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

Synopsis and conclusion

Ecologically sensitive, but relatively simple sub-Antarctic island ecosystems such as Marion and Prince Edward Islands, present unique models of terrestrial ecosystems to study the influence of anthropogenic changes, in particular climate change and species invasion on ecosystem functioning (Smith 1991). Marion and Prince Edward Islands are situated 22 km apart with only Marion Island colonised by mice (Watkins and Cooper 1986; Crafford and Scholtz 1987). Thus, the mouse-free Prince Edward Island represents an ideal natural control system in studies to assess the potential influence of climate change and mouse predation on the ecosystem functioning of the two islands (see Smith 1991; Smith and Steenkamp 1992, 1993; Gremmen et al. 1998).

More specifically, Marion and Prince Edward Islands offer an ideal opportunity to study the responses of macro-invertebrates such as weevils to changing global climate and/or biological invasions, through morphometric size and shape changes over time. The indirect effect of climate change on mice populations as well as the direct effect of size-selective predation by mice have been considered important contributors to weevil body size changes (Chown and Smith 1993; Smith 2002; Smith et al. 2002). In addition, the direct influence of climate change may also affect insect body size, with increasing temperatures leading to a decrease in body size (Atkinson 1994; James et al. 1997; Karan et al. 1998). Therefore, morphological changes in important contributors, such as weevil species, to nutrient cycling, that influence ecosystem functioning on both Marion and Prince Edward Islands (Crafford and Scholtz 1987; Crafford 1990), are of conservation concern. Van der Merwe et al. (1997) have shown that the upper lethal temperatures of the six weevil species that occur on the two islands correspond closely to the maximum microclimatic temperatures in their respective habitats. This suggests that temperature increase on the islands may be deleterious to weevil survival (Smith 2002).

Using a reduced set of 15 morphometric measurements (from an original set of 23 variables) that took into account correlations between variables and the morphological integration concept of Olson and Miller (1958), the present study was able to distinguish
between the six currently recognised weevil species on Marion and Prince Edward Islands (Chapter 2). Although sexual size dimorphism is common in virtually all insect species (Helms 1994; Anholt 1997; Fairbairn 1997), multivariate analyses of the weevil species from Marion Island suggested the absence of multivariate sexual dimorphism, leading to the pooling of sexes in all subsequent analyses. Willig et al. (1986) expressed reservations about using a univariate approach in the assessment of non-geographic variation such as sexual dimorphism because significance tests for each variable independently present the dilemma of having to consider the number of variables that must exhibit significance before overall significance is declared. The use of a multivariate approach to identify potential sexual dimorphism as adopted in this study is recommended since it evaluates overall differences as it utilises rather than ignores correlations among variables (Willig et al. 1986).

For the purposes of comparisons with previous studies, the present investigation was based on traditional morphometrics where linear measurements were used to assess multivariate size and shape changes in weevil morphology. While the analyses based on traditional morphometrics may have allowed some insight into aspects of weevil morphology with reference to climate change and mouse-predation, these could be investigated further using geometric morphometric techniques that are superior in partitioning organismal shape differences (Rohlf and Marcus 1993; Rohlf 1999).

The selected reduced set of morphometric measurements (Chapter 2) allowed the assessment of morphometric size and shape changes over time in weevils from Marion and Prince Edward Islands. However, the taxonomic status of both *Ectemnorhinus similis* and *E. marioni* has largely been uncertain (Kuschel 1971; Chown and Scholtz 1989; Chown 1991, 1992). While current taxonomic authorities treat both as valid species (Kuschel and Chown 1995), others have considered them as synonymous (see Kuschel 1971).

A multi-faceted approach involving both morphometric and molecular (COI gene) (G.C. Grobler) characterisation provided some insight into the taxonomic status of *Ectemnorhinus* species on both Marion and Prince Edward Islands (Chapter 3). The molecular analyses revealed the presence of two genetically distinct species on Prince Edward Island, while evidence for a single species, comprising diverse genetically discrete populations was found on Marion Island (G. C. Grobler). These results were supported by multivariate analyses that showed neither multivariate size nor shape variation in individuals of *Ectemnorhinus* from Marion Island, but indicated the presence of two multivariate size-related phenetic groupings on Prince Edward Island. The congruence between molecular and morphometric data suggest that previous morphologically- and ecologically-defined groups in *Ectemnorhinus* weevils from Marion and Prince Edward Islands (Crafford et al. 1986; Chown and Scholtz 1989; Chown 1990) need to be re-evaluated.
Currently, the morphological identification of *Ectemnorhinus* species in the field is problematic such that it may have constrained the morphological analyses in the present study. However, the analyses were largely based on *a priori* analyses that made no prior assumptions about group membership, and more importantly included some genetically identified individuals as references to the *a priori*-derived morphometric groupings. Based on the findings in Chapter 3, all *Ectemnorhinus* species on Marion Island may be considered a single species. However, distinguishing between *Ectemnorhinus* species on Prince Edward Island should be investigated further and taxonomic descriptions and the nomenclature for *Ectemnorhinus* species on both Marion and Prince Edward Islands should be revised. In addition to the revised taxonomic descriptions and the nomenclature for these species, it is proposed that the *Ectemnorhinus* species on both Marion and Prince Edward Islands be investigated further using geometric morphometric techniques in order to assess potentially subtle morphological differences between the genetically-distinct groups delineated.

It is also possible that an on-going parallel population genetic study (G.C. Grobler) of *Ectemnorhinus* populations on both Marion and Prince Edward Islands will allow additional taxonomic and evolutionary insight into this group of weevils. It is proposed that an additional further investigation should also consider expanding the cytogenetic study by Chown (1989) to include weevils from both Marion and Prince Edward Islands.

The question of morphological change over time was investigated for the remaining four weevil species which were not of equivocal taxonomic status, namely, *Bothrometopus elongatus*, *B. randi*, *B. parvulus* and *Palirhoeus eatoni* occurring on both Marion and Prince Edward Islands. Morphometric analyses of these weevil species suggest morphometric size differences between samples collected in the mid-1960s and 1970s and recently collected material on both Marion and Prince Edward Islands. Similarly, samples collected in the early-to mid-1980s and recently collected samples for Prince Edward and Marion Islands respectively, suggest morphological changes over time during a period characterised by the green-house effect.

In addition, for all species, most of the deviance in Generalized Linear Models was explained by the full models of PCA III, supporting the separation of species on the third PCA axes in the multivariate analyses. Sampling year contributed highly significantly and explained the largest percentage deviance for the full models for principal components I (representing multivariate size) – III (representing multivariate shape) for all species. The only exceptions were *B. parvulus*, where none of the variables contributed significantly to the full model and *B. randi*, with gender explaining a larger percentage of the deviance than sampling year. Mice predation did not contribute significantly to the deviance in any of the *B. randi* PCA axes analysed, although it is a preferred prey species of mice (Chown and Smith 1993). However,
mice predation contributed towards a small portion of the deviance for other, non-preferred prey species, such as *B. elongatus* and *P. eatoni*.

For the Marion Island dataset, temperature contributed most to the percentage deviance explained by the full model for PCA III for all species, except *B. elongatus*. In addition, temperature contributed significantly to PCA I and II for all species, except *B. elongatus* and *B. parvulus*. In general, gender also contributed significantly to the percentage deviance explained for all PCA axes across species.

Although temperature data are only available for Marion Island, it is assumed that temperature increases on the mouse-free Prince Edward Island that is located 22 km away are fairly similar. The suggested multivariate size and shape changes in all weevil species over a similar time period on both Marion and Prince Edward Islands, and the direct link between temperature increase (1950 - 2004) and sampling year (1965 – 2003), with temperature increasing over time, also supports the potential primary effect of climate change on weevil morphological changes.

The effect of climate change on weevil morphometric parameters are further exacerbated by the separation of the 1986 data in all species (Chapter 4). 1986 represents the start of an El niño period (Turner 2004) and may support the argument that climate change plays a major role in weevil size and shape.

Other studies have reported that small increases in temperature or changes in precipitation may influence invertebrates to undergo range expansions or population changes (Masters et al. 1998; Bale et al. 2002; Beaumont and Hughes 2002). Given that adaptation to climate is a physiological response (Addo-Bediako et al. 2000), Bergstrom and Chown (1999) have argued that the short-term effect of a potential predator may be concealed by the effects of climate change.

It is possible that temperature may have an indirect effect on mouse population numbers that in turn may have an added influence on weevil morphological changes through size-selective mouse predation (Crafford 1990; Smith and Steenkamp 1990; Chown and Smith 1993; Smith et al. 2002). Smith and Steenkamp (1990, 1992) suggested that mouse populations may be increasing as a result of warmer temperatures, having an impact on weevil morphology as well as their population densities (Crafford and Scholtz 1987; Hänel and Chown 1998; Hänel 1999; Smith et al. 2002). However, van Aarde et al. (1996) suggested no relationship between minimum temperature and mouse mortality. More recently, van Aarde et al. (2004) reported that mouse numbers on Marion Island between 1991 and 2001 were habitat-dependent, with stable population densities occurring on biotically-influenced areas, but that population numbers increased by approximately 12% per annum on wetlands.
The question of morphological change over time was further investigated by examining sub-fossil weevil remains recovered from mire core samples on Marion Island (Chapter 5). Weevil remains from 2.0 m and 2.5 m depths were carbon-dated and found to be from 789 BC and 2331 BC, respectively. Head capsules, being the best-preserved components, formed the basis of the analyses in this part of the study. These sub-fossil weevil remains were identified as belonging to the *Ectemnorhinus* group of genera and were compared to recent samples collected in 1986/87 and 2001 from *Blepharidophyllum* mire communities on Marion Island.

Previous core peat samples studied by Scott (1985) from between 1.65 – 1.80 m (4140 ± 70 y BP) and 2.80 – 2.95 m (5440 ± 310 y BP) depths indicated vegetation type and climate to have remained virtually unchanged during these time periods. Mire core samples collected at 2.5 m (3910 ± 40 y BP) and 2.0 m (2641 ± 45 y BP) depths in the present study represent samples from similar time periods to those examined by Scott (1985). Consequently, it may be assumed that these core samples represent a time period that exhibited little variation in climate change. Since these core samples predate the onset of global warming due to the green-house effect and the introduction of mice on Marion Island, it was hypothesised that there would be no discernible morphological changes in weevil samples, between 2331 BC and 789 BC, a period spanning 1542 years.

As hypothesised, the analyses of this part of the study did not detect statistically significant morphometric body size and shape changes in sub-fossil material from the two sampled depths that were considered to represent different dimensions in time and space. However, significant differences between sub-fossil and recent material collected in 1986/87 and 2001 were detected in a single head capsule measurement. These results suggest a general lack of morphological change in sub-fossil material from Marion Island over a period of 1542 years.

Given the different views on the potential influence(s) of morphological change with reference to climate change and/or mouse predation, the present study suggests that further investigations based on long-term population density data for both macro-invertebrates and invasive species are required. Based on a five-year (1996 – 2000) mouse-exclusion experiment, van Aarde et al. (2004) recently reported no significant mouse effect on abundance, biomass and community structure based on diversity and composition in any of the mouse-prey species on Marion Island. They reported no significant changes over time in either biomass or abundance in enclosures that were independent of the potential influence of mice, but also indicated that their results may have been affected by a generally low statistical power.

Additional annual weevil and mice sampling on Marion Island and more frequent sampling of weevils on Prince Edward Island may allow the continual monitoring of weevil morphological changes and mice population changes over time. Such long-term datasets may
allow the partitioning of potential influences, such as climate change and mouse predation to be investigated. In addition, future core sampling of mires on the mouse-free Prince Edward Island may allow the investigation of weevil morphological changes over time that is independent on the potential influence of mice predation. These potential factors, together with various other factors such as resource limitations may manifest as a result of environmental changes due to global warming. As suggested by Smith et al. (2002) and van Aarde et al. (2004), these future studies may also have to include an assessment of long-term invertebrate population dynamics, the autecology of mouse-prey items, and the proximate controlling factors of invertebrate and mouse populations. For example, Klok and Chown (1997, 2001) have reported that desiccation, and to some extent, temperature may represent population-limiting factors in some invertebrates. In essence, an insight into the potential effect of mouse-predation may only be fully understood with additional data on the biology of both macro-invertebrate prey species and their predators.

Marion and Prince Edward Islands Management Plan Recommendations

With a temperature increase as a result of global warming, the ecosystems of both Marion and Prince Edward Islands will continually be in a process of change. Increased temperature may create a favourable environment for invasive species and facilitate their establishment as well as increasing the severity of their impact on ecosystem functioning (Bergstrom and Chown 1999; Dukes and Mooney 1999). Therefore, additional precautionary measures need to be implemented in order to avoid any further introductions of alien invasive species on both Marion and Prince Edward Islands.

For example, personal and issued gear should be washed and checked more thoroughly to prevent the introduction of seeds, fungus, or invertebrate species before boarding on voyagers to the islands, such as the SA Agulhas. Current methods of cleaning equipment and gear on board opens a potential gap for invasive species to “re-infect” visitors and their equipment before being flown to either Marion or Prince Edward Islands. In addition, the cleaning of voyagers such as the SA Agulhas should be prioritised and strict regulations implemented. For example, rat guards should always be present on anchor ropes to prevent rodents from boarding the ship and augmented by the fumigation of pesticides before each voyage to the islands, to ensure an “alien-free” ship (also see Frenot et al. 2005).

It is important to recognise that an increase in the number of visitors to the islands may also increase the probability of the introduction and establishment of invasive species that would lead to conservation problems (Chown et al. 1998). Already, human influence has
increased rapidly, through extensive commercial exploitation, for example whaling and sealing activities (Frenot et al. 2005). In addition, there has been an increase in scientific research on the islands that in turn, may have an impact on the ecosystems of the islands (Frenot et al. 2005). Chown et al. (1998) suggested that the number of human occupants and the interaction between humans and the island area are important determinants of the number of introduced species to the islands. It is, therefore, recommended that commercialisation of the islands through tourism should be strictly regulated or even prohibited, and that both tourism and scientific visits to the islands be limited (Chown et al. 1998). Currently, a strict permitting system exists, where the number of visitors to Prince Edward Island is restricted to six visitors for four days per year, with visitors being issued with new clothing and equipment and flown to Prince Edward Island directly from the ship on arrival. The sustained implementation of this current policy should curtail further introductions of invasive species on Prince Edward Island.

However, Redford (1992) and Terborgh (1999) suggested that even low-intensity human use may have significant effects on natural ecosystems. Therefore, islands not likely to be visited (e.g., Prince Edward Island) that are adjacent to frequently visited islands (e.g., Marion Island) are likely to exhibit conservation problems in future (Gremmen and Smith 1999; Chown et al. 2001). Alien species introduced to Marion Island have been shown to naturally disperse to Prince Edward Island (Gremmen and Smith 1999).

For already established invasive species, such as the house mouse, it is suggested that alternative mouse-control measures be investigated and implemented as soon as possible. Although the present study suggests that climate change may be the main potentially influential factor causing weevil morphological changes, it is possible that further increases in temperature may also facilitate an increase in mouse population numbers (Smith and Steenkamp 1990, 1992; also see Frenot et al. 2005). Indeed, adult weevils are contributing more to mice diet than found in previous studies (Smith et al. 2002). In addition to size-selective predation, increased mouse population numbers may have a devastating effect on the morphology and population densities of invertebrates on both Marion and Prince Edward Islands.

Of major concern is whether it is possible for these invertebrates to successfully maintain viable population densities and still serve as a main food source for predators. Huysier (2000) reported that the contribution of macro-invertebrates to the diet of the lesser sheathbill diet has declined dramatically and suggests that mice, through predation on macro-invertebrates are indirectly responsible for the decreased population numbers of the lesser sheathbill. It is possible that the eradication of mice may ensure sustainable macro-invertebrate population densities for natural predators. It is suggested that intense monitoring of population densities of both macro-invertebrates and invasive species over a similar time period be implemented in order to facilitate the assessment of predator-prey interactions. In addition,
Frenot et al. (2005) highlighted the urgent need for the establishment of long-term monitoring programmes on the Southern Ocean Province Islands to ensure appropriate risk management protocols to be implemented.

More importantly, it is further suggested that both Marion and Prince Edward Islands should be managed as separate ecosystems. From the genetic (G.C. Grobler) and morphometric differences between *Ectemnorhinus* species on both islands, it appears that the biodiversity of both islands differ with regards to species composition, such that Prince Edward island, as previously thought, can no longer be considered a potential backup source of biodiversity that may be lost on Marion Island (or vice-versa).

References


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