

*The % eggs eaten by skua are from counts of skua-eaten eggshells, assume 2-egg clutches, and do not include the Ravine sub-colony.

Population model

We modelled the population growth rate in Penguin Bay using a Leslie matrix and the PopTools add-in (Hood 2010) for Microsoft Excel (Microsoft Corporation). We assumed females began breeding in their fifth year (i.e., they laid for the first time just before turning five years old (Guinard et al. 1998; Dehnhard et al. 2014) and bred every year thereafter). The annual fecundity rate (female chicks produced by each female breeder) we used was the average of the 2010, 2011, and 2012 overall chicks/nest values (Table 5.1), divided by two under the assumption of an equal sex ratio of chicks produced ($0.387/2 = 0.1935$). The first-year survival rate we used was the average of the 2010 to 2011 and 2011 to 2012 first-year survival estimates from the 'First-year survival' section below (0.505). We assumed that females survived at a constant annual rate in their second-year and thereafter derived from the monthly 'background' survival rate of 0.985 (annual survival = $0.985^{12} = 0.834$). Elsewhere first-year survival of Rockhopper Penguins is lower than survival of sub-adult and adults, which are similar (Guinard et al. 1998; Dehnhard et al. 2014). For illustrative purposes we depict the theoretical survival rates (adult and sub-adult survival rates set to be equal for ease of interpretation) and reproductive success rates required for a stable population ($\lambda = 1.0$). For comparison to the present study we also calculated the population growth rate using a Leslie matrix of an increasing population of Southern Rockhopper Penguins on New Island, Falkland Islands, using demographic data from the literature: reproductive success of 0.69 (2006; Poisbleau et al. 2008), first-year survival of 0.81 (2006 and 2007 cohorts; Dehnhard et al. 2014), and a mean adult survival rate of 0.919 (2006–2010; Dehnhard et al. 2013)..

'Predation-free' population growth rate

We estimated a 'predation-free' population growth rate using estimates of reproductive success and adult survival rates without the effects of predation we describe below. We have assumed all sea lion mortality was of adult penguins, and so are unable to estimate a 'predation-free' first-year survival rate.

RESULTS

Egg fates

A-egg hatching success varied inter-annually and with nest shelter (Table 5.2). Hatching success was higher in 2011 than 2012 (36 of 134 eggs, 26.9%, versus 18 of 123, 14.6%, Figure 5.2) and was higher in cavity nests (24 of 58, 41.4%) than in lee or exposed nests (lee, 20 of 128, 15.6%; exposed, 10 of 71, 14.1%, Figure 5.3). Other strongly supported models ($\Delta_i < 2.0$) additionally included effects of colony, nest position, lay date, or laying synchrony, but only marginally increased the log-likelihood values over that of the most parsimonious model. In the global model only year and nest shelter had estimates larger than their standard errors (Table 5.3). Model rankings and relative support were very similar for the analysis considering A-egg survival to B-egg hatching, despite a large proportion of A-egg failure occurring after B-eggs hatched, as 55.4 and 45.0% of A-eggs alive at B-egg hatching failed post B-egg hatching in 2011 and 2012, respectively (Figure 5.2).

Table 5.2 Support for logistic regression models predicting fate (hatch or fail) of A-eggs of Eastern Rockhopper Penguins in 2011 and 2012.

Model	$\log(L)$	K	Δ_i	w_i
Year + Shelter ^a	-120.85	4	0.00	0.20
Year + Shelter + Colony	-120.52	5	1.35	0.10
Year + NestPos + Shelter	-120.69	5	1.69	0.09
Year + LayDate + Shelter	-120.81	5	1.92	0.08
Year + Synchrony + Shelter	-120.82	5	1.94	0.08
Year + Synchrony + Shelter + Colony	-120.48	6	3.28	0.04
Year + NestPos + Shelter + Colony	-120.48	6	3.28	0.04
Year + LayDate + Shelter + Colony	-120.50	6	3.31	0.04
Year + Synchrony + NestPos + Shelter	-120.64	6	3.60	0.03
Shelter	-123.67	3	3.63	0.03
Year + LayDate + NestPos + Shelter	-120.68	6	3.67	0.03
Year + LayDate + Synchrony + Shelter	-120.76	6	3.83	0.03
Null	-132.13	1	16.51	0.00

^aTop model; $AIC_c = 249.75$. Variables include Year (2011 or 2012), Colony (East or West sub-colony), Shelter (degree of nest shelter, increasing from exposed to lee to cavity), NestPos (nest position as the number of nests to the colony edge), Synchrony (days between the lay date and the median lay date in each year), and LayDate (days from 30-Oct for A-eggs, 2-Nov for B-eggs). The log-likelihood value is $\log(L)$, number of parameters in the model is K , AIC_c is Akaike's information criterion adjusted for small sample size, Δ_i is the difference in AIC_c value from that of the top model (i.e., lowest AIC_c), and w_i is the Akaike weight; $n = 257$ eggs. Models are presented from lowest to highest Δ_i . Except for the null model, only models with $\Delta_i < 4.0$ are shown.

Table 5.3 Parameter estimates and standard errors (SE) from the top-ranked and global logistic regression models predicting fate (hatch or fail) of A-eggs and B-eggs of Eastern Rockhopper Penguins in 2011 and 2012 in the East and West sub-colonies.

Parameter	<u>A-egg fate</u>				<u>B-egg fate</u>			
	<u>Top model</u>		<u>Global model</u>		<u>Top model</u>		<u>Global model</u>	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Intercept	-0.015	0.304	0.005	0.759	0.662	0.363	0.156	0.696
Colony- West			-0.293	0.461	0.989	0.428	0.902	0.452
Year (2012)	-0.775	0.333	-0.748	0.366			-0.200	0.287
LayDate			0.016	0.079			0.072	0.063
Synchrony			0.038	0.120			-0.014	0.095
NestPos			-0.024	0.091			0.075	0.071
Shelter- exposed	-1.476	0.439	-1.323	0.474	-1.985	0.460	-2.016	0.464
Shelter-lee	-1.341	0.366	-1.200	0.398	-1.275	0.417	-1.274	0.420

The East colony, year 2011, and 'cavity' nest shelter were used as the reference categories. Parameters are defined in Table 5.2.

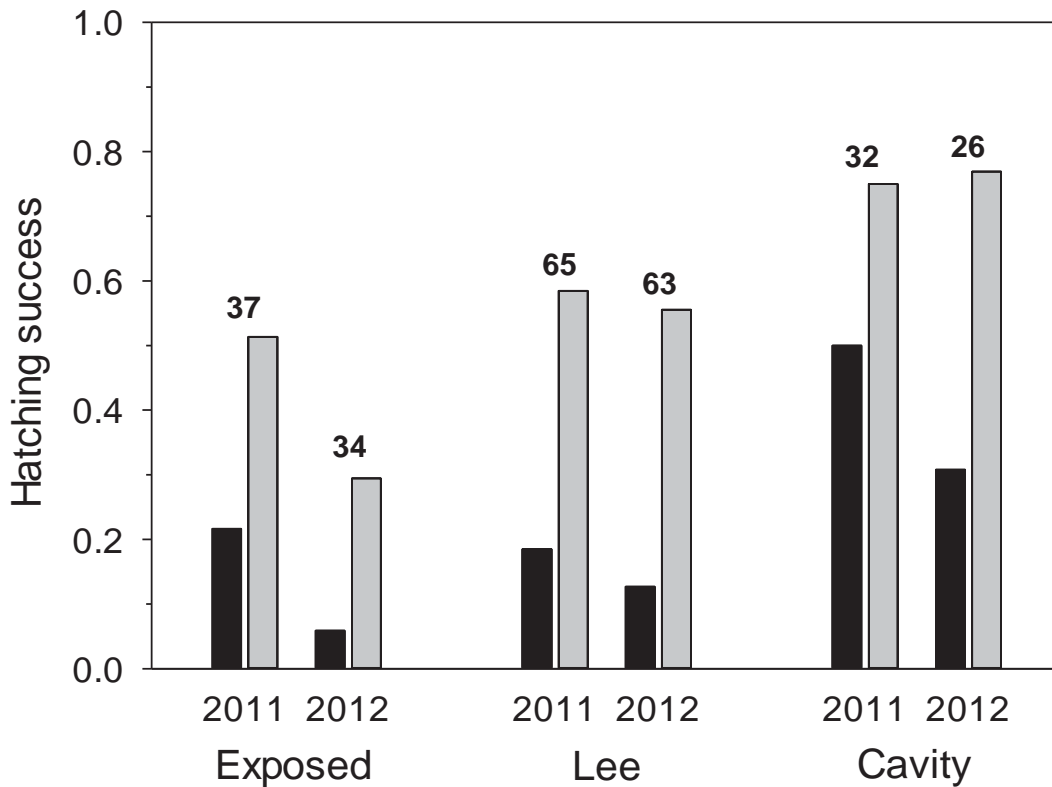


Figure 5.3 Hatching success (no. eggs hatched / no. eggs laid) of Eastern Rockhopper Penguin A-eggs (black bars) and B-eggs (grey bars) in 2011 and 2012 in relation to nest shelter category. Total number of nests in each year/shelter-type is given above bars.

B-egg hatching success was best explained by nest shelter and sub-colony (Table 5.4). It was highest in cavity nests (44 of 58, 75.9%), but differed between lee (73 of 128, 57.0%) and exposed nests (29 of 71, 40.8%, Figure 5.3), and was higher in the West (124 of 216, 57.4%) than the East sub-colony (22 of 41, 53.7%). Other strongly supported models additionally included effects of lay date, year, or nest position, or two of those effects (Table 5.4). Addition of these extra effects made modest improvements to the log-likelihood values over that of the most parsimonious model (by 0.41 to 1.58; Table 5.4). In the global model all terms except year and synchrony were larger than their standard errors (Table 5.3), suggesting the additional terms lay date and nest position (but not year) in the strongly supported models had smaller, but non-negligible effects.

Table 5.4 Support for logistic regression models predicting fate (hatch or fail) of B-eggs of Eastern Rockhopper Penguins in 2011 and 2012.

Model	$\log(L)$	K	Δ_i	w_i
Shelter + Colony ^a	-164.71	4	0.00	0.12
LayDate + Shelter + Colony	-163.77	5	0.14	0.11
Year + Shelter + Colony	-163.91	5	0.42	0.09
LayDate + NestPos + Shelter + Colony	-163.13	6	0.87	0.07
NestPos + Shelter + Colony	-164.30	5	1.20	0.06
Year + LayDate + Shelter + Colony	-163.45	6	1.51	0.05
Year + NestPos + Shelter + Colony	-163.53	6	1.67	0.05
Synchrony + Shelter + Colony	-164.71	5	2.01	0.04
LayDate + Synchrony + Shelter + Colony	-163.76	6	2.12	0.04
Year + LayDate + NestPos + Shelter + Colony	-162.89	7	2.40	0.04
Year + Synchrony + Shelter + Colony	-174.16	6	2.43	0.03
LayDate + Synchrony + NestPos + Shelter + Colony	-163.12	7	2.86	0.03
LayDate + NestPos + Shelter	-165.18	5	2.96	0.03
NestPos + Shelter	-166.26	4	3.10	0.02
Synchrony + NestPos + Shelter + Colony	-164.30	6	3.21	0.02
Year + LayDate + Synchrony + Shelter + Colony	-163.44	7	3.50	0.02
Shelter	-167.53	3	3.63	0.02
Year + Synchrony + NestPos + Shelter + Colony	-163.53	7	3.69	0.02
Year + NestPos + Shelter	-165.58	5	3.76	0.02
Null	-175.75	1	16.05	0.00

^a Top model; $AIC_c = 337.46$. Table headings are defined in Table 5.2; $n = 257$ eggs. Models are presented from lowest to highest Δ_i . Except for the null model, only models with $\Delta_i < 4.0$ are shown.

The mean lay date of B-eggs that hatched (7.56 ± 2.32 d) was only slightly later than for those which failed (7.13 ± 2.41 d). As found for A-eggs, hatching success of B-eggs was higher in 2011 (81 of 134, 60.4%) than in 2012 (65 of 123, 52.8%). Lay date and year are confounded, because the average lay date of B-eggs was later in 2011 (8.25 ± 2.22 d) than in 2012 (6.42 ± 2.15 d). However, within both years, B-eggs that hatched had a slightly later lay date (2011: 8.37 ± 2.15 d, 2012: 6.55 ± 2.14 d) than those which failed (2011: 8.06 ± 2.32 d, 2012: 6.28 ± 2.18 d). B-eggs that hatched came from more interior nests (mean nest position = 2.44 ± 2.14 nests to periphery) than those that failed (2.27 ± 2.01 nests to periphery). However, nest position is confounded with nest shelter, because cavity nests tended to be on the colony periphery (1.48 ± 1.83 nests to periphery) relative to lee nests (2.55 ± 2.09 nests to periphery) and exposed nests (2.76 ± 2.09 nests to periphery). Thus, nest position is likely to have a stronger effect on hatching success in a sample where cavity nests are more evenly distributed between interior and peripheral nests. In summary, nest shelter and colony had strong effects on B-egg hatching success, whereas lay date and nest position had lesser effects (Table 5.3). The global model predicted that the hatching probability of B-eggs increased from 0.56 to 0.78 over the range of lay dates measured, and from 0.54 to 0.70 over the range of nest positions measured. The greater increase in hatching success with lay date than nest position suggests that lay date had a larger effect than nest position.

Daily egg and chick survival rates

As predicted based on nest defence ability from skua predation, overall daily egg survival rates were highest during shared incubation, intermediate during male-only incubation, and lowest during female-only incubation (Table 5.5, Figure 5.2). A-eggs had a very high failure rate after B-eggs hatched. This post B-egg hatching period averaged only 1-day duration in both years, but 55.4 and 45.0% of A-eggs alive at B-egg hatching failed post B-egg hatching in 2011 and 2012, respectively (Table 5.5, Figure 5.2).

Table 5.5 Daily egg and chick survival rates and hatching success of first-laid A-eggs/chicks and second-laid B-eggs/chicks of Eastern Rockhopper Penguins in 2011 and 2012 with respect to incubation shift (shared, female-only, male-only), pre- and post-B-egg hatching, and the post-hatching guard period. Survival rates exclude inviable eggs. Durations (d) are mean values and for shared incubation and guard period are given with respect to A-eggs/B-eggs.

Year	No. laid	Shared	Female	Male	Pre B hatch	Post B hatch	Overall incubation	Hatch (%)	Guard	Survive guard (%)	Survive overall (%)
2011	Duration	14/10	13	8	35	1	36		23/24		
	A-eggs	0.982	0.974	0.984	0.980	0.554	0.964	26.9	0.950	30.6	8.2
	B-eggs	0.994	0.978	0.982			0.984	60.4	0.996	91.4	55.2
2012	Duration	13/9	16	9	38	1	39		22/23		
	A-eggs	0.971	0.972	0.969	0.971	0.450	0.952	14.6	0.951	33.3	4.9
	B-eggs	0.991	0.974	0.986			0.981	52.8	0.985	70.8	37.4
Mean		0.984	0.974	0.980	0.975	0.502	0.970		0.971		

Daily chick survival rates during the guard period were similar to overall daily egg survival rates for both A- and B-eggs in 2012; in 2011 A-chick survival was slightly lower and B-chick survival slightly higher than their respective egg survival rates (Table 5.5). As incubation lasted longer than the guard period, a higher proportion of A- and B-chicks survived the guard period than eggs hatched in both years (even though daily survival rates were similar for eggs and chicks in 2012). B-chicks survived considerably better in 2011 than 2012 (91.4 and 70.8% respectively), but there was no difference between years for A-chicks (30.6 and 33.3% surviving). The lack of a difference in survival rates for A-chicks reflects the higher frequency of both chicks hatching in 2011 than 2012 (28 of 134, 20.9%, versus 11 of 123, 8.9%). When both chicks hatched, the A-chick generally died (at 5.6 ± 2.1 d old), so mortality rates were similar, despite 2011 being a better breeding season overall.

First-year survival

Our first-year survival estimates were 0.587 over 2010 to 2011 and 0.422 over 2011 to 2012 (Table 5.6), for an average of 0.505. At the sub-colony level first-year survival rates appear to increase with increasing colony size, but we expect that this is an artefact of first-year penguins choosing to moult along the shoreline and at larger sub-colonies (i.e., the Foreshore sub-colony), rather than a true inter-colony difference in survival rates. Counts of first-year penguins were high around the time of hatching in mid-Dec when they came ashore to prospect, low late-Dec and early-Jan, and increased to a maximum in mid-to-late Jan as first-year penguins came ashore to moult (Table 5.6). Our maximum counts of first-year penguins were the last made each season, suggesting later counts may have been even higher. However, later counts may miss birds that had completed their moult and gone to sea.

Table 5.6 Number of first-year Eastern Rockhopper Penguins counted in and around each sub-colony in 2011 and 2012. No counts were made in the Ravine sub-colony before 24-Dec 2011. 'Survival' estimates are of the first-year survival rate calculated as the maximum count of first-year penguins divided by the count of chicks in the previous year from Table 5.2. Dates in 2012 were ± 1 d from those in 2011, except the final count was 18-Jan in 2012.

Date	No. first-year penguins counted 2011						No. first-year penguins counted 2012					
	East	West	Ravine	Foreshore	Overall	Overall	East	West	Ravine	Foreshore	Overall	
2-Dec	0	2	NA	13	NA	NA	0	0	9	23	32	
10-Dec	0	4	NA	242	NA	NA	0	1	59	164	224	
16-Dec	0	6	NA	266	NA	NA	0	8	146	247	401	
24-Dec	0	6	102	232	340	340	0	0	48	128	176	
31-Dec	0	2	25	56	83	83	0	1	15	38	54	
6-Jan	0	5	18	80	103	103	0	0	5	10	15	
15-Jan	0	18	187	360	565	565	0	11	197	372	580	
21-Jan	0	26	306	441	773	773						
Survival	0.0	0.133	0.705	0.647	0.587	0.587	0.0	0.046	0.412	0.575	0.422	

Adult survival and recapture rates

The global model of adult survival and recapture rates explained the data adequately ($\hat{c} = 1.273$). The most parsimonious model in the candidate set included a survival rate that differed between the sexes during late breeding/pre-moult of the 2012 breeding season and differed from all other years over which survival was constant and the same between the sexes (Table 5.7). This top model estimated that the monthly survival rate was 0.985 ± 0.002 in all intervals, except lower in males during late breeding/pre-moult in 2012 (0.947 ± 0.038) and lower still during the same period in females (0.882 ± 0.043 , Table 5.8). Thus, over the late breeding/pre-moult interval of the 2012 season, the mortality rate was higher from the background rate by 3.5 times for males and 7.9 times for females. The monthly background survival rate for both sexes, and the male and female monthly survival estimates during late breeding/pre-moult equate to annual survival estimates of 0.834, 0.520, and 0.222, respectively. The second-ranked model had one fewer parameter (no sex effect on survival during late breeding/pre-moult in 2012) and was also well supported (low Δ_i and similarly high proportion of the QAIC_c weights). Estimates from the second-ranked model differed only in the sexes having the same probability of monthly survival during late breeding/pre-moult in 2012 (0.920 ± 0.034 , mortality rate 5.3 times the background rate). No other model was as well supported (all $\Delta_i > 2$; Burnham and Anderson 2002). Together the two top-ranked models that allowed survival to differ during late breeding/pre-moult of the 2012 breeding season had 12 times the support of the third-ranked model in which survival was constant through time.

Table 5.7 Model rankings and ranking criteria for hypotheses to explain adult Eastern Rockhopper Penguin survival during Oct 2010 to Oct 2013. Δ_i is the difference in QAICc value from that of the top-ranked model, QAICc is Akaike's information criterion adjusted for small sample size and corrected for \hat{c} , QDeviance is the model deviance after correcting for \hat{c} , and w_i is the Akaike weight.

Model rank	Model ^a	Δ_i	K	QDeviance	w_i
1	φ (sex*pre-moult) ρ (sex*t)	0.00	15	69.40	0.45
2	φ (pre-moult) ρ (sex*t)	0.31	14	71.74	0.39
3	φ (.) ρ (sex*t)	3.64	13	77.11	0.07
4	φ (t) ρ (sex*t)	4.28	17	69.60	0.05
5	φ (sex*.) ρ (sex*t)	5.57	14	77.01	0.03
6	φ (sex*t) ρ (sex*t)	9.78	22	64.87	0.00
7	φ (sex*t) ρ (t)	11.07	17	76.39	0.00
8	φ (sex*t) ρ (sex*.)	595.58	14	667.02	0.00
9	φ (sex*t) ρ (.)	596.51	13	669.98	0.00

^aModel notation follows Cooch and White (2014): φ = survival probability, ρ = recapture probability, sex = sex effect, t = differs through time (between recapture occasions), (.) = constant through time, pre-moult = survival differs only during the Jan–Apr 2013 late breeding/pre-moult period, and an asterisk indicates interaction between factors.

Table 5.8 Intervals, durations, corresponding Eastern Rockhopper Penguin life history stages, and male and female monthly survival (ϕ) and recapture (p) probabilities (\pm 95% CI) estimated from the top-ranked model in Table 5.4.

Interval	No. months	Early breeding	Late breeding/ pre-moult	Over- winter	Male ϕ	Female ϕ	Male p	Female p
Oct 2010 to Oct 2011	12	X	X	X	0.985 \pm 0.002	0.985 \pm 0.002	0.976 \pm 0.017	0.984 \pm 0.013
Oct 2011 to Jan 2012	3	X			0.985 \pm 0.002	0.985 \pm 0.002	0.950 \pm 0.027	1.000 \pm 0.000
Jan 2012 to Oct 2012	9		X	X	0.985 \pm 0.002	0.985 \pm 0.002	0.992 \pm 0.007	1.000 \pm 0.000
Oct 2012 to Jan 2013	3	X			0.985 \pm 0.002	0.985 \pm 0.002	0.880 \pm 0.047	0.924 \pm 0.038
Jan 2013 to Apr 2013	3		X		0.947 \pm 0.038	0.882 \pm 0.043	0.150 \pm 0.084	0.185 \pm 0.097
Apr 2013 to Oct 2013	6			X	0.985 \pm 0.002	0.985 \pm 0.002	0.907 \pm 0.083	0.998 \pm 0.002

The best supported structure of recapture rate varied between occasions and the sexes. Monthly recapture rates were consistently higher in females than males (Table 5.8). Recapture rates of females from Oct 2011 to Jan 2012 and Jan 2012 to Oct 2012 were estimated to be 1.0 because there were no females not recaptured in Oct 2011 or Jan 2012 that were subsequently recaptured (Appendix 5.2). Recapture rates were especially low in both sexes in the late breeding/pre-moult period of the 2012 breeding season, when our recapture effort was limited to locating 45 individuals, but were otherwise ≥ 0.880 . It should be noted that we cannot evaluate the relative support for models differing from the two top ranked models by allowing the final survival probability to be estimated independently from all others, because the best supported model structure of recapture rate is time dependent (i.e., the terminal survival and recapture probabilities would not be individually identifiable; Lebreton et al. 1992; Cooch and White 2014).

Predation

Skua predation rates varied with colony size: while more eggs were taken from the larger colonies (annual average 103 eggs at the Foreshore, 85 at the West and 11 at the East sub-colonies), the proportion of eggs taken in each sub-colony was far greater for the smallest sub-colony (East, mean 44.2% of eggs laid from 2010–2012) than the others (West, 18% and Foreshore, 7.0%; Table 5.1, Figure 5.4). A- and B-eggs were consumed similarly at the East sub-colony in all three years, but proportionately more A- than B-eggs were eaten in the West and Foreshore sub-colonies (Figure 5.4). Predation rates on both egg types increased from 2010–2012 at the West and Foreshore sub-colonies.

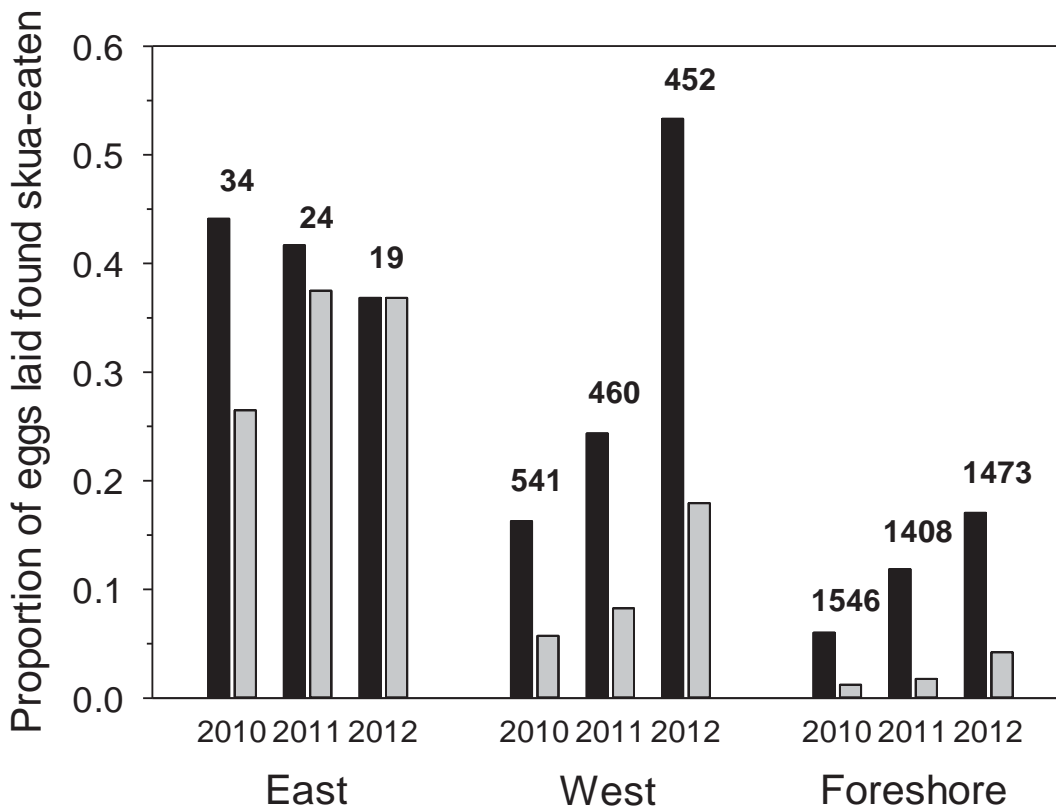


Figure 5.4 The proportions of Eastern Rockhopper Penguin A-eggs (black bars) and B-eggs (grey bars) laid in the East, West, and Foreshore sub-colonies that were found eaten by Brown Skuas in 2010, 2011, and 2012. Eggs of 'Unknown' type were not counted in 2010, but in 2011 and 2012 'Unknowns' were assigned as A-eggs or B-eggs as per the A-egg:B-egg ratio found at each sub-colony in each year. Total number of nests in each year/sub-colony is above bars.

Skuas ate the largest proportion of both A-eggs and B-eggs at the smallest sub-colony, the East (2010–2012 mean 44.2% of eggs laid), an intermediate proportion at the mid-sized West sub-colony (18%), and the smallest proportion at the relatively large Foreshore sub-colony (7.0%, Table 5.1, Figure 5.4). A similarly high proportion A- and B-eggs were consumed at the East sub-colony in all three years, but more A-eggs than B-eggs were eaten in the West and Foreshore sub-colonies, and at the latter two colonies an increasing proportion of both egg types were consumed through 2010 to 2012 (Figure 5.4).

Northern Giant Petrels were not attracted to the penguin sub-colonies until the crèche stage when we saw two successful attacks on chicks in three attempts. Giant Petrels were observed killing adult and first-year penguins by ambushing them as they used the pathway between the shoreline and the inland East and West sub-colonies (Figure 5.1). Before our

departure c. 20 Jan in 2011 and 2012 we estimated that Giant Petrels had killed c. 10 penguins in each year from counts of carcasses near the sub-colonies.

Sea lions killed an average of 4.75 ± 2.5 (SD) and 3.00 ± 1.0 penguins/d during chick-rearing in 2011 and 2012 respectively, or 3.64 penguin/d and 0.23 penguins/hour of observation over both years combined (Table 5.8). Extrapolating these predation rates across 75 and 74 d chick-rearing periods results in estimates of 6.0 and 3.6% of the breeding population being killed in 2011 and 2012, respectively, or an average of 4.8%. The estimated monthly adult survival rate of 0.985 (Table 5.9) translates to survival of 0.963 (mortality of 3.7%) over a chick-rearing period of 2.5 months. This mortality level matches or is exceeded by our estimate of sea lion depredation (6.0% in 2011 and 3.6% in 2012), suggesting that most or all adult penguin mortality during chick-rearing can be accounted for by sea lion predation.

Table 5.9 Numbers of predation events and predation rates of adult and sub-adult Eastern Rockhopper Penguins killed by New Zealand sea lions during ‘all-day’ predation watches (05:00–21:00) in 2011 and 2012 in Penguin Bay, Campbell Island.

Dates of systematic watches	Sea lion kills	
	2011	2012
1 st week of Dec	NA	8
2 nd week of Dec	NA	1
3 rd week of Dec	5	1
4 th week of Dec	2	1
1 st week of Jan	4	3
2 nd week of Jan	8	1
3 rd week of Jan	NA	6
Total kills	19	21
Predation rate (kills/d)	4.75	3.00
Opportunistic observations		
‘Confirmed’	30	25
‘Unconfirmed’*	11	5
Total confirmed	49	46
Grand total	60	51

* denotes that there was some uncertainty to whether it was a definite case of penguin predation by sea lions.

Population model

Based on the reproductive success, first-year, and adult survival parameters we measured from 2010–2013 we estimated the population growth rate (λ) to be 0.905. Figure 5.5 can be used to interpolate the rate of reproductive success required for population stability, given knowledge of sub-adult/adult survival rates, or vice versa. For ease of interpretation Figure 5.5 assumes sub-adult and adult survival rates are equal. However, we estimated first-year survival to be 0.505 and adult survival to be 0.834 and have no information on sub-adult survival beyond the first year. Typically penguin survival is lowest in the first-year, and thereafter similar between pre-breeders and adults (Dehnhard et al. 2014; Guinard et al. 1998). Figure 5.5 can still be used for interpolation in such instances. For example, our estimated annual adult survival rate (0.834) is 65.1% higher than our estimated first-year survival rate of 0.505, so that reproductive success would have to be 65.1% higher than that depicted at $\lambda = 1.0$ in Figure 5.5 (0.823 chicks/nest) to achieve a stable population (1.359 chicks/nest).

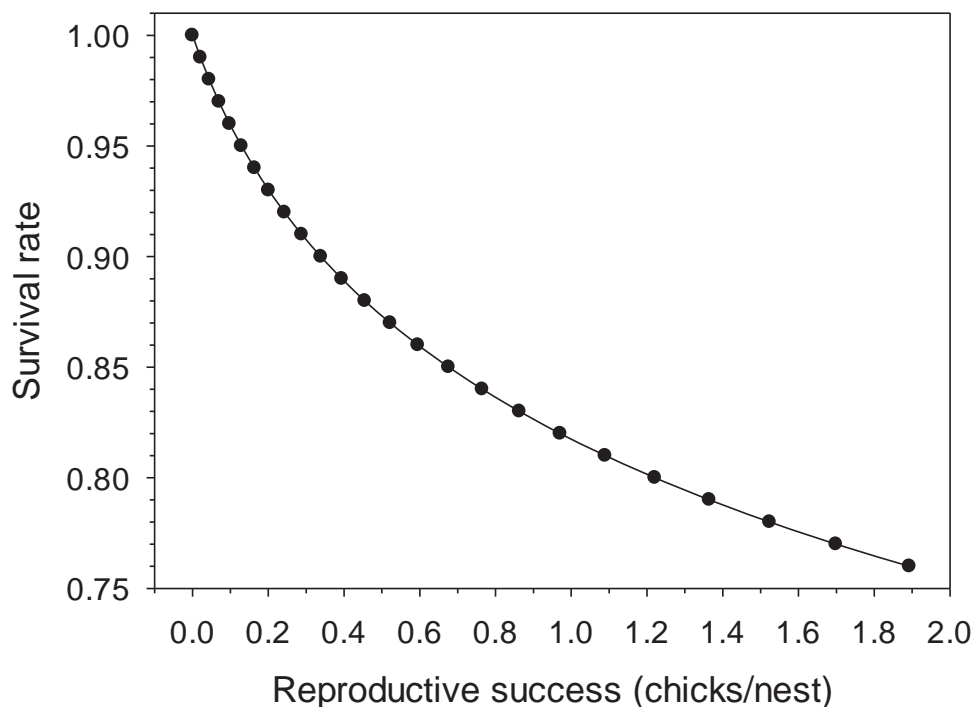


Figure 5.5 Theoretical Rockhopper Penguin adult and sub-adult survival rates (set to be equal) and reproductive success (chicks per nest). The line indicates a stable population ($\lambda = 1.0$) under assumptions of a stable age distribution and first breeding in the fifth year. Demographic rates above the line represent population growth, below the line population decline.

We estimated the population growth rate of Southern Rockhopper Penguins at New Island, Falkland Islands, to be $\lambda = 1.07$. We found the same rate from counts of breeding pairs in 2006 (5,687) and 2012 (8,318) reported by Dehnhard et al. (2014). This perfect agreement is likely partly coincidental, but can also be interpreted as validating the assumption of a Leslie matrix of a stable age structure in this population, and that the demographic rates estimated at New Island are accurate.

'Predation-free' population growth rate

Skua predation of eggs appeared to have a relatively minor effect on reproductive success at the large Foreshore colony; we therefore assume that without predation by skuas, the overall Penguin Bay reproductive success rate would be at least as high as the average reproductive success rate at that sub-colony 2010–2012 (0.40 chicks/nest). If 2012 is excluded as an anomalously poor year because of environmental conditions (Chapter 4), then the average reproductive success at the Foreshore sub-colony is 0.45. The realized insurance value of A-eggs was 11% and 15% in 2010 and 2011 (average 13%, K.W.M. unpub. data), so that the average proportion of B-eggs laid found eaten in 2010 and 2011 at the Foreshore sub-colony (1.5%) likely depressed reproductive success by 1.3% ($= 1.5\% - (1.5\% * 13\%)$). The average of 4.8% of the breeding population that we estimated as being depredated by sea lions during incubation and chick-rearing would cause failure of a similar proportion of nests, so that a reasonable estimate of reproductive success without predation effects is 51.1% ($= 45 + 1.3 + 4.8$) of nests producing a chick. The relatively small amount of Giant Petrel predation we observed is negligible. If, as suggested above, sea lion predation lowers the adult survival rate by 6% annually, then the annual adult survival rate without sea lion predation is 0.894 ($= 0.834 + 0.06$). At the first-year survival rate we measured (0.505), the 'predation-free' reproductive success and adult survival rates result in a population growth rate much nearer stability ($\lambda = 0.983$) than we estimated with predation effects ($\lambda = 0.905$).

DISCUSSION

The rates of reproductive success, first-year survival, and adult survival we measured for the declining population of Eastern Rockhopper Penguins in Penguin Bay, Campbell Island were all low across three years of study. The 'bottom-up' effect of oceanographic conditions causing poor food availability resulted in especially poor reproductive success in 2012, and reduced

adult survival rates in the subsequent late-breeding/pre-moult period. However, we also found that 'top-down' effects of predation, especially by New Zealand sea lions and Brown Skuas, contributed to low overall demographic rates so that predation is likely to be the primary cause of the Penguin Bay population's localized decline.

Skua predation

The amount of shelter around a nest was an important determinant of the fate of both A- and B-eggs, suggesting that skua predation is in addition to the expected egg failure rate and therefore reduces reproductive success (i.e., it is additive mortality). Hatching success was highest in cavity nests where skuas were rarely observed attempting to depredate eggs or chicks. Hatching success is also likely to vary for reasons unrelated to skua predation. More exposed nests are vulnerable to conspecific disturbance that contributes to egg displacement and trampling (St. Clair and St. Clair 1996). We observed that birds in cavity nests tended to incubate facing the nest opening, whereas other birds rotate on their nests more frequently to confront their neighbours and passing birds and as the wind direction changes. Changing position on the nest can cause egg displacement (St Clair et al. 1995; St. Clair and St. Clair 1996), so a reduced need for changing position is another benefit that likely increases the reproductive success of more sheltered nests. B-egg hatching success was also higher at more interior nests. Hatching success is typically higher in the interior of a penguin colony than on the periphery because avian predators have easier access to peripheral nests (Tenaza 1971; Emslie et al. 1995; Liljestrom et al. 2008). A tendency for more experienced and larger individuals to breed at interior nests would also contribute to their higher success (Ainley et al. 1983; M^onguez et al. 2001).

Differences in avian predation rates caused by differences in the availability of cavity nests appear to have led to a counter-intuitive sequence of sub-colony extinction in Penguin Bay. Cavity nests tended to be on the colony periphery, suggesting that cavity nests and their associated large rocks may anchor colony boundaries that would otherwise have contracted. In 1984 the Central sub-colony was larger (999 pairs) than the East (753 pairs), but by 2010 the Central sub-colony was extinct while the East sub-colony persisted at least through 2013 (Cunningham and Moors 1994; P. Moors unpub. data, Figure 5.1). If both sub-colonies were subject to the same predation rates and zero or equal immigration/emigration rates, then the East sub-colony should have gone extinct first. In 2012 the pairs hanging on in the East were primarily in cavity nests (12 of 18 nests, 67%) and only cavity nests hatched eggs. We judged

that the former area of the Central sub-colony in 2009 contained only two cavity nests. In 2009 there were c. 50 pairs in the Central sub-colony, but none attempted to breed there in 2010. We expect that repeated breeding failure caused by Brown Skuas, and predation of large chicks and adults during moult by Northern Giant Petrels at this relatively flat, exposed sub-colony caused its abrupt abandonment. *Eudyptes* penguins typically moult at their nest sites as we observed in the predominantly cavity nests in the East sub-colony in April 2013. However, the flat and exposed lower portion of the West sub-colony was empty of moulting adults. We located some of them in the steeper interior of the colony, and expect they had retreated there, as crèching chicks do, to escape avian predators.

Overall, skuas ate a higher proportion of the eggs laid at smaller sub-colonies. The smallest sub-colony had the lowest overall reproductive success and the largest sub-colony the highest success, whereas the two sub-colonies of intermediate size had similar success. Smaller sub-colonies suffered higher predation rates not only because of their greater ratio of peripheral to interior nests (Jackson et al. 2005), but because each sub-colony was the territory of a pair of Brown Skuas nesting nearby. Therefore, smaller sub-colonies had a higher ratio of predators per nest. The only exception was the Foreshore sub-colony, which may have been too large to be effectively defended by one skua pair. Aggressive confrontations between skuas over the Foreshore colony were common, and may have limited the effects of predation. One might expect that a sub-colony as small as the East would become unprofitable for the resident skua pair so that they would invest less effort in nest predation than would skuas at larger sub-colonies (Type III function response). Although we observed the East skuas attempting to 'steal' eggs from other sub-colonies, they also invested much time and effort in depredating every nest possible within the East sub-colony, to the extent of confronting incubating birds within well-defended cavity nests.

Although skua predation of eggs and young chicks lowers reproductive success, environmental conditions affecting food availability can have a larger effect. In 2011 when adult body condition and diet quality was high (Chapter 3), reproductive success was relatively high across sub-colonies (0.46–0.52 chicks/nest), regardless of their size. In 2012 when body condition and diet quality were poor, the largest Foreshore colony had only a slightly higher reproductive success than the smaller sub-colonies (Foreshore 0.31 chick/nest, others sub-colonies 0.24–0.27 chicks/nest). The greatest variation in reproductive success in relation to sub-colony size occurred in 2010 (Foreshore 0.44 chicks/nest, East 0.18 chicks/nest). Chick growth (K.W.M. unpub. data) and a comparison of overall reproductive success rates (2010 0.41 chicks/nest, 2011 0.47 chicks/nest, 2012 0.28 chicks/nest) suggest that food availability in

2010 was intermediate to 2011 and 2012. There were also more nests in the East and West sub-colonies in 2010 than thereafter, and because exposed and peripheral nests were the ones that became vacant (K.W.M. pers. obs.), the effect of predation in relation to colony size is most evident in 2010. Although hatching success was lower in 2012 than 2011, in 2012 higher B-chick mortality through predation and starvation during the guard phase had a greater effect in driving down reproductive success.

Adult body condition is likely to act synergistically with skua scavenging and predation rates, in that adult penguins in poorer condition appear to have lower nest defence and brood care abilities. Daily egg survival rates were lowest during female-only incubation. Females lost c. 40% of their arrival mass over their 6.5 week fast by the end of their incubation shift (Chapter 3; K.W.M. unpub. data). Skuas boldly attacked these c. 2.1 kg females, and were even seen to grab an incubating female by the back and pull it off its eggs, whereas solo-incubating males, already larger-billed and more aggressive and weighing c. 3.5 kg after their incubation foraging trip, were rarely overtly attacked (Chapters 3 and 4). In addition, a higher proportion of pairs had their A-egg fail after B-egg hatching in 2012 than in 2011, and none maintained two chicks through the guard phase in 2012. Successfully hatching an A-egg in the presence of a B-chick typically requires careful attention and repeated retrieval of the A-egg after displacement (St. Clair and St. Clair 1996; K.W.M. pers. obs.). The nutritionally-stressed breeders in 2012 were apparently less willing or able to make the effort required to hatch both eggs. The timing of egg failure in Rockhopper Penguins elsewhere has been shown to vary between populations and inter-annually (St. Clair and St. Clair 1996). Peak periods of A-egg loss occur either soon after laying, or as we found, after B-egg hatching (Gwynn 1953; Williams 1980; St. Clair and St. Clair 1996). At Macquarie Island a high proportion of the loss of both A- and B-eggs of Eastern Rockhopper Penguins occurred during the middle of the incubation period (Hull et al. 2004), in line with our result that daily egg survival rates may also be low during female-only incubation.

Giant Petrel predation

Giant Petrels are not *Eudyptes* penguin egg predators, nor have they been described taking brooded chicks during the guard period. We observed only two successful attacks by Giant Petrels on chicks during the early crèche period, but expect petrel predation was more important on older chicks and fledging chicks, as found for King Penguins (*Aptenodytes patagonicus*; Descamps et al. 2005) and Snares Penguins (Warham 1974a). Giant Petrels killed

a small proportion of healthy breeding adults and pre-breeders by ambushing them on their route into the inland East and West sub-colonies before c. 20 Jan. Northern Giant Petrels kill adult Northern Rockhopper Penguins in the water near landing places (Ryan et al. 2008), but we did not observe this hunting technique. It appears as though the opportunity to scavenge penguins killed by sea lions attracts Giant Petrels to Penguin Bay and helps sustain the local population, thereby facilitating increased rates of Giant Petrel predation on penguins. Likewise, scavenging of Antarctic fur seal (*A. gazella*) kills of Macaroni Penguins (*E. chrysolophus*) by Giant Petrels is believed to have contributed to a population increase of Giant Petrels at Bird Island, South Georgia (Bonner and Hunter 1982).

Sea lion predation

New Zealand sea lions prey upon penguins everywhere they co-occur (Moore and Moffat 1992; Childerhouse et al. 2001; Lalas et al. 2007). Pinniped predation of penguins has been reported as either a frequent behaviour of a few specialized individuals (Strange 1982; du Toit et al. 2004; Lalas et al. 2007) or a rare, opportunistic behaviour of many individuals (Casaux et al. 2004; Makhado et al. 2008). We observed that while one or two sea lions were likely responsible for the majority of penguin kills, at least six different individuals were observed making kills based on simultaneous events and sea lion age/sex classes, so that hunting penguins was seemingly both a specialized and opportunistic behaviour.

Interestingly, we observed individual sea lions investing much time and energy in swimming along the shoreline of Penguin Bay searching for penguins to attack in the water, or after a short chase from the sea onto the shore (e.g., up to a few hours per day), but the same sea lions ignored the opportunity to depredate the same penguins on land within breeding colonies. Other pinnipeds similarly display the same paradoxical behaviour in depredating seabirds in/near water, but not in breeding colonies, with only a few observations of 'rogue' individuals killing seabirds on nests (Crawford and Cooper 1996; Moore et al. 2008). Although free of sea lion predation within colonies, we observed sea lions trampling to death eggs, chicks, and one brooding adult penguin. Twice we saw penguins defending their nests bitten and thrown by sub-adult males. Typically sea lions avoided traversing through penguin sub-colonies, but on three occasions pregnant cows sought refuge from bulls within colonies (including a stillbirth within the West sub-colony in 2010), and at other times sub-adult males fled through colonies to avoid larger males. Such interactions with negative outcomes for penguins are likely to increase if the sea lion population in Penguin Bay continues to grow.

Similarly, rapidly growing fur seal populations have displaced *Eudyptes* penguin colonies elsewhere (Huyser 2001; Cuthbert et al. 2009).

We estimated that sea lions killed an average of 4.8% of the adult breeding population during chick-rearing. Breeding penguins are also vulnerable to sea lion predation at their first colony arrival, when departing and returning from their incubation foraging trip, and when returning and departing for moult, so that we predict that the total mortality of the breeding population caused by sea lion predation is likely similar to 6% each year. Some unknown proportion of penguins killed by sea lions are first-year birds and other sub-adult pre-breeders, although this proportion may be low if these birds only arrive and depart twice, for prospecting and moulting periods ashore. However, first-year birds are likely depredated at rates higher than their transit frequency would suggest, as they sometimes lingered naïvely in the surf zone where most kills took place.

The predation rate we documented of 0.23 kills/h is an order of magnitude below that calculated from observations of South American sea lions (*Otaria flavescens*) depredating Southern Rockhopper Penguins (2.36 kills/h; Cursach et al. 2014) and Antarctic fur seals depredating Macaroni Penguins (2.44 kills/h; Bonner and Hunter 1982). These estimates are likely to be biased high because timing of observations was not randomized or systematic in either study and occurred primarily in the afternoon and evening when penguins typically return to land (Raya Rey et al. 2007; Chapter 4) and overlapping with our observed peak in kills 17:00–21:00 (K.W.M. unpub. data). Despite our relatively low kill rate, the effect of sea lion predation on the penguin population we estimated as mortality of 6% of breeders per year is the same or larger than estimates of the proportion of Adélie Penguin breeding populations killed by leopard seals (*Hydrurga leptonyx*; Ainley et al. 2005 and references therein).

Population model

We estimated the Penguin Bay population growth rate (λ) to be 0.905 from 2010 to 2013. The corresponding rate of decline of 0.095% per year is 2.9 times faster than the 1984–2012 estimate by Morrison et al. (Table 5.6, Chapter 2) of 0.033% per year ($\lambda = 0.967$). A faster recent rate of decline may indicate that demographic rates were lower in recent years than they had been previously, which would forecast a sharp drop in the breeding population size in the next few years as the recently low reproductive success rate leads to a lagged effect in the recruitment rate dropping further below that required to replace dying breeders. Demographic rates in Penguin Bay were slightly higher in 1985 and 1986, when the annual adult return rate

was 87.2% and reproductive success was 47.4 and 50.5%, respectively (Marchant and Higgins 1990). Alternatively, changing demographic rates will result in an unstable age structure, contradicting the stable-rates assumption of the Leslie matrix method and producing a population growth rate that differs from that observed.

The low adult survival rate in Penguin Bay appears to be the most important contributor to the population's decline. Theoretically, adult survival rate is also the most influential parameter affecting the population growth rate of long-lived species (Sæther and Bakke 2000). We have illustrated how a small decrease in adult survival requires an increase of reproductive success of larger magnitude to maintain a stable population. The reproductive success rates of Southern Rockhopper Penguins in the Falkland Islands, averaging 0.74 over 15 years and ranging from 0.49 to 0.95 (Baylis et al. 2013) are exceptionally high for *Eudyptes* penguins, but even a 0.74 chicks/nest reproductive success rate is too low to balance the low 0.834 adult survival rate we measured in Penguin Bay (Figure 5.5). In contrast, the average reproductive success in Penguin Bay of 0.39 chicks/nest is sufficient for population stability with a biologically plausible adult (and first-year) survival rate of 0.89. Demographic rates in Penguin Bay were similar to those for a rapidly declining population of Northern Rockhopper Penguins (*E. moseleyi*) at Amsterdam Island: reproductive success (0.38 chicks/nest), first-year survival (0.39), adult survival (0.84; Guinard et al. 1998). Anomalously cold sea-surface temperatures lowering prey availability and predation from a greatly expanded population of sub-Antarctic fur seals (*A. tropicalis*) were implicated in the decline (Guinard et al. 1998).

'Predation-free' population growth rate

At the average first-year survival rate we measured (0.505) we estimated that 'predation-free' reproductive success and adult survival rates would result in a population growth rate of $\lambda = 0.983$, compared to $\lambda = 0.905$ with predation effects. Therefore, predation is sufficient to be the primary driver of the localized population decline in Penguin Bay, even without accounting for the effect of predation on first-year survival rates. A stable population ($\lambda = 1.0$) would require an average first-year survival rate of 0.65, equivalent to that we measured from 2010 to 2011. A 'predation-free' first-year survival rate is likely to be ≥ 0.65 because sea lions and Giant Petrels killed an unknown proportion of first-year penguins and predation danger may cause emigration (reduced natal and/or breeding site fidelity) away from Penguin Bay, lowering our estimate of first-year survival.

Our estimate of the first-year survival rate assumes all first-year penguins hatched in Penguin Bay returned to moult in Penguin Bay. Natal site fidelity of first-year *Eudyptes* penguins has not been studied in detail. The detection probability of PIT-tagged first-year Southern Rockhopper Penguins was lower than in subsequent years (Dehnhard et al. 2014), and only 10% of surviving Macaroni Penguins were detected at their natal colony in their first year (Horswill et al. 2014). This suggests that first-year birds less frequently enter their natal colony than do older birds, but does not invalidate our assumption that most first-year birds moult nearby.

As most penguin populations around the world decline because of climate change and other anthropogenic effects (Trathan et al. 2014), the importance of predation on penguin populations of reduced size is likely to grow. Our study demonstrates that predation rates can be an additive source of mortality beyond the bottom-up control of food availability and sufficient to drive the decline of a small penguin population. We encourage further research on the importance of predation in driving the population growth rate of penguins at this and other sites.

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Appendix 5.1 Recapture matrix for adult male Eastern Rockhopper Penguins Oct 2010 to Oct 2013. 'Tagged at t ' is the number of individuals added to the marked population at occasion t , 'Released at t ' is the number of individuals in each release cohort, i.e., tagged at t plus the total number of individuals first recaptured (reencountered through PIT tag reading) at the previous occasion, and 'First recapture occasion' is the number of individuals of each release cohort first recaptured at each subsequent occasion.

Occasion t	Tagged at t	Released at t	First recapture occasion						Total recaptured
			Oct 2011	Jan 2012	Oct 2012	Jan 2013	Apr 2013	Oct 2013	
Oct 2010	165	165	131	3	0	0	0	0	134
Oct 2011	35	166		155	8	0	0	0	163
Jan 2012	0	158			135	1	0	0	136
Oct 2012	45	188				158	2	14	174
Jan 2013	0	159					21	94	115
Apr 2013	0	23						19	19
Total	245	859	131	158	143	159	23	127	741

Appendix 5.2 Recapture matrix for adult female Eastern Rockhopper Penguins Oct 2010 to Oct 2013. Table headings are defined in Appendix 5.1.

Occasion <i>t</i>	Tagged at <i>t</i>	Released at <i>t</i>	First recapture occasion						Total recaptured
			Oct 2011	Jan 2012	Oct 2012	Jan 2013	Apr 2013	Oct 2013	
Oct 2010	157	157	128	2	0	0	0	0	130
Oct 2011	37	165		158	0	0	0	0	158
Jan 2012	0	160			138	0	0	0	138
Oct 2012	44	182				160	1	7	168
Jan 2013	0	160					21	81	102
Apr 2013	0	22						20	20
Total	238	846	128	160	138	160	22	108	716

Chapter 6

A CARRY-OVER EFFECT OF MIGRATION DOES NOT UNDERLIE WITHIN-INDIVIDUAL VARIATION IN EXTREME EGG-SIZE DIMORPHISM IN EASTERN ROCKHOPPER PENGUINS



Figure 6.0 Top: Eastern Rockhopper Penguin incubating smaller A-egg in anterior position, larger B-egg in posterior position. Rob Dunn removing a penguin egg for measurement from a cavity nest in the East sub-colony. Photos by Kyle Morrison.

ABSTRACT

Penguins of the genus *Eudyptes* are unique among birds in that their first-laid A-egg is 54-85% the mass of their second-laid B-egg. Although the degree of intra-clutch egg-size dimorphism varies greatly among the seven species of the genus, obligate brood reduction is typical of each, with most fledged chicks resulting from the larger B-egg. Many authors have speculated upon why *Eudyptes* penguins have evolved and maintained a highly dimorphic 2-egg clutch, and why it is the first-laid egg that is so much smaller than the second, but only recently has a testable, proximate mechanism been proposed. In Macaroni Penguins (*E. chrysolophus*), females that apparently had greater overlap between egg-formation and migration lay more dimorphic eggs, suggesting a physiological conflict may constrain growth of the earlier-initiated A-egg. This migratory carry-over effect hypothesis (MCEH) has yet to be examined in any other species or in more than one year. I tested the MCEH in Eastern Rockhopper Penguins (*E. chrysocome filholi*) on Campbell Island, New Zealand, by recording the arrival and laying dates, body sizes, and egg masses of transponder-tagged females over two years. Females that presumably had less migration/egg-formation overlap laid less dimorphic clutches, as predicted by the MCEH. However, repeated measures of individual females revealed that changes in egg-size dimorphism between years were unrelated to changes in overlap. Egg masses, and to a lesser extent egg-size dimorphism, were highly repeatable traits related to body size and mass. These results and a detailed consideration of the MCEH suggest that egg-size dimorphism in *Eudyptes* penguins is unlikely to be caused by a migratory carry-over effect.

INTRODUCTION

A key component of avian investment in reproduction is the resources females allocate to egg production. Larger eggs and clutches may be produced by higher quality females or those in better body condition, and result in greater reproductive fitness (Williams 1994; Hipfner and Gaston 1999). Eggs laid at an early date may also have higher fitness, such as when high quality or more experienced females breed earlier, or food availability declines during the breeding season (Verhulst and Nilsson 2008). The allocation of investment within a clutch is also an important means of facilitating brood reduction in order to match brood size to available resources (Slagsvold et al. 1984; Lamey 1990). Despite their important fitness consequences, females may be constrained from optimal egg investment and timing of breeding by effects that carry-over between stages or because of their evolutionary history. For example, pre-breeding diet quality may carry-over to influence resources available for egg production

(Sorensen et al. 2009). Furthermore, the variation in a trait expressed by individuals may be limited by their genotype and phenotypic plasticity (Nussey et al. 2007; Reed et al. 2009).

There is no more anomalous pattern of investment in egg production than that which occurs within the seven species of *Eudyptes* penguins, which lay two eggs more different in size than in any other bird species (Slagsvold et al. 1984). In other species with less dimorphic eggs, egg size, hatching, and fledging success typically decrease with laying order. In *Eudyptes* penguins it is the first-laid “A-egg” that is much smaller, hatches later, and is far less successful than the second-laid “B-egg”, although both eggs are equally viable when reared independently (Williams 1990). Additionally, the degree of egg-size dimorphism (ESD) varies greatly between species of *Eudyptes* penguins, with species’ mean A-egg masses being 54–85% those of B-eggs (St. Clair 1992; Davis 2013). Within each species, inter-individual variation in ESD varies over a similarly wide range (St. Clair 1993; Crossin et al. 2010; Crossin et al. 2012). The key questions are 1) Why is it the first-laid A-egg that is smaller? 2) What causes the inter- and intra-species variation in ESD? 3) Why is this pattern of investment unique to *Eudyptes* penguins? 4) Why do *Eudyptes* penguins lay two eggs but typically only raise one chick?

Researchers have had a long-standing interest in the evolution and maintenance of this bizarre reproductive pattern (Lack 1968; Johnson et al. 1987; Lamey 1990). More recent hypotheses have continued the historic focus on ultimate causation (St. Clair 1998; Davis and Renner 2003). Crossin et al. (2010) used a novel approach by examining the proximate cause of ESD in Macaroni Penguins (*Eudyptes chrysolophus*), which have among the most dimorphic eggs in the genus. In Fiordland Penguins (*E. pachyrhynchus*), the Eudypid that lays the least dimorphic eggs and the only species for which egg formation times have been studied, A- and B-egg rapid yolk growth takes c. 16 days, followed by a c. 7 day ‘lag’ period before laying during which albumen, membranes, and shell are formed and deposited, for a total egg formation period of c. 23 days (Grau 1982, Grau 1984). Rapid yolk growth of A-eggs is initiated c. 4 days before that of B-eggs, corresponding to the subsequent c. 4 day laying interval between eggs. *Eudyptes* penguins over-winter at sea. After arriving from their return migration breeders fast at their nest sites until after laying (the pre-laying interval). In six of the seven species of *Eudyptes* (excluding Fiordland Penguin, Grau 1982), females’ pre-laying interval is sufficiently short (< 23 d) to infer that rapid yolk growth begins during migration, setting up the potential for a physiological conflict between migration and reproductive development that could affect final egg sizes. Rapid yolk growth occurs through uptake of the yolk precursors vitellogenin (VTG) and yolk-targeted very-low-density lipoprotein (VLDL_y) from blood plasma, which form the primary sources of yolk protein and lipid, respectively (Williams 2012). Under

the migratory carry-over effect hypothesis (MCEH) of Crossin et al. (2010), production of yolk precursors is constrained by return migration, contributing to ESD by causing a slower rate of yolk growth for A-eggs compared to later-developing B-eggs. A critical assumption of the MCEH is that there is no-interindividual variation in yolk and albumen formation periods among *Eudyptes* penguins, and that the mean durations reported by Grau (1982) for Fiordland Penguins are representative of the entire genus. Crossin et al. (2010) found that female Macaroni Penguins with a longer pre-laying interval ashore before laying their A-egg (and therefore presumably reduced migration/yolk formation overlap) had higher VTG levels at colony arrival and laid less dimorphic clutches. The authors concluded that the MCEH was strongly supported and was likely to explain the occurrence of extreme ESD across the genus (Crossin et al. 2010; Crossin et al. 2012). The MCEH was invoked in a subsequent phylogenetic comparative analysis of ESD in *Eudyptes* that concluded their dimorphic two-egg clutch became a canalized trait c. 7 million years ago, before the diversification of the extant species, and is maladaptive given their slow life-history strategy (Stein and Williams 2013).

I extended analysis of the MCEH by evaluating it in a second species, the Eastern Rockhopper Penguin (*E. chrysocome filholi*), which lays eggs of intermediate ESD relative to other *Eudyptes*. Additionally, I considered effects on variation in ESD both between and within individuals by using repeated measures of individual females in two years. Unlike Crossin et al. (2010), I also considered effects of the structural size of females and their raw body mass at arrival. I predicted that larger and heavier females would lay larger eggs and less dimorphic clutches, as occurs in some other bird species (Slagsvold et al. 1984; Christians 2002).

Specifically, I:

1. Tested whether egg size and dimorphism were affected by females' laying date, arrival mass, pre-laying interval and body size (bill depth and flipper length).
2. Determined the individual repeatability between years in breeding chronology, egg masses, and ESD.
3. Tested whether variation between years in pre-laying interval was related to ESD within females.

MATERIALS AND METHODS

Data collection

The breeding chronology and egg masses of female Eastern Rockhopper Penguins were measured in study plots in the East and West sub-colonies of Penguin Bay, Campbell Island, New Zealand (52° 32' 12" S, 169° 2' 10" E) in October and November of 2011 and 2012. Data included 50 females in 2011, and 62 in 2012 (total n = 112). Repeated measures were obtained from 34 individuals, and data from only one year from 44 females. All study females were individually marked with an 11 mm-long subcutaneous passive integrated transponder (PIT tag: Allflex Australia Pty.) one or two years prior to their inclusion in the study. Female arrival dates were recorded using an automated gateway on the penguin's travel pathway into the study sub-colonies that logged PIT tag code, date, and time (gateway developed by Stu Cockburn, Department of Conservation, Wellington). Female identity at their nest site was confirmed using an RS320 stick reader (Allflex Australia Pty.). In 2012 female arrival body mass was measured with a 5 kg spring scale (± 50 g), bill depth with calipers (± 0.05 mm), and flipper length with a ruler (± 1 mm) within one day of their logged arrival date. Bill depth and flipper length of 2011 females were taken from measurements when they were tagged in 2010. The date of first recording at a nest site was not always a reliable indicator of arrival date, as some females occupied a nest within the study plots two or more days after their colony arrival was logged by the automated gateway. Evidently, assuming that first nest occupancy equates to colony arrival may bias chronological and arrival body mass data. For this reason only females whose arrival date was logged by the gateway and (in 2012) whose body mass was measured within one day of their logged arrival date were included in the study. Otherwise all females breeding in the study plots for which both A- and B-egg masses were measured on their lay dates were included.

Lay dates were determined by checking nest contents daily from arrival until females completed their two-egg clutch. The duration of the pre-laying interval was the time between a female's arrival date and its A-egg lay date. The masses of first-laid A-eggs and second-laid B-eggs were measured using a digital scale (± 0.1 g).

Data analysis

A:B egg mass ratio (intra-clutch egg-size dimorphism, ESD) was calculated as A-egg mass / B-egg mass, so that less dimorphic clutches have a higher A:B egg mass ratio. Clutch mass equals A-egg mass + B-egg mass. Means are presented \pm SD unless otherwise noted. Arrival and lay dates were standardized between years by analysing dates in days from the first such date in each year.

An information-theoretic approach to model selection was used to evaluate factors that influenced egg masses and ESD. Separate analyses were used to consider whether A-egg lay date, pre-laying interval, bill depth, or flipper length had additive effects on A- and B-egg masses using the same all-subsets model structure, plus a null model (16 models). The ESD analysis was the same, except for including clutch mass (32 models). A-egg, B-egg, and clutch masses were strongly positively correlated (A- and B-egg mass: $R^2 = 0.50$, $F_{1,110} = 108.073$, $p < 0.001$, A-egg and clutch mass: $R^2 = 0.83$, $F_{1,110} = 520.293$, $p < 0.001$, B-egg and clutch mass: $R^2 = 0.88$, $F_{1,110} = 781.896$, $p < 0.001$), and A- and B-egg mass are confounded with ESD, so of these potential factors only clutch mass was included in the ESD analysis. As a test of the MCEH the primary interest was in the effect of pre-laying interval, but because pre-laying interval = A-egg lay date – arrival date both lay date and arrival date could not be included as additional factors. A-egg lay date was included because it was expected to more closely reflect a female's body condition and investment in reproduction than arrival date (Williams and Croxall 1991). A random effect of female identity (PIT-tag code) was included in all models because a global model including this effect was better supported than a model without in all three analyses. Analyses were conducted using linear mixed-effect models with the arm package in R Studio (Gelman et al. 2012; R Core Team 2012). Measures of the variance explained by fixed factors were calculated as marginal R^2 values (R^2_m), and by both the fixed factors and the random factor of female identity as conditional R^2 values (R^2_c), after Nakagawa and Schielzeth (2013) using the MuMIn package in R Studio (Barton 2014). AIC_c , Δ_i , and w_i values were calculated manually, after Burnham and Anderson (2002). A *post-hoc* information theoretic analysis was conducted using linear models to evaluate whether the addition of female arrival body mass explained additional variance in A:B mass ratio in 2012.

The individual repeatability of all measures of breeding chronology and egg size was assessed by calculating their intra-class correlation coefficients (R) using the method and rptR package (in R Studio) of Nakagawa and Schielzeth (2010). As noted by Nakagawa and Schielzeth (2013), R and R^2 values are closely linked.

RESULTS

Females whose egg masses were measured arrived to breed 18–25 Oct in 2011 and 16– 22 Oct in 2012. A-eggs were laid 2–9 Nov, 12–19 d after arrival in 2011, and 31 Oct to 8 Nov, 13–21 d after arrival in 2012. The breeding chronology of the study females is a good representation of a larger sample reported in Chapter 3. Mean female arrival and laying dates of study females

were slightly later in 2011 than 2012 (arrivals 21 Oct \pm 1.7 d in 2011 and 18 Oct \pm 1.4 d in 2012; laying 5 Nov \pm 1.8 d in 2011 and 3 Nov \pm 1.9 d in 2012). Mean pre-laying interval duration was longer in 2011 (16.2 \pm 1.8 d) than in 2012 (15.3 \pm 1.5 d). Females that arrived later laid later ($r^2 = 0.267$, $F_{1,110} = 39.984$, $p < 0.001$), and had a shorter pre-laying interval ($r^2 = 0.125$, $F_{1,110} = 15.696$, $p < 0.001$). Longer pre-laying intervals were associated with later lay dates ($r^2 = 0.383$, $F_{1,110} = 68.216$, $p < 0.001$). The interval between A- and B-egg lay dates was nearly identical in 2011 (4.4 \pm 0.6 d) and 2012 (4.5 \pm 0.6 d). Overall, A-egg mass (83.2 \pm 7.6 g) was 28% smaller than B-egg mass (115.3 \pm 9.1 g), equivalent to mean ESD of 0.72 \pm 0.05. However, the degree of ESD varied greatly between clutches, from A-eggs being close to half the mass of B-eggs (0.58) to nearly the same mass (0.93).

A-egg mass

Females with deeper bills, longer pre-laying intervals, and later lay dates laid heavier A-eggs (Table 6.1). The parameters bill depth and pre-laying interval were most strongly correlated with A-egg mass (Figure 6.1, Figure 6.2), whereas lay date was less important. Flipper length had a negligible relationship with A-egg mass, as its standard error was larger than its parameter estimate (Table 6.2). Fixed factors in the top-ranked model explained only a small proportion of the variance in A-egg mass ($R^2_m = 0.12$, Table 6.1). Individual females laid A-eggs of similar mass between years (ID-only model $R^2_c = 0.73$, Table 6.1; $R = 0.729 \pm 0.073$, Table 6.3). A post-hoc linear regression analysis revealed that arrival date was unrelated to A-egg mass.

Table 6.1 Support for linear mixed-effect models predicting mass of A-eggs of Eastern Rockhopper Penguins.

Model	deviance	K	Δ_i	w_i	R^2_m	R^2_c
PreLay+BillDepth+ID ^a	736.73	4	0.00	0.30	0.12	0.71
ALayDate+PreLay+BillDepth+ID	735.28	5	0.43	0.24	0.13	0.72
ALayDate+BillDepth+ID	737.52	4	0.65	0.22	0.12	0.72
PreLay+BillDepth+Flipper+ID	736.19	5	3.40	0.06	0.12	0.72
ALayDate+PreLay+BillDepth+Flipper+ID	734.46	6	3.61	0.05	0.14	0.72
ALayDate+BillDepth+Flipper+ID	736.64	5	3.70	0.05	0.13	0.73
BillDepth+ID	743.29	3	4.11	0.04	0.07	0.73
PreLay+ID	744.13	3	6.65	0.01	0.04	0.72
ID	750.13	2	10.39	0.00	NA	0.73

^aTop model; $AIC_c = 744.35$. Parameters include the random effect of individual identity (ID), and fixed effects of A-egg lay date (ALayDate), duration of the pre-laying interval (PreLay), bill depth (BillDepth), flipper length (Flipper), and clutch mass (ClutchMass). Results include the model deviance, number of parameters in the model (K), Akaike's information criterion adjusted for small sample size (AIC_c), Δ_i is the difference in AIC_c value from that of the top model (i.e., lowest AIC_c), and w_i is the Akaike weight, R^2_m is the marginal R^2 (variance explained by the fixed factors), R^2_c is the conditional R^2 (variance explained by the random and fixed factors); n = 112 eggs. Models are presented from lowest to highest Δ_i . Except for the null model (ID only), only models with $\Delta_i < 7.0$ are shown.

Table 6.2 Parameter estimates and standard errors (SE) from the top-ranked and global linear mixed-effects models predicting A- and B-egg masses and A:B egg mass ratio of Eastern Rockhopper Penguins.

Parameter	<u>A-egg mass</u>			<u>B-egg mass</u>			<u>A:B egg mass ratio</u>					
	<u>Top model</u>	<u>Global model</u>	<u>Top model</u>	<u>Global model</u>	<u>Top model</u>	<u>Global model</u>	<u>Top model</u>	<u>Global model</u>				
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE				
Intercept	25.566	16.611	6.150	28.410	57.900	19.026	14.575	34.563	0.536	0.041	0.652	0.170
ALayDate			0.619	0.480			0.060	0.543			0.002	0.003
PreLay	0.969	0.377	0.655	0.454			-0.245	0.472	0.012	0.003	0.010	0.003
BillDepth	2.389	0.870	2.225	0.905	3.242	1.065	2.755	1.100			0.000	0.006
Flipper			0.149	0.168			0.342	0.205			-0.001	0.001
ClutchMass											0.001	0.000

Parameters are defined in Table 6.1.

Table 6.3 Repeatability in egg size and breeding chronology of Eastern Rockhopper Penguins between 2011 and 2012; $n = 112$. R is the intra-class correlation coefficient. Mean parameter values are for 34 females with repeated measures, and include masses (g), dates in days from the first such date in each year, and pre-laying interval in days.

Parameter	R	SE	-95% CI	+95% CI	2011 mean	2011 SE	2012 mean	2012 SE
A-egg mass	0.729	0.073	0.565	0.850	81.8	41.9	82.9	42.1
B-egg mass	0.829	0.049	0.717	0.907	114.1	48.5	114.3	54.3
Clutch mass	0.860	0.040	0.767	0.923	195.9	83.4	197.2	83.0
A:B egg mass	0.385	0.144	0.050	0.621	0.72	0.26	0.73	0.38
Arrival date	0.455	0.132	0.168	0.680	4.4	9.9	3.4	9.1
A-egg lay date	0.861	0.039	0.765	0.918	4.6	10.6	4.7	10.2
Pre-laying interval	0.464	0.132	0.176	0.693	15.2	9.4	16.3	10.7

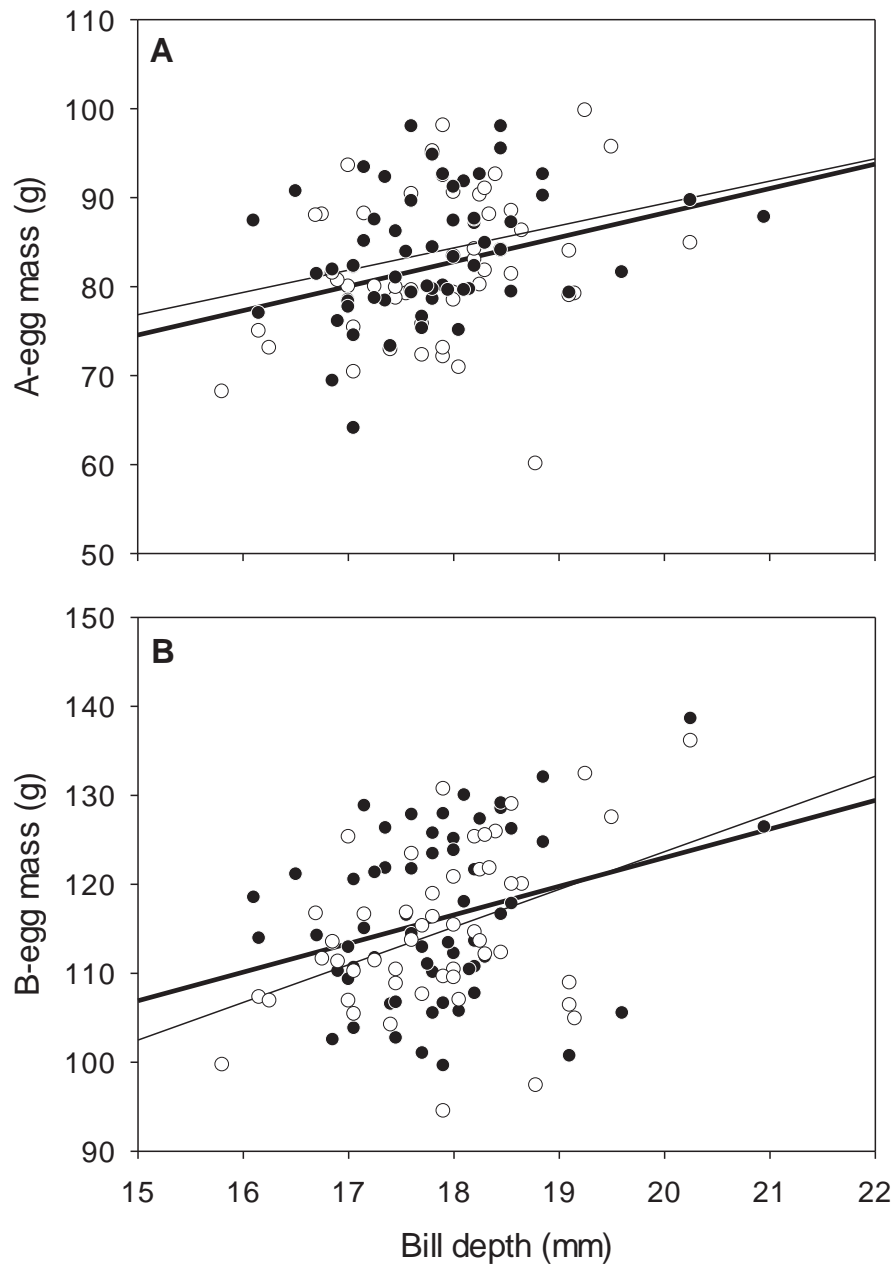


Figure 6.1 A-egg mass (A) and B-egg mass (B) in relation to bill depth in 2011 (filled circles and thin regression lines, $n = 50$) and 2012 (hollow circles and thick regression lines, $n = 62$, including $n = 34$ repeated measures). Deeper-billed females laid heavier A-eggs in both years (2011: $R^2 = 0.084$, $F_{1,48} = 4.38$, $p = 0.042$, 2012: $R^2 = 0.094$, $F_{1,60} = 6.22$, $p = 0.032$) and heavier B-eggs in both years (2011: $R^2 = 0.173$, $F_{1,48} = 10.02$, $p = 0.003$, 2012: $R^2 = 0.090$, $F_{1,60} = 5.94$, $p = 0.018$).

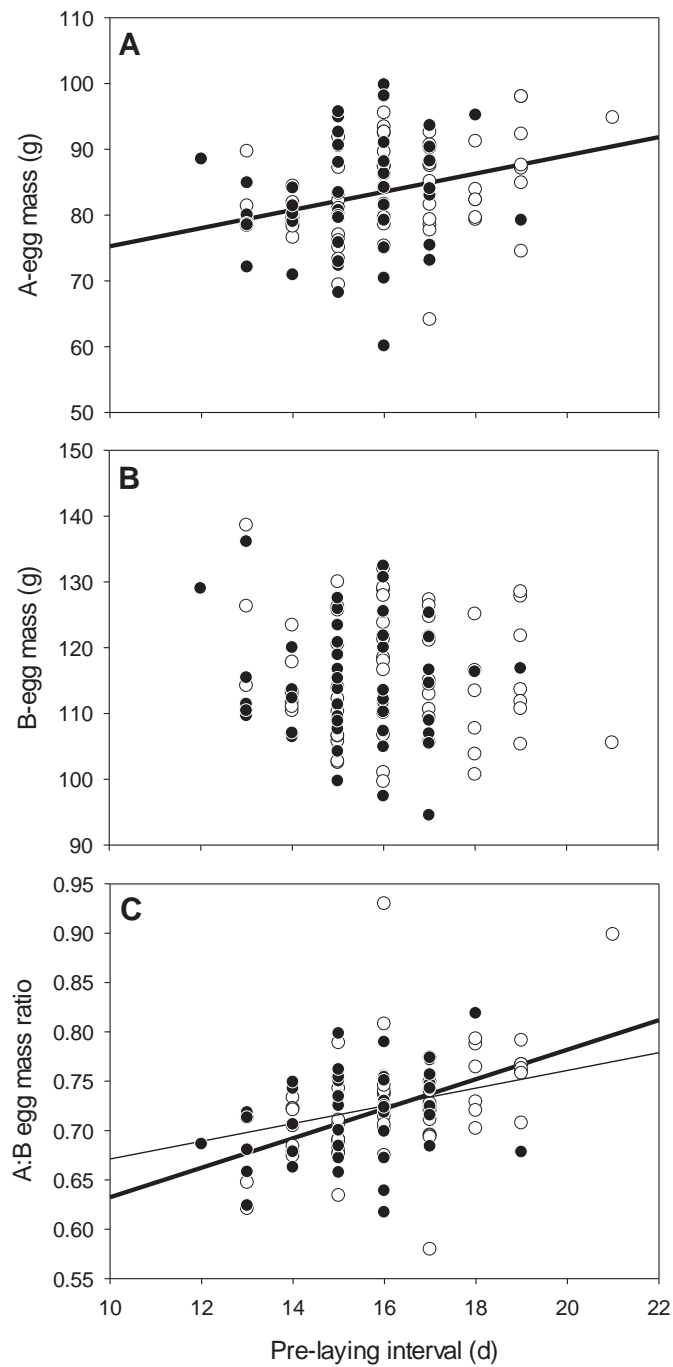


Figure 6.2. A-egg mass (A), B-egg mass (B), and A:B egg mass ratio (C) in relation to the duration of the pre-laying interval in 2011 (filled circles and thin regression lines, $n = 50$) and 2012 (hollow circles and thick regression lines, $n = 62$, including $n = 34$ repeated measures). Females that spent more time ashore before laying laid heavier A-eggs in 2012, but not in 2011 (2011: $R^2 = 0.012$, $F_{1,48} = 0.935$, $p = 0.338$, 2012: $R^2 = 0.123$, $F_{1,60} = 8.383$, $p = 0.005$). Additionally, females with longer pre-laying intervals laid B-eggs of similar mass, and less dimorphic clutches in both years (2011: $R^2 = 0.092$, $F_{1,48} = 4.833$, $p = 0.033$, 2012: $R^2 = 0.237$, $F_{1,60} = 18.585$, $p < 0.001$).

B-egg mass

Females with deeper bills and longer flippers laid heavier B-eggs. Bill depth was factor most strongly correlated with B-egg mass (Table 6.4), as found for A-egg mass (Figure 6.1). In contrast to relationships with A-egg mass, flipper length was positively related to B-egg mass, whereas pre-laying interval and lay date were unimportant (Table 6.2). Fixed factors explained B-egg mass poorly ($R^2_m = 0.09$, Table 6.4). Individual females laid B-eggs of similar mass between years, with an even higher repeatability than for A-eggs (ID-only model $R^2_c = 0.83$, Table 6.4; $R = 0.829 \pm 0.049$, Table 6.3). As found for A-egg mass, there was no relationship between arrival date and B-egg mass.

Table 6.4 Support for linear mixed-effect models predicting mass of B-eggs of Eastern Rockhopper Penguins.

Model	deviance	K	Δ_j	w_j	R^2_m	R^2_c
BillDepth+ID ^a	765.33	3	0.00	0.28	0.09	0.83
BillDepth+Flipper+ID	762.39	4	0.64	0.20	0.13	0.83
ALayDate+BillDepth+ID	765.15	4	1.68	0.12	0.09	0.83
PreLay+BillDepth+ID	764.94	4	1.76	0.12	0.10	0.83
ALayDate+BillDepth+Flipper+ID	762.36	5	2.50	0.08	0.13	0.83
PreLay+BillDepth+Flipper+ID	762.08	5	2.53	0.08	0.13	0.83
ALayDate+PreLay+BillDepth+ID	764.92	5	3.33	0.05	0.10	0.83
ALayDate+PreLay+BillDepth+Flipper+ID	762.06	6	4.14	0.04	0.13	0.83
Flipper+ID	768.66	3	6.61	0.01	0.07	0.83
ID	774.27	2	8.68	0.00	NA	0.83

^aTop model; AIC_c = 769.83. Parameters are defined in Table 6.1.

Egg-size dimorphism

Females with a longer pre-laying interval laid less dimorphic eggs (Figure 6.2). Only pre-laying interval affected ESD (Table 6.5). Pre-laying interval explained a modest proportion of the variance in ESD ($R^2_m = 0.16$, Table 6.5). Relative to A- and B-eggs masses, ESD was less repeatable (ID-only model $R^2_c = 0.39$, Table 6.5; $R = 0.385 \pm 0.144$, Table 6.3).

Table 6.5 Support for linear mixed-effect models predicting A:B egg mass ratio of Eastern Rockhopper Penguins.

Model	deviance	K	Δ_i	w_i	R^2_m	R^2_c
Prelay+ID ^a	-380.84	3	0.00	0.94	0.16	0.41
ID	-362.01	2	6.41	0.04	NA	0.39

^aTop model; $AIC_c = -353.60$. Parameters are defined in Table 6.1.

In contrast to a second prediction derived from the MCEH, females that extended their pre-laying interval from one year to the next did not lay a less dimorphic clutch in the second year ($r^2 = 0.012$, $F_{1,32} = 0.372$, $p = 0.546$, Figure 6.3). These variables were unrelated despite individual changes in pre-laying interval and ESD of 46% and 50% of the observed ranges of each variable in 2012, respectively. Females that laid a larger A-egg from one year to the next did not lay a smaller B-egg, or vice versa ($r^2 = 0.019$, $F_{1,32} = 0.435$, $p = 0.624$).

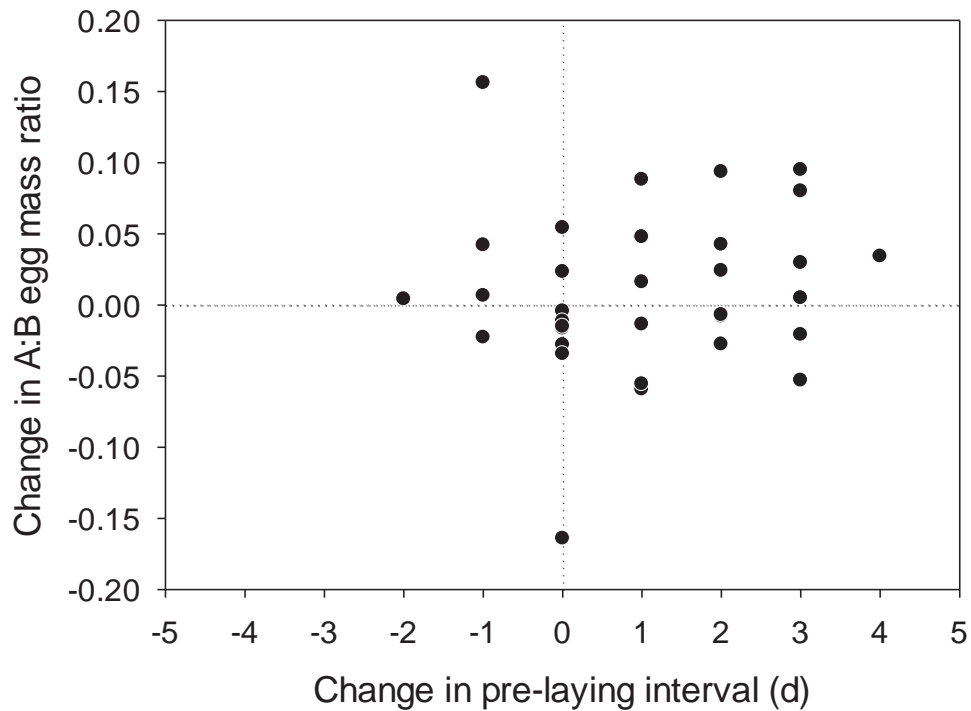


Figure 6.3 Change in A:B egg mass ratio in relation to change in the duration of the pre-laying interval from the same females between 2011 and 2012 ($n = 34$). Changes in time ashore before laying were unrelated to changes in egg-size dimorphism ($R^2 = 0.013$, $F_{1,34} = 0.443$, $p = 0.510$).

In 2012, females that arrived at a heavier mass laid a more dimorphic clutch. The best-supported model including arrival body mass explained more variance in ESD in 2012 ($R^2 = 0.29$), relative to the second-ranked model including only pre-laying interval ($R^2 = 0.24$, Table 6.6). Arrival mass was associated with more dimorphic clutches because heavier females did not lay heavier A-eggs ($r^2 = 0.047$, $F_{1,60} = 2.989$, $p = 0.089$), but did lay heavier B-eggs ($r^2 = 0.224$, $F_{1,60} = 17.279$, $p < 0.001$). Heavier females also had deeper bills ($r^2 = 0.106$, $F_{1,60} = 7.112$, $p = 0.010$) and longer flippers ($r^2 = 0.336$, $F_{1,60} = 30.319$, $p < 0.001$). Arrival mass was unrelated to arrival date, laying date, or pre-laying interval in 2012.

Table 6.6 Support for linear models predicting A:B egg mass ratio of Eastern Rockhopper Penguins in 2012.

Model	deviance	K	Δ_i	w_i	R^2
Prelay+BirdMass	0.13	4	0.00	0.74	0.29
Prelay	0.14	3	2.05	0.26	0.24
BirdMass	0.17	3	14.97	0.00	0.07
Null	0.18	1	16.87	0.00	NA

^aTop model; $AIC_c = -197.65$. Parameters include duration of the pre-laying interval (Prelay) and female body mass at arrival (BirdMass); $n = 62$. Results defined in Table 6.1, except that R^2 is the variance explained by the model.

DISCUSSION

Female Eastern Rockhopper Penguins with deeper bills and longer flippers laid heavier eggs, but not more dimorphic clutches. Egg masses and lay date were highly repeatable individual traits. As predicted by the migration carry-over effect hypothesis (MCEH), females with a longer pre-laying interval (i.e., those having less migration/egg-formation overlap) laid less dimorphic eggs. However, intra-individual variation in egg-size dimorphism (ESD) between years did not support the MCEH. A review of the assumptions and predictions of the MCEH reveal that it requires further refinement and testing.

Correlates of egg masses

Female body size was most strongly correlated with egg masses. Females with deeper bills laid heavier A-eggs and B-eggs, and longer-flipped females laid heavier B-eggs. Females with deeper bills may lay heavier eggs because of an allometric relationship between egg size and body size in birds, evident between species of *Eudyptes* in B-eggs, but not A-eggs (Stein and Williams 2013), and within some other bird species (Christians 2002). Alternatively, larger females may be of higher quality (Mínguez et al. 2001) or mate assortatively by size (Forero et al. 2001) and produce larger eggs when mated with a heavier mate (Poisbleau et al. 2013a). In female Macaroni Penguins, flipper length was strongly correlated with arrival body mass, and heavier females laid heavier B-eggs, but not A-eggs (Williams and Croxall 1991). Likewise, I

found that heavier female Eastern Rockhopper Penguins had longer flippers and laid heavier B-eggs, but not A-eggs, so that heavier females laid more dimorphic clutches. This suggests that females with the resources available to do so preferentially invest in the larger, more successful B-egg. However, heavier clutches were not more dimorphic in the present study or in Macaroni Penguins (Williams 1990; Crossin et al. 2010). Instead, A-egg and B-egg masses were strongly positively correlated within a clutch. Females that laid at a later date laid heavier A-eggs, in contrast to the pattern found in Macaroni Penguins in one of two years of study (Williams and Croxall 1991). The relatively weak positive correlation between lay date and A-egg mass I found is counter to the prediction that earlier-laying females would lay larger eggs, and requires confirmation by additional study.

Correlates of egg-size dimorphism

In agreement with the main prediction of the MCEH, females with a longer pre-laying interval (less migration/egg-formation overlap) laid less dimorphic eggs, although this factor alone explained only 16% of the variation in ESD. The duration of the pre-laying interval explained a similar c. 23% of the variation in ESD in Macaroni Penguins (from data in Figure 1A, Crossin et al. 2010). No other factor considered in the present study, or by Crossin et al. (arrival date-corrected body mass or clutch mass) had a detectable effect on ESD. In Southern Rockhopper Penguins (*Eudyptes chrysocome*) at the Falkland Islands, females paired with a new mate or a heavy mate laid less dimorphic clutches (Poisbleau et al. 2013a). Such females were apparently responding to an increased probability of fledging two chicks and sought to reduce the size disadvantage of the A-chick (Poisbleau et al. 2013a). A similar response to mate quality would be maladaptive in Macaroni, Royal (*E. schlegeli*), or Erect-crested (*E. sclateri*) Penguins, which typically lose their A-egg soon after it is laid and have never been observed to fledge two chicks (St Clair et al. 1995).

Repeatability in egg masses and breeding chronology

If migration/egg-formation overlap had a causative, rather than correlative relationship with ESD, then a change in overlap should be reflected in a change in ESD, but there was no evidence of this in the current study. Furthermore, individual identity was a better predictor of ESD than was pre-laying interval, because individual females tended to lay similarly dimorphic clutches between years (repeatability of 0.39). Nevertheless, A-egg mass, and especially B-egg mass and clutch mass were even more repeatable traits. Their repeatability values ($R = 0.73$,

0.83, and 0.86, respectively) exceed the average repeatability of egg size in birds of 0.68 reported in the review by Christians (2002), although calculation methods may vary. As shown here, A-egg mass was less repeatable in Macaroni Penguins than was B-egg mass (Williams and Croxall 1991). A relative constancy in egg investment and lay dates has also been shown in Southern Rockhopper Penguins, in which indices of regional and local environmental variation had little or no influence on egg masses, clutch mass, or ESD over seven years (Dehnhard et al. 2015). The infrequent and non-repeatable occurrence of dimorphic clutches in Magellanic Penguins (*Spheniscus magellanicus*) is maladaptive and has been attributed to noise in the system (Boersma and Rebstock 2009). Likewise, noise may account for much of the intra-individual variation in ESD in *Eudyptes* penguins. Arrival dates and the duration of the pre-laying interval were similarly repeatable to ESD (both 0.46), whereas A-egg lay date was as highly repeatable as B-egg mass and clutch mass (0.86). The high individual repeatability of A-egg lay date may be attributable to migratory penguins initiating egg formation at sea in response to a photoperiod cue (Williams 1995), and an individual's sensitivity to photoperiod having a genetic component (Coppack et al. 2001; Visser et al. 2011).

Migratory carry-over effect hypothesis

The MCEH is based on the idea that there is a direct physiological conflict between migration and reproductive development that constrains production of the yolk precursor vitellogenin (VTG) at sea and therefore limits rates of yolk growth, especially for the earlier-initiated A-egg. We are accustomed to thinking of avian migration as a period of great energetic stress where birds must depart fat (and arrive thin, if at all) because of prolonged periods of flight relative to feeding. However, the opposite is true for migratory penguins. While at sea during migration *Eudyptes* penguins can feed and potentially fatten, whereas after arrival they fast while completing egg formation and partway through incubation. At arrival female *Eudyptes* penguins are heavier than at any other time in the following 4-month long breeding season, and may go on to lose 40% of their body mass over a fast of > 40 days (Williams 1995; Chapter 3). Intuitively, one would expect that forming eggs while fasting during the pre-laying interval ashore would be more physiologically challenging than forming eggs during migration, reasoning opposite to that of the MCEH.

The MCEH hypothesizes that females with a longer pre-laying interval (less migration/egg-formation overlap) are released from a migration-dependent physiological constraint earlier in their yolk formation periods, allowing them to produce higher plasma VTG

levels and increase their yolk growth rates earlier relative to yolk completion than females that lay sooner after arriving. Crossin et al. (2010) found that those females that would go on to have longer pre-laying intervals had higher VTG levels at arrival, and interpreted this as strong evidence supporting the MCEH. However, a relationship between VTG levels at *arrival* and the duration of the pre-laying interval is not a logical prediction from the MCEH. VTG levels at arrival reflect VTG levels obtained while migrating, when the MCEH proposes VTG production is constrained for all females. Females that inexplicably had high VTG levels at arrival could not have been able to produce them during migration because of their longer pre-laying interval, because all females have experienced the same brief (< 24 hr) period ashore before being sampled at arrival. A robust demonstration of a link between VTG levels, pre-laying interval, and ESD would need to show that females with the longest pre-laying intervals reached their individual maximal VTG levels sooner before laying, and laid less dimorphic clutches, than females with greater migration/egg-formation overlap. As Crossin et al. (2010) demonstrated that mean VTG levels increased between arrival and A-egg laying, individual maximal levels are presumably attained during the pre-laying interval, some days after arrival.

Female *Eudyptes* penguins lay an A-egg that is smaller than their B-egg, so the rate of egg formation and/or the duration of the egg formation period must differ between each egg. However, the MCEH does not account for the possibility of intra-clutch variation in egg formation times and assumes that the overall mean times reported by Grau (1982) in Fiordland Penguins are the same for both A- and B-eggs of Macaroni Penguins. Data from Grau (1982) demonstrated that for Fiordland penguins the average yolk formation period of A-eggs is sufficiently shorter than that of B-eggs to explain the difference in average yolk mass. For A-eggs, a 24.5 g yolk formed over 15.7 d gives a rate of yolk formation of 1.6 g/d. For B-eggs, a 28.0 g yolk formed over 17.3 d also results in a rate of yolk formation of 1.6 g/d. Therefore, the assumption of a slower yolk formation rate for A-eggs, central to the MCEH, is unsupported in the only Eudyptid in which formation times have been studied. Additionally, any intra-clutch variation in the c. 7 day lag period between yolk completion and laying is especially relevant to ESD, because albumen, membranes, and shell are formed and deposited during this time (Grau 1982; Grau 1984). Albumen accounts for 86% of the difference in the mean wet mass of egg contents between A- and B-eggs in Macaroni Penguins (from Table 1 in Crossin et al. 2010), but its deposition does not overlap with migration in Macaroni Penguins (Crossin et al. 2010) or in Eastern Rockhopper Penguins in this study (all pre-laying intervals ≥ 7 d). This suggests that the focus of the MCEH on yolk growth/migration overlap is too narrow. Clearly, the potential effect of intra-clutch variation in albumen formation times and deposition rates on ESD is

large. The assumptions of the MCEH of equal formation times between eggs, between individuals, and across the *Eudyptes* genus, requires validation.

The genus-wide trait of ESD presumably evolved only once in the ancestral Eudyptid. ESD appears to be a canalized trait exhibited independently of a migratory carry-over effect, as it is evident in the dimorphic eggs of Fiordland Penguins that do not appear to initiate egg formation prior to arrival (Grau 1982) and the dimorphic eggs of captive Eudyptids that have undergone no migration (Stein and Williams 2013). If a migratory carry-over effect was important in the evolution of ESD, then how do other penguin species with a similar degree of overlap avoid a carry-over effect and lay similar-sized eggs? As Crossin et al. (2010) demonstrated for Macaroni Penguins, female Adélie (*Pygoscelis adeliae*), Chinstrap (*P. antarctica*) and Magellanic Penguins may be migrating, on average, during the first half of their A-egg formation period (Astheimer and Grau 1985; Boersma et al. 1990; Trivelpiece and Trivelpiece 1990). In contrast to expectations from the MCEH, Adélie penguin A-eggs are heavier, on average, than B-eggs (ESD = 1.07; Astheimer and Grau 1985) and typically A- and B-eggs are of equal size in Magellanic (Boersma et al. 1990) and Chinstrap Penguins (de León et al. 2001).

The novel approach of Crossin et al. (2010) in considering the proximate, physiological cause of ESD in Macaroni Penguins represents a major innovation in methods applied to this enigmatic trait of *Eudyptes* penguins, but requires further refinement and testing: (1) the relationship between overlap and plasma VTG levels at arrival does not follow logically from the MCEH as yet described, (2) the additional factors of body size that were correlated with egg sizes and raw body mass that was related to ESD in the present study warrant further consideration, (3) alternative hypotheses for variation in ESD such as intra-clutch variation in egg formation times require investigation, and (4) further tests of the MCEH should again utilize repeated measures, while assessing changes in the relative masses of yolk and albumen may prove especially insightful.

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Chapter 7

GENERAL DISCUSSION

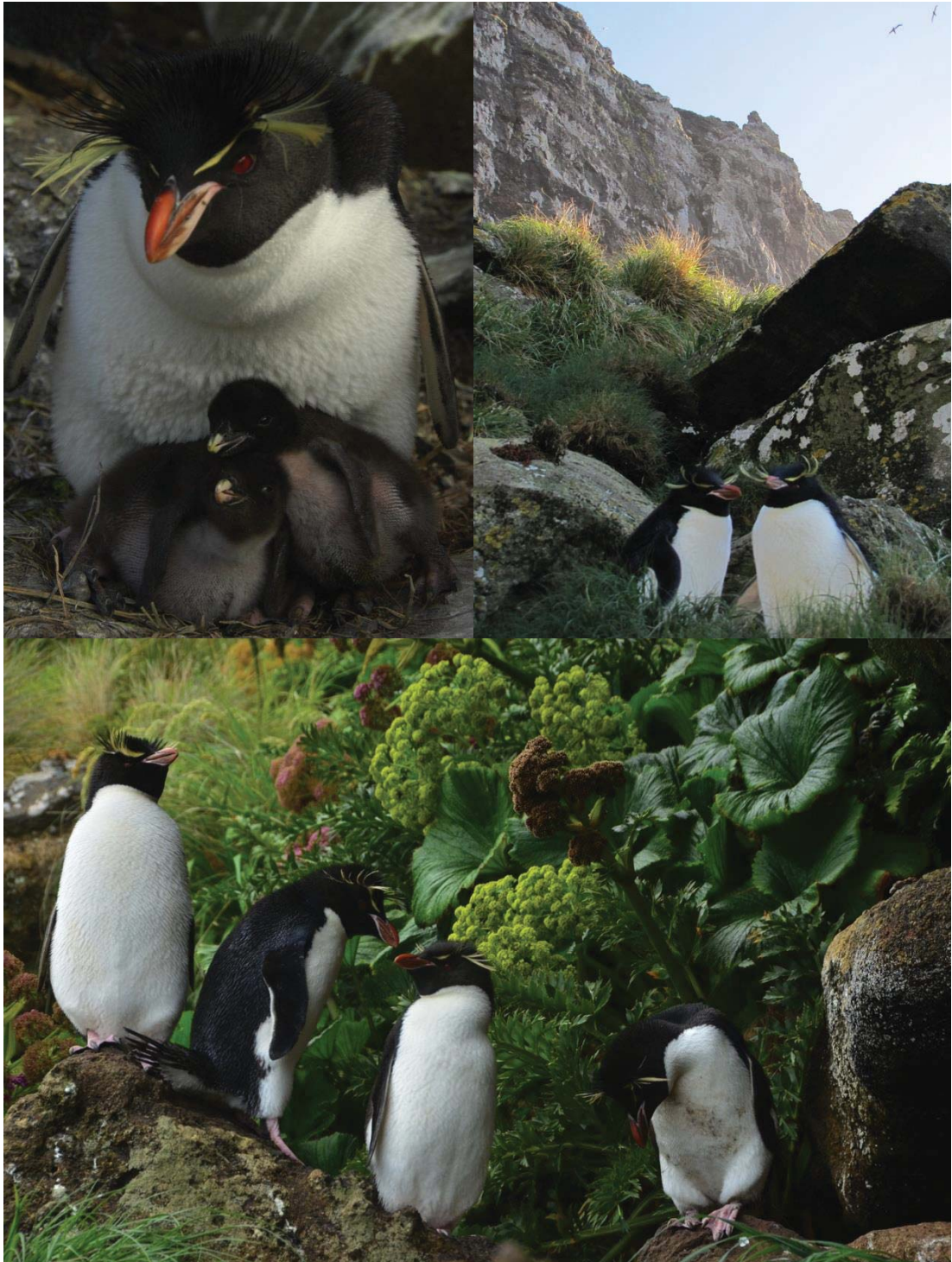


Figure 7.0 Clockwise from top-left: Eastern Rockhopper Penguin with a rare two-chick brood, newly arrived pair below Yvon's Dagger and Light-mantled Sooty Albatrosses in Penguin Bay, penguins and megaherbs in Smoothwater Bay. Photos by Kyle Morrison.

KEY FINDINGS

The aims of this thesis were to investigate what factors were affecting the population dynamics of Eastern Rockhopper Penguins on Campbell Island, including to determine the relative importance of food availability and predation on reproductive success, first-year survival, and adult survival. Fortuitously, a sharp difference in diet quality and associated nutritional stress between the two intensive years of my study allowed for a comparison of the relative importance of both top-down and bottom-up effects on demographic rates. Each of the five research chapters examined different effects on penguin population parameters. The later three chapters also considered constraints that restricted penguins' responses to the factors affecting their demographic rates.

Chapter 2 estimated the total Campbell Island Eastern Rockhopper Penguin population size to be 33,239 breeding pairs in 2012, a 21.8% decrease from an adjusted estimate of 42,528 pairs in 1984. However, the recent decline occurred before 1996 with most colonies being stable or growing thereafter. The recent decline represents just 0.7% of the 1942 population size and occurred at a much slower rate ($\lambda = 0.991$) than the 94% decline 1942–1984 ($\lambda = 0.940$). Population growth after 1996 appears related to the current global warming hiatus, lower sea surface temperatures (SSTs), and increased abundance of a key prey species. This result supported the conclusion of previous research in the 1980s, that periods of penguin population decline were associated with warm SST. In Chapter 2 differences in predation rates were suggested to be the cause of contrasting population trends between neighboring colonies, a hypothesis examined in Chapter 5.

Chapter 3 found that male penguins returned from their incubation foraging trip at a heavier mass if they had consumed a lower-trophic level diet. On average, chicks were fed a lower trophic level diet in 2011, when chicks were larger and heavier than in 2012. These results and a review of other studies relating dietary trophic level to body mass or condition contradicted the assumption typically made in retrospective studies of marine predator diet; that historic declines in predator populations are caused by shifts to lower-trophic level diets of lower quality. Instead, my results indicate that Eastern Rockhopper Penguins do better on a lower trophic level diet. A similar inference was drawn in the 1980s when the rapidly declining Campbell Island population's diet was found to be more fish-based than at other, more stable colonies.

Chapter 4 found that the canalized parental roles of Eastern Rockhopper Penguins during early chick-rearing resulted in some females, but especially males, making a long self-

feeding trip in the crèche stage, lowering the number of feeds chicks received. As expected, chicks were heavier when fed more often. On average, chicks received a lower rate of provisioning in a year of nutritional stress, in part because a higher proportion of males made a self-feeding trip, and because such trips were of longer duration in the poor year than in the good year. It appears as though the canalized division of labour strategy of *Eudyptes* penguins limits chick growth and survival to recruitment in years of nutritional stress, an important finding if such years become more frequent under climate change. *Eudyptes* penguins are likely constrained from evolving a strategy of shared brood guarding and provisioning throughout chick-rearing by the vulnerability of chicks guarded by females to loss through conspecific abuse and predation.

Chapter 5 determined that, as predicted, penguin nests in exposed, peripheral sites, in small sub-colonies were most strongly affected by skua predation, especially of eggs. More surprising was the high rate of New Zealand sea lion predation of adult penguins. Population modelling suggested that the low adult survival rate was the most important factor causing the localized decline in Penguin Bay. Analyses indicated that without skua and sea lion predation, estimated demographic rates would result in a stable penguin population, supporting the hypothesis of Chapter 2 that high predation rates were driving the continued localized decline in Penguin Bay.

Chapter 6 tested the migratory carryover effect hypothesis (MCEH), which suggests that migration/egg-formation overlap results in sub-maximal rates of yolk growth, especially for the earlier-initiated A-egg, underlying the enigmatic trait of extreme intra-clutch egg-size dimorphism in *Eudyptes* penguins. As predicted by the MCEH, female Eastern Rockhopper Penguins presumed to have less migration/egg-formation overlap laid less dimorphic clutches, but within-individual variation in egg-size dimorphism between years was unrelated to changes in overlap. Egg masses, and to a lesser extent egg-size dimorphism, were highly repeatable traits related to body size and mass. These results and further evaluation of the MCEH suggest that migration-related conflicts are unlikely to be the underlying cause of egg-size dimorphism in *Eudyptes* penguins.

BOTTOM-UP CONTROL OF POPULATION DYNAMICS

Bottom-up control of marine predator populations occurs when food availability regulates the population growth rate. In Chapter 4 I demonstrated how in a year when adults were nutritionally stressed they made longer self-feeding trips and lowered their chick-provisioning

rates. Adults buffering their own survival rate at the expense of the current year's reproductive success under poor environmental conditions is a key aspect of a slow-life history strategy, and is evident in other species of long-lived seabirds and mammals (Drent and Daan 1980; Forcada et al. 2008). I found that chicks that received fewer feeds were smaller at a given age, and because penguin chicks that fledge at lower body masses have a lower probability of survival to recruitment, the nutritional stress experienced by adults will carry through to negatively affect the population growth rate. This strategy is likely to result in population growth or stability when years of low food availability are relatively rare, but if factors such as climate change result in extended periods of poor conditions or more frequent years which vary outside of an optimal range, then repeatedly poor reproductive success and recruitment will cause population declines. This is likely the mechanism driving the overlap between periods of higher and more variable SST and declining numbers of Eastern Rockhopper Penguins on Campbell Island described in Chapter 2. Similarly, at Marion Island a warming SST trend is linked to adult Macaroni and Eastern Rockhopper Penguins arriving to breed at lower body masses and to declines in their populations (Mélise et al. 2003; Crawford et al. 2006). Presumably these adults have insufficient body reserves to endure the extended fasts required of successful breeders and provision their chicks at the required rate to support their survival to fledge and recruit. In the poor food year of 2012 I found that earlier-arriving females fed their chick at a higher rate, but females that were heavier at arrival did not. The earlier arrival of higher quality (but not necessarily heavier) females may explain that pattern. In Chapter 3 I showed that arrival body masses were similar in the good year of 2011 and poor year of 2012, so that poor conditions may have been localized to the vicinity of Campbell Island or developed after arrival in 2012. I expect that female body mass at return from their incubation foraging trip (and after their long courtship/incubation fast and major mass loss) and just prior to their commencement of chick provisioning, is likely to be a better predictor of provisioning rate than arrival body mass. I did not weigh a suitably large sample of females at their incubation return to relate their mass to their subsequent provisioning rate.

In Chapter 3 I found that penguins were heavier when consuming a lower trophic level diet, composed of more zooplankton than fish or cephalopods. This result was counter to the assumption of some studies, that the higher energy density of fish prey results in their being a higher quality diet (Hilton et al. 2006; Norris et al. 2007; Wiley et al. 2013). I assumed that penguin body masses reflected diet quality, by which I meant the net gain in energy and nutrients provided by prey. Such a holistic definition of diet quality was necessary because I did not measure the quantity or energy density of prey delivered, as some studies do (Jodice et

al. 2006; Schrimpf et al. 2012). However, it is really net energy gain that matters to a seabird, as prey of high energy density are not profitable if they are too fast or few and far between to catch. I suggest the penguins in my study, and other marine predators in the literature I cite, can achieve higher masses on a low trophic level diet because they target zooplankton when they are super abundant and efficiently captured. At times when fish are as readily caught, they are likely to be the higher quality diet, but those circumstances appear to be exceptional for most marine predators. This insight has broad relevance to the increasing number of studies of marine trophic relationships and diet which utilize stable isotopes (Hobson et al. 2004; Hobson 2011; Bond and Lavers 2014), as it emphasizes that assumptions about trophic level and diet quality require verification in the system of study. I suggested in Chapter 2 that the overall penguin population growth I found since 1996 was associated with cooler SSTs and strong year classes of southern blue whiting (*Micromesistius australis*, SBW), a fish species common in chick diets during the mid-1980s (Marchant and Higgins 1990). SBW may have been abundant enough at this time for them to represent a higher quality diet than one composed of more zooplankton. Alternatively, strong year classes of SBW are likely to represent strong production of zooplankton that both SBW and penguins feed upon (Willis et al. 2007). Detailed studies of dive efficiency and prey capture rates in relation to energy balances and the type and amount of prey captured will help to further understand the relationship between trophic-level and diet quality (Green et al. 2002; Green et al. 2005).

TOP-DOWN CONTROL OF POPULATION DYNAMICS

Logistics and access restricted my study to the penguins in Penguin Bay, the colony which declined fastest since 1984, a decline that has seemingly not slowed when others did since 1996 (Chapters 2, 5). This restriction was partly unfortunate, in that the demographic rates recorded in Penguin Bay are unlikely to reflect those elsewhere, but also fortuitous in allowing an investigation into the cause of the localized decline. I found that reproductive success, and especially adult survival rates were being depressed below those required for a stable population growth rate by Brown Skua and New Zealand sea lion predation, respectively. I found that the poor food year of 2012 resulted in the lowest rates of reproductive success and adult survival, but such bottom-up effects would occur in the growing, neighbouring colonies as well. Hence, top-down control of the Penguin Bay population growth rate requires an explanation of why predation rates were higher there than elsewhere. The results of Chapter 5 support the hypothesis put forth in Chapter 2, that colony topography increases the predator/penguin ratios in Penguin Bay and facilitates higher predation success. Both A- and B-

eggs were more likely to hatch at sheltered nests, and the few nests that raised both chicks beyond the guard stage tended to be at sheltered nests. The distribution of boulders that provide the best nest shelter is irregular in Penguin Bay, and the fragmentation of the single large colony in the main part of Penguin Bay into four sub-colonies and the subsequent extinction of one of these appears related to the distribution of sheltered nests.

The number of sea lion pups produced in Penguin Bay has grown since the mid-1980s, and sea lion numbers observed in Penguin Bay were higher than at other penguin colonies (Chapter 5). This appears to be because of Penguin Bay's proximity to the major haul-out site in Sandy Bay, its greater shelter from the predominant southwesterly winds and swell, and access to the uplands where a few cows choose to pup and socially immature males follow. Leopard seals (*Hydrurga leptonyx*) have the largest proportional effect on Adélie Penguin colonies of intermediate size (Ainley et al. 2005), as the territoriality of hunting seals restricts the number hunting along a section of shoreline and the penguin transit rate is too low from the smallest colonies to attract hunting seals. Likewise, the intermediate size of the Penguin Bay penguin population relative to others on Campbell Island may contribute to the important effect of predation on the population growth rate. This may suggest that the Penguin Bay population will eventually decrease to a size at which sea lion predation is no longer important. However, New Zealand sea lion predation has strong local effects on Yellow-eyed Penguin populations, which are small and dispersed relative to other penguins (Moore and Moffat 1992; Lalas et al. 2007). In the same way small sub-colonies of penguins would presumably become unattractive to skuas, but I found that the territoriality of skuas meant that predation by the resident pair of the smallest penguin sub-colony was proportionately larger than elsewhere (Chapter 5). Furthermore, single large colonies cannot be readily defended by a single breeding pair, so that disputes between competing pairs seems to lower the proportional effect of skua predation on larger colonies.

Predation effects may be synergistic when two or more predator species target the same prey, if the activities of one facilitate predation by another. For example, in attacking a large colony of cliff-nesting Common Murres (*Uria aalge*), a Bald Eagle (*Haliaeetus leucocephalus*) will kill at most one murre, but the whole colony may temporarily abandon its eggs, causing many to fail through displacement and predation by Glaucous-winged Gulls (*Larus glaucescens*; Hipfner et al. 2011). Interactions between the suite of penguin predators in Penguin Bay appeared to be similarly synergistic. Brown Skuas and Northern Giant Petrels scavenged the penguin kills of New Zealand sea lions, presumably boosting the avian predators' attendance, reproductive success, and predation rates on penguins (Chapter 5).

Giant Petrels sometimes stole penguin chicks killed by skuas, presumably causing skuas to kill more chicks than they would have otherwise. When incubating or brooding penguins were forced from their nests by sea lions traversing through breeding colonies, unattended eggs and small chicks were vulnerable to skua predation. Giant Petrel predation attempts on sub-adult and adult penguins appeared to be most successful when the petrel could isolate one victim from the many targets presented by a large group of penguins moving along the pathway into the inland sub-colonies. Penguins came ashore in larger rafts formed by the amalgamation of smaller rafts that had been delayed from landing by sea lions hunting along the shoreline, so that sea lion predation risk likely increased petrel predation success indirectly.

CONSTRAINTS ON BEHAVIOURAL PLASTICITY

Observations of Rockhopper Penguins suggest they have a difficult existence. They are small-bodied, and appear to be pushing the boundaries of fasting and resisting predators in their breeding ecology, raising the question of why selection has not favoured an easier route. Firstly, why not be a bit larger, better able to defend yourself, and have a slower metabolic rate? The answer may be that the bigger Eudyptid niche was already filled. Southern and Eastern Rockhopper Penguins are the only Eudyptids that sometimes breed sympatrically with another Eudyptid. Warham (1975) pointed out that in all such instances, the larger Eudyptid breeds earlier by 2–4 weeks than the Rockhopper Penguin, and that niche partitioning by time, depth, and size-class of prey may be important to their ability to coexist. Secondly, why not have shorter incubation/pre-laying fasts by arriving closer to laying, make feeding trips between arrival and laying as some other penguin species do, or have one sex depart immediately after clutch completion? Additionally, why not eliminate the second long male fast altogether by sharing chick guarding and provisioning duties between the sexes? It would seem clear that shorter fasts would be beneficial by removing the risk of abandonment of eggs I reported in Chapter 4 and would allow for increased parental investment in chick-rearing through more frequent provisioning, producing bigger, more successful chicks. However, it may be that *Eudyptes* penguins are constrained from making adjustments towards shorter fasts by other factors that would negatively affect their fitness. I argued in Chapter 4 that nest site quality likely varied more for *Eudyptes* penguins than for other genera, owing to their small body size and the rocky slopes of many colonies. I demonstrated the importance of nest quality in Chapter 5 in the finding that the degree of nest shelter strongly influenced hatching success of both A- and B-eggs and the proportion of well-sheltered nests in a sub-colony influenced its probability of persistence. Furthermore, I argued in Chapter 4 that the greater

sexual size dimorphism of *Eudyptes* penguins relative to other penguin genera appears to disadvantage females in defending nests against conspecifics and predators. Such factors likely explain why selection has favoured arriving early and staying days after clutch completion over a shorter fast, as well as why only males guard chicks at the cost of a potentially higher provisioning rate.

In contrast to their relatively fixed breeding schedule and dimorphic clutches of a fixed two-egg clutch size (Chapter 6), Rockhopper Penguins appear to have considerable plasticity in their diet and foraging behaviour. As shown in Chapters 3 and 4 and by Tremblay and Cherel (2003; 2005), foraging behaviour and prey selection may vary greatly between years and breeding locations, including multi-day provisioning trips versus two trips in a single day, and different dive depths and rates. Plasticity in reproductive investment is apparent in my recording one female in the good year of 2011 who was raising two chicks (of combined mass c. 50% heavier than chicks being raised without a sibling) by commonly making two provisioning trips in a single day, a rare behaviour for females rearing a single chick (K.W.M. unpub. data). This suggests that when food is abundant and sufficiently near shore, Rockhopper Penguin behaviour is plastic enough to increase their provisioning rate and chick production. Near shore food availability was evident in 2011 by observations of rafts of penguins continuing to make foraging dives within Penguin Bay < 500 m offshore, as Cape Petrels (*Daption capense*) and Campbell Albatrosses fed amongst such rafts of penguins. Evidently, Rockhopper Penguins can readily exploit favourable conditions, and have high demographic rates resulting in rapid population growth, as described in Chapter 5 for Southern Rockhopper Penguins on the Falklands Islands where the total population grew by 51% from 2005–2010 (Baylis et al. 2013).

A species' genotype may also constrain its behavioural plasticity (Nussey et al. 2007). A number of the unusual traits of *Eudyptes* penguins are shared by all species in the genus, such as long fasts including male-only chick guarding and highly dimorphic two-egg clutches. The most parsimonious explanation of genus-wide traits is that they evolved only once in the ancestral species where they became a canalized trait and were inherited by each daughter species, rather than having evolved multiple times independently. This is likely also true of fasting and egg-size dimorphism in *Eudyptes* penguins, but inter-species comparisons also demonstrate that differences in ecological context can cause micro-evolution that modifies expression of these traits over time (Nussey et al. 2007). In terms of fasting duration, Macaroni Penguins breeding at low latitudes such as South Georgia are able to exploit the abundant prey of the Polar Front, but their southerly location shortens the time period of suitable

environmental conditions for breeding and moult (Williams and Croxall 1991). These conditions likely selected for their relatively short pre-laying interval ashore, and allow for shorter incubation foraging trips to regain mass and rapid chick growth so that chicks crèche at a younger age than elsewhere, shortening the duration of the second male fast. Intra-clutch egg-size dimorphism ranges from A-eggs being 54% the mass of B-eggs, on average, in Erect-crested penguins, to A-eggs being 85% the mass of B-eggs in Fiordland Penguins (St. Clair 1992; Davis 2013). The more similar-sized eggs of Fiordland Penguins likely reflect a foraging environment that increases their propensity to fledge two chicks (McLean 2000; Mattern 2013). Alternatively, the migration carry-over effect hypothesis of egg-size dimorphism (Chapter 6) argues that the relatively less dimorphic eggs of Fiordland Penguins occur because they have little or no migration/egg-formation overlap, so that the growth of their A-egg yolk is not constrained by a physiological conflict between migration and egg-formation (Crossin et al. 2010). This reasoning suggests that Erect-crested Penguins, which lay the most dimorphic eggs, should have the greatest degree of overlap and shortest pre-laying interval ashore between arrival and laying. However, the limited available information suggests that the pre-laying interval of Erect-crested Penguins is c. 2 weeks in duration (Davis 2001), similar to the 15-16 days of Eastern Rockhopper Penguins reported in Chapter 5, and not shorter than the 10 days of Macaroni Penguins (Crossin et al. 2010).

SHIFTING BASELINES: PERCEPTIONS OF ECOSYSTEM HEALTH AND FUNCTION

John Sorensen was a naturalist and coast-watcher of the 1940s whose photographs and note-taking provide hard evidence of the huge Eastern Rockhopper Penguin population on Campbell Island of that time (Bailey and Sorensen 1962; Cunningham and Moors 1994). Without such historical information, I might have looked down at the Paris Coast in 2012 at some 13,500 pairs of penguins and concluded that was a lot of penguins which must be thriving in a productive marine ecosystem. Of course, if John Sorensen were standing beside me he would undoubtedly have been shocked and saddened by his perception that, relative to a 1940's baseline of 472,500 pairs, the penguins were nearly gone and their population crash must mean the marine ecosystem was now ill-suited to their persistence. This is the problem of shifting baselines in ecology; our perception of what is 'normal' and 'healthy' is limited by our range of experience (Pinnegar and Engelhard 2008; Papworth et al. 2009). Of course, Sorensen's baseline may also be a misperception of the longer-term average population size, as the 1940's population may have been exceptionally large following the previous 30 years of favourable, cool SST conditions outlined in Chapter 2, and because humans had removed most

of the region's pinnipeds and whales in the 19th century, potentially reducing competition for prey, and predation with respect to pinnipeds.

New Zealand's Department of Conservation (DOC) defines its outcome as having, "New Zealanders gain environmental, social and economic benefits from healthy functioning ecosystems, recreation opportunities and living our history," (www.doc.govt.nz). The problem of shifting baselines means that it is hard to know whether the current penguin population size is one of a 'healthy functioning ecosystem'. If it is not, or we are concerned about its future under threats such as climate change, then what can be done to maintain and restore the population?

IMPLICATIONS FOR CONSERVATION MANAGEMENT

One potential conclusion from Chapter 5 would be that the sea lions responsible for killing penguins could be removed to captivity or culled to preserve the penguin population. There is a precedent for such action on Campbell Island, where a single sub-adult male New Zealand sea lion was killed to stop its aberrant behaviour of killing nesting Southern Royal Albatrosses (*Diomedea epomophora*; Moore et al. 2008). Similarly, it was suggested that a particular female sea lion responsible for causing the decline of a localized population of Yellow-eyed Penguins on the Otago Coast of the South Island, New Zealand, be removed to captivity (Lalas et al. 2007). Such action in the case of Penguin Bay would be ill-advised and unlikely to be effective, given the critically endangered status of sea lions, and my observation that depredating penguins was not a behaviour restricted to one or two sea lions. Furthermore, the Penguin Bay population is relatively small and insignificant to the island's total population, the dynamics of which over the past 70 years appear to have been under bottom-up control through food availability, rather than the top-down control of predation (Chapter 2).

Action to control the rate and degree of climate change would be the most effective means of ensuring the persistence of the Rockhopper Penguin population on Campbell Island. Although I have provided evidence of the importance of SST, food availability, and nutritional stress to penguin demographic rates and population dynamics in Chapters 2–5, a single penguin population's plight will obviously do very little to alter humanity's use of fossil fuels. However, penguins are charismatic creatures that do grab the public's attention, so that concern for Campbell Island's Rockhopper Penguins may make a small contribution to the growing public sentiment that serious action on climate change is necessary.

More realistic conservation management options for DOC to consider surround the idea of maintaining the penguin population's adaptive capacity to environmental change (Canale and Henry 2010; Towns et al. 2012). In simple terms, we need to ensure that we don't make things any worse for them than they are already. For example, precautions on shipping and oil drilling near penguin breeding locations, foraging areas, migration routes, and over-wintering areas, would reduce the risk of mass mortality through large oil spills or chronic pollution through small spills (Pütz et al. 2006). Such a reduction in population size may reduce genetic diversity important to adapting to climate change (Urban et al. 2014), and a smaller population would be more vulnerable to predation effects (Chapter 5). Marine Protected Areas in important foraging and over-wintering areas could be created to restrict additional activities such as commercial fishing and sea bed mining, which may further reduce the carrying capacity of the marine environment for penguins. A fundamental obstacle in employing such conservation management action is our poor understanding of *Eudyptes* penguin foraging areas, diet, and over-winter distribution in the New Zealand region.

FUTURE DIRECTIONS

Tracking studies to establish penguin foraging areas in relation to diet, and shifts in areas and diet between years, stages of breeding, and sex and age classes are among the highest research priorities for *Eudyptes* penguins (Taylor 2000). Such information is a critical prerequisite for the realistic conservation management actions suggested above. Studies that will begin to provide such information are already underway for Eastern Rockhopper Penguins on Campbell Island, Snares Penguins, and Fiordland Penguins, but not yet for the declining Erect-crested Penguin, the world's least-studied penguin species. Global positioning system and geo-location sensor tracking technologies have led to an explosion in our knowledge of seabird marine ecology. Likewise, diet analysis through next-generation sequencing of faecal DNA may develop into an affordable, informative, low-disturbance technique to identify seabird prey to the species level and to infer their relative proportions in the diet (Deagle et al. 2010; Jarman et al. 2013). Seabird diet and demography have the potential to provide information to fisheries management. The relevance of such metrics from Eastern Rockhopper Penguins, Grey-headed and Campbell Albatrosses at Campbell Island to assessing the year-class strength in the commercially important fishery for southern blue whiting of the Campbell Plateau warrants investigation (Cherel et al. 1999b).

My thesis has offered support to the existing hypothesis that warm (and more variable) SSTs underlie Rockhopper Penguin population declines on Campbell Island, but understanding this relationship will require more regular estimates of penguin demographic rates and population size, and oceanographic studies of how SST affects marine productivity and prey availability to penguins. My work has established a permanently marked population of penguins, including some marked as chicks, but obtaining additional information from this population will require regular monitoring and the addition of new marked birds to replace those lost through the high adult mortality rate.



Figure 7.1 Top: Eastern Rockhopper Penguins porpoise ashore in Penguin Bay. Bottom: chick brooded by parent. Photos by Kyle Morrison.

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