

A morphological analysis of weevils from sub-Antarctic Prince Edward Islands: an assessment of ecological influences

Introduction

Anthropogenically-induced global environmental modifications, such as green-house gas-driven climate change and biological invasions and their effect on species biodiversity and species changes, are of great conservation concern (Dukes and Mooney 1999; Pimm et al. 2001; Luck et al. 2004). The effects of human-induced change on mainland as well as island ecosystems, influencing physiology, distribution, life cycle events (phenology) and adaptation of organisms may have serious consequences for the future survival of organisms (Hughes 2000). A diverse range of studies show species are already exhibiting changes with regard to population densities, distributional ranges and morphological change as a result of the anomalous global climate (Huyser et al. 2000).

There is increasing concern that higher CO₂ production due to human activities is affecting global climate (Dukes and Mooney 1999). Long-term climatic monitoring programmes indicate that the earth is warming up and continual temperature increases in future are anticipated (Mitchell et al. 1990; Schneider 1992; Hughes 2000). It has been predicted that over the next century, the earth's average temperature will increase by between 1 – 3.5°C, and precipitation regimes will change continually (Dukes and Mooney 1999). Such climatic changes have far-reaching consequences on both ecosystems and species (McCarty 2001).

Anomalous climate changes have already been reported to be affecting species' distributions, abundance, physiology and phenology (Hill and Hodkinson 1992; Lawton 1995; Parmesan 1996; Kuchlein and Ellis 1997; Parmesan et al. 1999; Hughes 2000). For example, a 90% decline in population numbers of sooty shearwaters (*Puffinus griseus*) occurred in North America between 1987 and 1994 (Veit et al. 1996, 1997). Similarly, 75% of 65 bird species in the United Kingdom showed a tendency towards earlier breeding between 1971 and 1995 (Crick et al. 1997; for more examples, see McCarty 2001). Invertebrates are also affected by temperature increases that are most likely to influence insect distribution and abundance (Whittaker 2001).

Both temperature and precipitation play an important role in the life cycles of many organisms (Block 1990; Erelli et al. 1998; Karan et al. 1998), therefore, important conservation

issues for species' survival (either extinction, genetic, or morphological change) are highlighted as a result of a continuously changing environment, due to, for example, global warming. Temperature is an important determinant of body size in insects, with warmer environments favouring smaller body size, and vice-versa (Atkinson 1994; David et al. 1994; Chown and Gaston 1999). Increasing temperatures as a result of global warming are considered to decrease developmental time in organisms, particularly in insects, shortening larval stages and allowing these organisms to reach adult stage much faster (Hughes 2000).

Long-term morphological changes, including body size changes in various organisms resulting from human activities have already been reported (see Bas and Sarda 1998; Roy et al. 2003). Body size is closely related to insect life history traits, such as fecundity, mating success and dispersal ability (see Peters 1983; Partridge 1988; Prout and Barker 1989; Reiss 1989; Harvey and Pagel 1991). Thus, temperature-induced modifications in body size may change insect life history traits (Karan et al. 1998; Bitner-Mathé and Klaczko 1999; Hodkinson et al. 1999). However, not only are changes evident in individual organisms, but global temperature change currently poses a real threat to ecosystems (McCarty 2001).

Removal of barriers preventing long-distance dispersal of both plants and animals, as a result of human activities, leads to an increase in the number of ecosystems altered in their composition and functioning (Vitousek et al. 1997; Dukes and Mooney 1999). Dukes and Mooney (1999) reported that most aspects of global change, especially climate change and habitat fragmentation, will favour invasive species, therefore, increasing the severity of their impact on ecosystems. For example, the majority of endangered vertebrate species in south Florida are threatened by habitat fragmentation and destruction (Humphrey 1992; Moler 1992), and are considered to favour the establishment of non-indigenous invasive species (Forys and Allen 1998), such as the Cuban tree frog (*Osteopilus septentrionalis*) and is linked to the decline of some native hylids (Wilson and Porras 1983). Invasive species tend to be 'generalists', making them successful in a wide range of habitats, thus, mainly 'specialist' species dependent on specific habitats will be greatly influenced by environmental change (Dukes and Mooney 1999). Consequently, the prevalence of invasive species is most likely to increase as a result of global anthropogenic changes (Dukes and Mooney 1999).

The increase in human-facilitated biological invasions constitutes one of the most important conservation threats to the functioning of ecologically sensitive ecosystems, particularly in the isolated sub-Antarctic South Indian Ocean Province Islands (Bonner 1984; Chown et al. 1998; Bergstrom and Chown 1999). A large number of both plant and animal species are endemic to the Southern Ocean Islands (Gremmen 1981; Crafford et al. 1986; Kuschel and Chown 1995; Huyser et al. 2000), highlighting the critical need for the biological conservation of these isolated sub-Antarctic land masses (Chown et al. 1998). So far, the

relatively small surface area and the isolation of sub-Antarctic islands, together with limited human activities, have facilitated the continuous monitoring of the arrival, establishment, and the impact of alien species on island ecosystem functioning (Bergstrom and Chown 1999). These ecologically sensitive, but relatively simple ecosystems are, therefore, ideal for addressing questions relating to the partitioning of the potential influences of anthropogenic changes, such as climate change and alien species invasions on ecosystem functioning (Smith 1991).

Since the late 1960s, mean annual temperature on various sub-Antarctic islands has increased by approximately 1°C, while mean annual precipitation has declined (Adamson et al. 1988; Smith and Steenkamp 1990; Weimerskirch et al. 2003). Not only are indigenous island fauna and flora directly influenced by these climatic changes, but in many instances, alien invasive species are responding favourably, in for example, increasing their reproductive success and in broadening their distributional ranges (Ernsting et al. 1995; Dukes and Mooney 1999; Jones et al. 2002; Smith 2002).

The sub-Antarctic Prince Edward archipelago has two islands (Marion and Prince Edward Islands) with long-term climatic records since the 1950s for Marion Island (South African Weather Bureau) and regular vegetation surveys to monitor the number of alien invasive species and their establishment for both Marion and Prince Edward Islands (Gremmen 1981, 1997; Crafford et al. 1986; Watkins and Cooper 1986). Marion and Prince Edward Islands are located 22 km apart and the latter is house mouse-free (see below for more details). These two islands are essentially similar in their species composition, vegetation and insect fauna, and have fairly similar weather regimes. Both islands have a cool oceanic climate, with precipitation in excess of 2000 mm per annum (Crafford et al. 1986; Smith 1987). While Marion Island exhibits a mean annual air temperature of about 5.5°C (Smith and Steenkamp 1990), Prince Edward Island is thought to have a milder local climate with a tendency for drier weather conditions (Verwoerd 1971).

The ecosystem functioning of both islands is to a large extent, dependent on arthropods and other invertebrates that act as herbivores and detritivores (Gremmen et al. 1998). These macro-invertebrates play an important role in nutrient cycling, where for example, moth and weevil larvae, and earthworms have been reported to play a key role in enhancing rates of nitrogen, phosphorus and potassium mineralisation from peat on Marion Island (Smith and Steenkamp 1992a, 1993). Instead of nutrient flow through a grazing cycle, most of the energy and nutrients trapped during primary production go through a detritus cycle (Smith 1977; Smith and Steenkamp 1992b).

The increase in temperature and elevated CO₂ concentration as a result of global warming, and its drying effect, are expected to increase vegetation productivity and hence

nutrient demand (Smith 1991). Consequently, the detritus cycle remains a main source of nutrient cycling, highlighting the importance of invertebrate detritivores on the ecosystem functioning of both Marion and Prince Edward Islands (Klok and Chown 1997).

Since the introduction of the house mouse (*Mus musculus*) on Marion Island more than 180 years ago (Watkins and Cooper 1986), populations of this species have increased in association with elevated temperatures, and appear to have an increasing impact on Marion Island's invertebrate fauna and its flora through seed consumption (Smith and Steenkamp 1990; Chown and Smith 1993; Bergstrom and Chown 1999; Smith 2002). For example, it has been reported that weevil species contribute even more to the diet of *M. musculus* than previously observed (Crafford and Scholtz 1987; Smith et al. 2002). In addition, pronounced population declines have been observed for *P. marioni* and *Ectemnorhinus* weevil species between Burger's (1978) study, and a study conducted in similar vegetation types in 1996 (Hänel 1999).

While mouse predation has been implicated in the decline of insect population numbers, it is also considered to be responsible for changes in body size distributions of various macro-invertebrates important in nutrient cycling on Marion Island through size-selective predation (Crafford 1990; Chown and Smith 1993; Smith et al. 2002). For example, it has been reported that size-selective mouse predation may be contributing significantly to body size changes in especially *Bothrometopus randi* and *Ectemnorhinus similis* (Chown and Smith 1993; Smith et al. 2002), and that it may also be responsible for accelerating speciation in *Ectemnorhinus* weevil species on Marion Island (Chown and Smith 1993). The continual and extensive feeding of mice on especially *Ectemnorhinus* weevil species and *P. marioni* has led to an overall concern for the survival of these species on Marion Island (Chown and Smith 1993; van Aarde et al. 1996).

Indirectly, the reduction of insect prey populations through mouse predation is also considered to have a significant impact on indigenous predator species such as the lesser sheathbill (*Chionis minor*) (Huyser et al. 2000). Traditionally, predation by the lesser sheathbill, a natural predator on the islands, has been considered to impact on weevil and flightless moth populations, with weevils and *P. marioni* larvae contributing 16.8% and 21.4% to its diet, respectively (Burger 1978). However, Huyser (2000) considers that the contribution of macro-invertebrates to the diet of the lesser sheathbill has declined dramatically, leading to a decrease in lesser sheathbill population numbers.

With limited and highly restricted human visits to the mouse-free Prince Edward Island (Cooper and Avery 1986), the introduction of invasive species has been kept to a minimum. In contrast, Marion Island has been exposed to a relatively higher rate of invasions by alien species, which includes the introduction and establishment of mice due to frequent human

visits and a high rate of human activities (Cooper and Condy 1988; Hänel and Chown 1999). Consequently, both Marion and Prince Edward Islands provide ideal terrestrial ecosystem models to investigate the potential influences of climate change and alien invasive species on macro-invertebrate morphology.

The present study, therefore, attempts to partition the potential influences of climate change and/or alien invasive species on body size and/or shape changes by using six currently recognised weevil species endemic to the Prince Edward archipelago. These species include: 1) the coastal *Palirhoeus eatoni*; 2) *Bothrometopus elongatus*, *B. parvulus*, and the mainly coastal *B. randi*; and 3) *Ectemnorhinus similis* and *E. marioni* that jointly occur on *Azorella selago*-dominated habitat communities.

The *Ectemnorhinus*-group of weevils comprises 36 species, representing 80% of the Coleoptera on all of the sub-Antarctic islands and is the most diverse taxon on the South Indian Ocean Province Islands (Chown and Scholtz 1989; Chown 1993; Kuschel and Chown 1995). The 36 species comprise 6 genera with two major feeding habits that include angiosperm and cryptogam herbivory (Chown 1994).

Feeding habits of the *Ectemnorhinus*-group of genera determine their distributions on the islands (Chown 1994). Present data indicate the *Ectemnorhinus*-group of genera to be polyphagous, except for the supra-littoral *Palirhoeus eatoni*, an oligophagous species feeding on three species of marine alga (Chown 1994). Although the majority of weevils are polyphagous cryptogam-feeding species, members of the genera *Canonopsis*, *Christensenia* and *Ectemnorhinus* are the only species known to feed on angiosperms, but also incorporate bryophytes and other cryptogams in their diets (Chown 1989).

The feeding adaptations of the *Ectemnorhinus*-group gives them the ability to feed on a wide range of food plants and make them one of the most successful groups on the sub-Antarctic islands (Kuschel 1971). Species belonging to the genera *Palirhoeus*, *Bothrometopus* and *Ectemnorhinus* (*vanhoeffenianus* group - four species restricted to Îles Crozet) are restricted to the cryptogam-dominated epilithic biotope, comprising fellfield, shoreline rocks and outcrops, where they feed on lichens, cyanobacteria, algae and bryophytes (see Chown 1994). The remainder of the *Ectemnorhinus* weevils (*viridis* group - cosmopolitan within the South Indian Ocean Province Islands) are mainly associated with the vegetated biotope or with angiosperms at high altitudes, although some species such as *E. marioni* are always found in association with bryophytes irrespective of altitude (see Chown 1994). Smith (1977) reported that the largest and the most conspicuous herbivorous arthropod species is *Ectemnorhinus similis* (C.O. Waterhouse), the only weevil species on the Prince Edward Islands that feeds on angiosperms (Chown 1989; Chown and Scholtz 1989). Despite the different climatic histories

of Marion and Prince Edward Islands (Verwoerd 1971), no morphological or ecological differences were found between weevil assemblages (Chown 1992).

Palirhoeus eatoni (C.O. Waterhouse 1876) are restricted to the upper- to supra-littoral zone, regularly inundated and exposed to sea spray, where they feed on marine algae (Kuschel 1971; Crafford et al. 1986). To facilitate a firm grip on rocks, *P. eatoni* adults have small hooks on the lower angle of the tibiae, elongated claw segments and long claws (Kuschel 1971; Crafford et al. 1986). Adults vary in length between 4.0 – 5.5 mm, and are easily distinguishable from other weevil species by the presence of a tarsal claw segment that is longer than the first three tarsal segments. In addition, the species lacks any vestiges of meta-thoracic wings or a lateral flange on the inner surface of the elytra (Crafford et al. 1986). Larvae associate with debris and vegetation in both intertidal and supra-littoral zone and are distinguished on the presence of a darkly sclerotised peritreme on the thoracic spiracle (Crafford et al. 1986).

Adults of *B. elongatus* (Jeannel 1953) are restricted to the central highlands (300 – 1000 m a.s.l.) of Marion and Prince Edward Islands, where they feed on lichens and epilithic moss (*Andreaea acuminata*) (Crafford et al. 1986). It is the smallest weevil species present on Marion and Prince Edward Islands, ranging between 2.5 mm and 4.0 mm. The species is distinguished from other species, based on the presence of long transverse hairs on the elytra and pronotum (Crafford et al. 1986). Larvae feed on both moss and detritus, with larvae and pupae occurring inside clumps and balls of moss (*Andreaea* and *Ditrichum* spp.) (Crafford et al. 1986).

The distribution of *B. parvulus* (C.O. Waterhouse 1885) ranges from the supra-littoral zone, overlapping with the distribution of *P. eatoni*, up to 900 m a.s.l. (Crafford et al. 1986). Adults mainly feed on lichens, algae, mosses and certain vascular plants (e.g., *A. selago*; Kuschel 1971) (Crafford et al. 1986). Adults range between 3.0 mm and 5.0 mm and are characterised by a compressed and carinate humeral area. Larvae are white with labial sclerotisation with lateral arms broad at the base as well as air-tubes of abdominal spiracles directed dorso-caudad (Crafford et al. 1986).

Bothrometopus randi (Jeannel 1953) occurs from sea level up to approximately 750 m a.s.l. (Chown 1992), and rarely up to 1000 m a.s.l. (L. Janse van Rensburg and G.C. Grobler pers. obs.), and are distinguished by a distinctive green elytral scale pattern. Large adults (5.0 – 7.5 mm) occur abundantly on lichen-covered rocks and both adults and larvae appear to be specialised algae- or lichen-feeders. Larvae are large and have a grey-green colour (Crafford et al. 1986).

The taxonomic status of the currently recognised *E. marioni* (Jeannel 1940) and *E. similis* (Waterhouse 1885) has been the subject of considerable debate (Kuschel 1971; Crafford

et al. 1986; Chown 1989; Chown and Scholtz 1989; Chown 1990). Waterhouse (1885) first described *E. similis* from Marion Island followed by Jeannel's description of *E. marioni* in 1940 and is distinguished from *E. similis* on the basis of humeri, interstriae and striae morphology. Kuschel (1971), however, synonymised the two species due to lack of consistent differences in internal or external characteristics and ecological preferences. Later, Dreux and Voisin (1978) again recognised *E. marioni*. Thereafter, Crafford et al. (1986) recognised three distinct ecotypes within the *Ectemnorhinus* species complex, considered to be correlated with three morphs distinguished on body size and colour.

The brown morph ranged between 6.5 mm and 9.0 mm, covered by dense brown scales, interspersed with sparse, erect setae. Adults associated mainly with *A. selago* and *Poa cookii* grassland but also fed on *Acaena magellanica* and mosses (Crafford et al. 1986). The brown morph larvae were characterised as detritus-feeders, associated predominantly with *A. selago* litter, but also with albatross nests and well-manured vegetation.

An intermediate-sized group (5.0 – 7.0 mm) labelled as the green morph, were characterised by a brown integument covered with simple rows of dense green scales, interspersed with sparse, erect setae. Adults occur in a wide range of habitats, from the supralittoral up to 800 m a.s.l. associated mainly with *Poa cookii* grassland and drainage line communities on the coastal plain. Main food sources included *Acaena magellanica* and the moss, *Brachythecium rutabulum*. The larvae were primarily detritivores, but may also feed facultatively on mosses and lichens (Crafford et al. 1986).

The black morph, smallest of the three morphs (4.0 – 5.5 mm), were distinguished from the other morphs by the virtual absence of body scales and a black integument. This morph was chiefly associated with *Agrostis magellanica* mire vegetation, but has also been found on *A. selago* and drainage line communities adjacent to mires. Adults, larvae and pupae were often found submerged in the saturated litter of mire communities, with larvae feeding predominantly on detritus, but also on fresh fragments of the mire-associated mosses *Jamesoniella* and *Drepanocladus* (Crafford et al. 1986).

However, Chown (1990) noted that the use of vestiture colour and body length to distinguish between ecotypes was not justified, and the species complex was instead separated into two morphologically similar but ecologically distinct species. Bryophyte-feeding individuals (3.77 – 7.79 mm) associated with *Azorella selago*, *Agrostis*, *Campylopus* and *Ptychomnion* mires as well as diverse bryophytes including *Ditrichum strictum*, were designated *E. marioni* (Chown 1990). The larger (4.51 - 8.69 mm) angiosperm-feeding individuals associated with *Acaena* herbfields, *Callitriche antarctica*, *Pringlea antiscorbutica* and *A. selago* were designated *E. similis*. Although *E. similis* feeds mainly on angiosperms, at the end of the growing season when vascular plant foliage deteriorates, bryophytes and other

cryptogams are incorporated into their diet (Chown 1989; Chown and Scholtz 1989; Chown 1990). In addition, Chown (1990) noted that *E. marioni* and *E. similis* also differ in the length of their life cycles and time of emergence. *Ectemnorhinus marioni* adults are present throughout the year and are characterised by shorter life cycle with fewer instars, while *E. similis* adults emerge during summer months, synchronised with the first flushes of angiosperm growth and flowering. Apart from body size, no consistent differences in the male genitalia of the two taxa are present (Chown 1990). Similarly, females show no differences in either the ovipositor or the spermatheca (Chown 1990). It has been suggested that *E. marioni* and *E. similis* evolved sympatrically, as a result of differences in food preference and reproductive isolation induced by individual body size differences (Chown 1990; Crafford and Chown 1991).

If the *Ectemnorhinus* species complex is considered as two separate species, their body length and dietary variability becomes considerably reduced, bringing them within the range found in other weevil species occurring on other sub-Antarctic Islands (see Chown 1991). Chown (1991) reported that the variation in both diet and morphology of the *Ectemnorhinus* complex on Marion Island may be a result of the between-phenotype component and suggested that the radiation of *Ectemnorhinus* species on Marion Island is relatively far advanced (see Roughgarden 1972; explanation in Chown 1991). Therefore, Chown (1991) suggested that taxonomic decisions concerning species present on each island should be based on intensive studies of morphology, biology, ecology and island history, rather than morphology based on museum material.

The present study uses a morphometric approach as well as molecular (COI gene) data from a parallel study (G.C. Grobler) in an attempt to assess the taxonomic status of *Ectemnorhinus* weevil species from the Prince Edward archipelago. In addition, long-term morphometric size/shape changes in weevil species sampled on both Marion and Prince Edward Islands over the last five decades are assessed. This analysis of the long-term data includes data from up to approximately 4000 year-old sub-fossil weevil remains recovered from mire core samples on Marion Island. Given that both Marion and Prince Edward Islands are thought to have fairly similar temperature regimes, the latter island being mouse-free, would serve as a control in the partitioning of the potential effects of climate change and mouse predation on weevil morphology. Furthermore, altitude above 750 m a.s.l. was initially considered as an additional control because of previous reports that, unlike weevils, mice only occur up to 750 m a.s.l. in the summer months on Marion Island (Chown and Klok 2003). However, mice and/or mice pellets have since been observed to occur from 800 m up to 1000 m a.s.l. on Marion Island (L. Janse van Rensburg and G.C. Grobler, pers. obs.). Body size changes together with increased mice predation may eventually alter fundamental processes of

ecosystem functioning, which may lead to weevil species extinctions (Chown and Smith 1993). The problem in body size changes is exacerbated further by reports of elevation-linked declines in size for some weevils from Marion Island (Chown 1992; Chown and Klok 2003).

Given the background above, the objectives of the present investigation are:

- 1) To clarify the taxonomic status of the *Ectemnorhinus* weevil species occurring on both Marion and Prince Edward Islands using morphometric data complemented by molecular data from a parallel study (G.C. Grobler).
- 2) To assess weevil morphological changes on both Marion and Prince Edward Islands over time, with reference to climate change and mouse predation.

Relevance of Study

Both Marion and Prince Edward Islands are under the jurisdiction of the South African government, with their management being vested under the administration of its Department of Environmental Affairs and Tourism (DEA&T). As two of its major management objectives, the Prince Edward Islands Management Plan by the department's Prince Edward Islands Management Committee seeks to:

- 1) "... maintain biological diversity, including genetic diversity, species diversity and the diversity of ecological processes"; and
- 2) "... minimise interference with natural processes and the destruction or degradation of natural features resulting from human interference" (Anonymous 1996).

Invasive species pose one of the greatest threats to indigenous biodiversity on both Marion and Prince Edward Islands (Chown et al. 1998; Bergstrom and Chown 1999). The need to prevent further introductions and mitigate the impacts of alien species already present is entrenched into the current Management Plan for the Islands. One aspect of concern in the Prince Edward Islands Management Plan is the ecological impact arising from the introduction of the alien, invasive house-mouse (*Mus musculus*, sensu lato) on Marion Island because mice arguably constitute one of the main threats to biodiversity and ecosystem functioning on the Prince Edward and other Southern Ocean Islands (Jones et al. 2003). Similarly, climate on Marion and Prince Edward Islands is changing (Smith and Steenkamp 1990) and could also

have an effect on the ecosystem functioning of the islands. Therefore, there is a critical need to partition potential ecological influences that could affect weevil morphology, that in turn impact on the islands' ecosystem functioning.

To exacerbate these potential problems further, the taxonomic status of some of the affected weevil species is largely uncertain. It is, therefore, not clear which species occur on Marion Island and/or Prince Edward Island, and whether the populations/species which also appear to be in the process of speciation are sufficiently indistinct to be managed as single conservation units (Moritz and Faith 1998). Similarly, it is not clear whether the weevil populations occurring on the mouse-free Prince Edward Island are sufficient to ensure the conservation of weevil species diversity on Marion Island.

For the Prince Edward Islands Management Committee to take informed decisions regarding threats to indigenous biodiversity and ecosystem functioning, it clearly needs information on the distinctiveness of the weevil species and the extent to which their roles are changing in the Marion Island ecosystem. The present investigation has as its major rationale, the provision of information that will be of direct relevance to the management strategies for both Marion and Prince Edward Islands.

Key Questions and Thesis Outline

To this end, the following key questions (and their associated parts of the thesis) will be addressed in the present study:

- **Key Question I: Can the currently recognised weevil species be distinguished using a selected set of morphometric characters?**

The first part of this study (Chapter 2) is directed towards selecting meaningful morphometric characters for use in the assessment of the taxonomic status and morphological changes over time in weevils from Marion and Prince Edward Islands. This includes a morphometric assessment of functional units of weevil morphology that attempts to conform to the morphological integration concept advocated by Olson and Miller (1958). This part of the study will also include a series of univariate and multivariate procedures undertaken with the primary objective of establishing whether sexes should be treated separately or pooled in all subsequent analyses.

- **Key Question II: Do the two currently recognised *Ectemnorhinus* species on Marion and Prince Edward Islands show sufficient morphological and/ or genetic differences for them to be considered separate species?**

Chapter 3 addresses questions relating to the taxonomic status of *Ectemnorhinus* species on both Marion and Prince Edward Islands using multivariate morphometric and molecular analyses. The molecular aspect forms part of a parallel study (G.C. Grobler) that attempts to genetically characterise weevil species from Marion and Prince Edward Islands. Both morphometric and molecular analyses will be included in the assessment of the taxonomic status of *Ectemnorhinus* weevil species occurring on both islands.

- **Key Question III: Have there been morphological changes in weevil populations on both Marion and Prince Edward Islands over time with reference to potential influence, particularly climate change and mouse predation?**

Chapter 4 addresses the question of morphological change over time using *B. elongatus*, *B. parvulus*, *B. randi* and *P. eatoni* from both Marion Island and Prince Edward Island and attempts to partition its potential influence particularly with reference to climate change and mouse predation. Potential influential factors examined include temperature, rainfall, altitude, year of sampling, gender and mouse predation.

- **Key Question IV: Have there been morphological changes in weevil populations on Marion Island over time during a period that predates the potential influence of climate change and mouse predation, and with reference to recent times?**

Chapter 5 extends the question of weevil morphometric changes over time by examining sub-fossil weevil remains recovered from mire core samples on Marion Island. This part of the study includes the identification of sub-fossil remains with reference to the currently recognised weevil species on both Marion and Prince Edward Islands, followed by a comparison between sub-fossil and recently collected material in Marion Island mire habitats.

The final chapter (Chapter 6) provides a synthesis and general discussion of the major findings of the study and includes recommendations to the Department of Environmental Affairs and Tourism's Prince Edward Islands Management Committee.

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“I’ve never failed at anything in life. I was simply given another opportunity to get it right”

Winston Churchill