DOCTOR OF PHILOSOPHY

Natural selection and evolutionary ecology in Anolis oculatus

Reardon, James T.

Award date:
1999

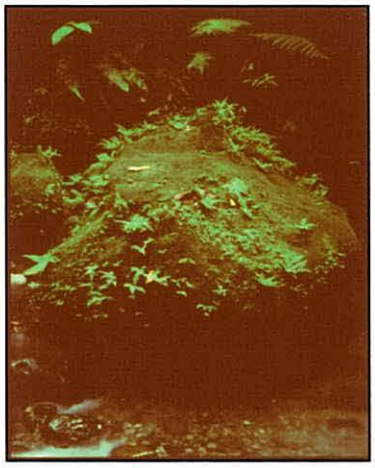
Awarding institution:
University of Wales, Bangor

NATURAL SELECTION, AND EVOLUTIONARY ECOLOGY IN *Anolis oculatus.*

A THESIS PRESENTED FOR THE DEGREE OF DOCTOR OF PHILOSOPHY, AT THE UNIVERSITY OF WALES, BANGOR.

BY JAMES T. REARDON, BSc(Hons.).

AUGUST, 1999.



For my Mother, and her memory of my Father.

ABSTRACT.

A juvenile male Anolis oculatus, displaying characteristic juvenile tail banding and lateral striping.

ABSTRACT.

The lizard, *Anolis oculatus* (Squamata: Iguanidae), is endemic to the Commonwealth of Dominica in the Lesser Antilles. A manipulative experimental approach was adopted to test for the causes of natural selection operating in natural environments. Four large enclosures were constructed in xeric Caribbean coastal woodland in which both control and environmentally translocated populations could be maintained and monitored.

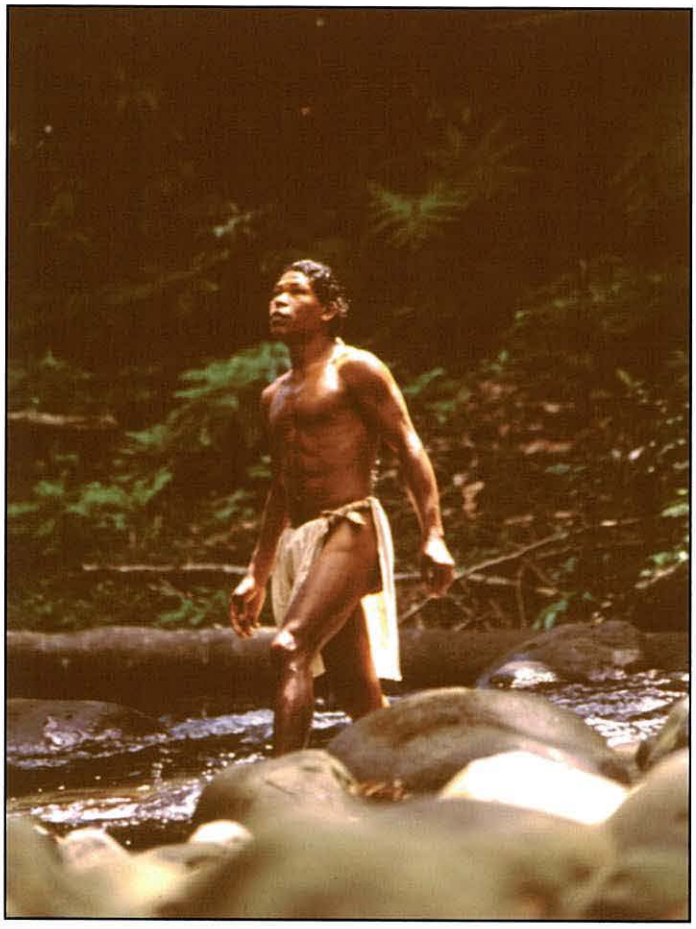
Both wet and dry season translocation experiments were carried out, with two replicate enclosures filled with control populations and two replicate enclosures filled with montane rainforest specimens. The intensity of selection was calculated from multivariate differences between survivors and non-survivors. Partial regressions allowed selection coefficients to be calculated for specific character traits permitting speculation on trait specific directional selection. Results indicate that significant and rapid selection occurs in the montane populations following the selection event.

Due to the pronounced geographic variation in phenotype of *Anolis oculatus*, shown to be congruent to several environmental parameters, it is suggested that the observed natural selection, is at least partly due to environmentally induced selection from current ecological conditions. To further test this theory, twelve experimental populations, sourced from an environmental gradient from across Dominica, were translocated to the enclosures. The results show a gradient of selection intensity, strongly suggesting an environmental component is significantly present in the natural selection experienced by the experimental populations.

To investigate an aspect of the evolutionary ecology of *Anolis oculatus*, sexual size dimorphism was recorded across the species range and tested against a variety of behavioural, ecological, environmental, and phylogenetic variables. This study reveals that sexual selection, in the form of male-male competition, appears to be the most closely linked trait to the observed patterns of sexual size dimorphism. However, gender specific diet selection is also a significant component in the ecology of sexual size dimorphism.

Finally, a common garden experiment was conducted to test for the presence of environmentally induced phenotypic plasticity in many of the character traits used to assess natural selection. This was done by incubating, hatching, and raising anoles from nine environmentally distant habitats in a common garden enclosure and testing the common garden juvenile phenotypes against those of source population specimens. Results suggest that environmentally induced developmental phenotypic plasticity does not significantly effect the character traits under analysis.

ACKNOWLEDGEMENTS.



Paulinus, a friend, and a native Dominican Carib (Tieno) tribesman.
He did a great roast Cockoy.

ACKNOWLEDGEMENTS.

I must thank my supervisor, Professor Roger Thorpe, for his time and guidance, without which, this thesis would not be possible. I am also indebted to my good friend, Mr. Percy Pierre, and to his wonderful family, without whom, my enclosures would have disappeared under vegetation, and for providing great company at Fort Shirley. I also hold gratitude for the help of Mr Arlington James, Senior Forestry Officer, for his support of my research within the National Parks of Dominica, and I thank the Forestry and Wildlife Department for their help. Forester Mr Randolph Winston worked hard to help me build enclosures and was a fine friend. I thank BBSRC for their kind funding of the studenship, and NERC for grant support to RST and AM. I am most grateful for the discussion of sexual size dimorphism and analytical guidance, provided by Dr Nick Giannasi, as well as being a great housemate. I must also thank Dr Anita Malhotra, for help in collecting lizards for the first enclosure experiments, and making available phylogenetic data. Alex Jones was also a help and good company; our afternoon on a beach full of French girls, on Isles du Gossier, will stay with me forever.

My time at Bangor University has been made pleasant by the friendly support of many people. Ms Ann Pennel and Dr Richard Arnold made me feel welcome, and helped feed my enthusiasms, and Ann has become a wonderful 'agony aunt' during my various academic traumas. In Dominica my fine Rastafarian guide to life, Bobby, helped me focus on life in the present, and chilling out with Clem was always fun. I thank Rufus and Vera for good beer, fine roties, and fun. I also have fond memories of my kind friend, Kris, at Seabird Café, for timeless conversation, good juice and great books. A truly enlightened lady. My great friend and comrade, Andrew Routh deserves my thanks for keeping me sane, for top wildlife fun during his visits, for providing a good ear, for proof-reading of my unintelligible English, and for joining me in making crawling up to birds in rivers an art. I'll never forget our afternoon swimming amongst Sperm whales, and I doubt he will either. I also thank Helena, Mel, Holly, and Camilla, for being good companions, and great diversions during my PhD. The analysis and writing up of my PhD has been made sufferable by the high jinks, and various capers of the BWA of D2. Dave Gay Wilcockson has been a great sporting companion, despite his legendary delusions of grandure; Sport Ken AKA Nick Hardman, has been a great mate, and I love his kids. Si Creer has amused us all with his alcoholic antics and Pat 'Velcro' Whithers is always on hand to lighten the mood with his gesticulations of self-pleasure. Amber has been kind company and good conversation, and Leigh and Cathy have been good lab mates.

However, my true gratitude is to my Mother, who raised me to love the world, without prejudice. Without her time, care and selflessness in encouraging me, none of this would have been conceivable.

CONTENTS.

A male *Anolis oculatus*, pictured in silhouette, through a banana leaf.

CONTENTS.

CHAPTER 1: GENERAL INTRODUCTION.

CHAPTER 2: TESTING FOR NATURAL SELECTION.

CHAPTER 4: SEXUAL SIZE DIMORPHISM

CHAPTER 1:

GENERAL INTRODUCTION.

A distinctive female *Anolis oculatus*, from the Elfin woodland habitat above Borie Lake.

1.0 GENERAL INTRODUCTION.

1.1 EVOLUTION.

"A major problem in evolutionary biology is to understand why the organic world is as diverse as it is, both in terms of its extraordinary variety in structure, function, and life histories, and its sheer numbers." – Grant 1998.

This statement represents the motivational crux of investigations into the complexities and processes of evolution presented to the modern biologist.

Wallace (1865) and Darwin (1874), with original thought, brought the first sense of reasoned logic to observations of diversity in the organic world. By identifying some of the basic processes of evolution, they laid open the natural world, with its seeming inexhaustible complexity of structure, and process, to the equally complex, and inexhaustible study of evolution and ecology.

If we embrace the concept of evolution then any organism, or group of organisms, exist in there present state as a consequence of evolutionary process. A variety of causes of evolutionary change in populations have been described. These including natural selection, when environmental and biotic factors influence the frequency at which genes are passed on to the next generation, and genetic drift (Lande 1975). This is when random changes in gene frequency can induce a population shift, in terms of phenotype means within the population. This will result in a 'direction' movement on the phenotypic landscape. Bottle necking or founder effect (Ambrose 1998; Lawler et al 1995) is also a significant factor in evolutionary change. This

results when a constriction in numbers of individual in a population bias the transfer of gene frequencies in the gene pool of future generations. However, it is the processes of natural selection (Wade and Kalisz 1990), together with sexual selection (Stamps 1983), that are largely regarded as the predominant force of evolutionary change and ultimately speciation (Magurran 1998; Foster et al 1998; Coyne and Orr 1998; Losos et al 1994). Natural selection forces may act to cause directional, disruptive or stabilising selection (Wagner 1996; Lande 1995).

In this study, it is the function of natural selection that is the topic of investigation together with its cause and/or consequences. Phylogenetic reconstruction of closely related species or populations can give valuable insight into the processes of evolution but remains a poor explanation for extant variation in phenotype observed in many subjects. However, a phylogenetic tree can be invaluable in assessing the degree to which the state of an observed trait exists as a consequence of its phylogenetic history. This study does not dwell on the molecular analysis of its subject but is an analysis of present phenotype and ecology with regard to each other. However, mitochondrial DNA phylogenetic reconstruction of previous investigators of the model, are used to assist in the interpretation of selection processes under discussion.

1.2 NATURAL SELECTION.

Natural selection may be seen as the effect of environment, and ecology, on lifetime fecundity of an individual (i.e., its fitness), with its ability to contribute to the future gene pool of its species or population. While lifetime fecundity is difficult to assess, it has been shown to be feasible to demonstrate a measure of fitness in field studies. Various studies indicated fitness through terms of survivorship, mating success, fertility and condition (Tinkle 1965; Lennington 1980; Grant 1998, Endler 1985; Brodie et at 1995).

When investigating natural selection, it is essential to first distinguish clearly the difference between selection and evolutionary response to selection (Arnold and Wade 1984). Recordable changes in mean character states within a generation are, according to Arnold and Wade (1984), the result of natural selection. This has been exemplified by Schluter and Smiths' (1986) study of beak and body size in the song sparrow *Melospiza melodia*. Natural selection as a force can be described in both phenotypic and genotypic terms within a population over time. Evolutionary response to selection, however, will be detected in a change in phenotypic mean and genotype from one generation to the next, and is dependent on inheritance. Such selection may be directional as in Endlers (1985) field studies of the guppy, *Poecilia reticulata*, which illustrates the role of predation, and sexual selection on body size and coloration. Directional natural selection is also observed in such models as the common house sparrow where the phenotype shift observed is a result of climatic selection forces (Johnston and Fleischer1981). Natural selection may also be stabilising. This occurs when the extremes at both ends of the frequency distribution are selected against. Disruptive natural selection occurs when the extremes are

favoured at the expense of the centre of the distribution. In Gray and Cades (1999) study of the field cricket, *Gryllus integer*, male song pulse frequency is disrupted in its distribution by the parasitoid fly, *Ormia ochracea*, that locates the cricket by its song. The fly prefers to target male crickets with average song pulse frequency within the population, as does the female cricket. Therefore the female cricket exerts stabilising selection in contrast to the disruptive influence of the parasitoid fly.

As stated above, it is believed that fitness is a quantifiable variable (Wade and Kalisz 1990). A statistical relationship may be deduced between fitness and phenotypic characters. This can be calculated from changes that occur in the character trait means *within* a generation. The measure of covariance between relative fitness and a quantitative change observed in a character trait is equivalent to the mean change induced within a generation, by selection forces (Robertson 1966; Bulmer 1980). It is this shift in covariance that has been termed the selection differential. When observed in a character trait, it is a simple mistake to assume that it is the observed trait that is under direct selection. This may be so, but is not necessarily the case. Pearson (1903) demonstrated clearly that such an observed shift in a character trait may be entirely the result of correlation to another unobserved character trait that is under selection pressure. This emphasises the need to include as many variables as is feasible in such studies. Under multivariate investigation, as in this study, selection can be partitioned if the correlated characters under selection pressures are included in the analysis. It is of course impossible to claim that all variables have been accounted for in such studies, due to the complex expression of traits and their sheer numbers in any organism. It is suggested that a partial regression (Lande 1979; Lande and Arnold 1983) can deduce the degree to which a character trait is selected for or against and

produce a selection coefficient to illustrate this. However, bearing in mind the points made above, such results must be met with caution.

By considering and observing the overall change in mean character states within a population both before and after a selection event, selection intensity may be derived. This constitutes a within generation measure of selection intensity. By calculating selection coefficients for individual character traits from partial regression coefficients, it is possible to assess character specific directional change within the population under selection and therefore the effect on fitness. Such selection coefficients are occasionally referred to as selection gradients in the literature (Brodie et al 1995), but will be referred to as selection coefficients throughout this study. An assessment of fitness may also be conducted by measuring survival, ontogeny, and fecundity in individual organisms. By recording such variables throughout a selection event, changes in fitness may also be deduced. Thus, with the use of a multivariate approach, selection intensity (difference in means before and after selection), selection coefficients (selection gradient), and fitness (measured as survival, condition, or reproductive success) may be assessed (Brodie et al 1995).

However, in assessing selection intensity, and selection coefficients, it becomes valuable to test for phenotypic plasticity operating in a character trait (Holopainen et al 1997). Any observation of phenotype frequency, or shift in mean, within a population cannot be absolutely attributed to selection until phenotypic plasticity is accounted for.

Ecology must be an integral consideration of any investigation of natural selection. As stated above, regardless of phylogenetic history, the present phenotype of any group of organisms may be at least partly attributable to selection resulting from immediate ecological conditions. Orr and Smith (1998) demonstrate in a variety of subjects as diverse as the apple maggot fly, and Cichild fishes, that natural selection caused by shifts in ecology has led to adaptive divergence between populations, and is implicated in speciation. They have integrated both laboratory, and field experiments to demonstrate that ecological shift can result in rapid rates of evolutionary divergence in the apple maggot fly. Taylor and McPhail (1999) also illustrate the important role of natural selection acting on trophic ecology as a major component of ecological speciation in *Gasterosteus* sticklebacks. In this model benthic and planktonik trophic divergence is suggested. Many other studies illustrate natural selection as a response to a shift in ecology (Vitt et al 1997; Carlier and Lefebvre 1996). A broad ecological address is essential if one is to postulate cause in observations of natural selection.

1.3 ISLAND STUDIES.

The reason for focusing on island studies when investigating evolution and natural selection is that islands represent simplified models. This is both in terms of species diversity coupled with a generally higher density of those species present than would be anticipated in a mainland system (Grant 1997). It is essentially a difference in scale that differentiates islands from mainland. Ecological release is also more commonly noted to occur on islands. It was this fact that aided both Darwin (1871)

and Wallace (1865) in there formulation of evolutionary theory. However, it was the publication of MacArthur and Wilsons '*The Theory of Island Biogeography*' (1967) that established the island model theory as ideal for the investigation of both evolution and ecology. Island communities are generally non-representative, or at least highly simplified in relation to mainland communities. In the case of islands of oceanic origin, (for islands may result from the loss of a land bridge) the different dispersal abilities of different taxa and their differing adaptability to compete as colonists, allows great opportunity for divergent evolution from ancestral states. Islands are considered experimentally favourable as specimen densities tend to be high and so sample size becomes less of an issue. The fact that islands occupy a discrete area makes it possible to sample the complete range of a species. Clusters of islands also provide the opportunity to observe parallel systems in evolution, in many cases (Brown et al, 1991; Endler 1985; Thorpe and Malhotra 1996). One must also note that 'islands' are not necessarily surrounded by water. Altitude is capable of creating an ecological island in terms of an area of specific habitat type that is separated from other similar ecological islands. A set of generalities tend to apply to islands including an attenuated climate (in the case of oceanic islands as temperature extremes are reduced by oceanic buffering), abundant food supplies, wide ecological niche availability and relatively few predators or ecological competitors as a result of the reduction of total number of species present.

A consequence of these factors is that island species tend to exhibit high population density and high intraspecific competitive pressure. It is these elements that make an abundant species ideal for the study of evolution and ecology.

1.4 THE COMMONWEALTH OF DOMINICA.

Situated near the centre of the Lesser Antillean arc of volcanic islands in the Eastern Caribbean, the Commonwealth of Dominica represents a classical young tropical volcanic island in both geological and biological terms illustrated in the map of figure 1.1.

Although the geological history of the eastern Caribbean is broadly understood (Pindell and Barret 1990), it is complex and open to some contradictions (Morris et al. 1990). Although volcanic activity has occurred in the region since the early Eocene approximately 40mya (million years ago), volcanic activity giving rise to Dominica is not believed to have begun until approximately 15mya in the late Miocene period. It is likely that Dominica did not stabilise as an island until the Pliocene approximately 5mya but subsequent oceanic submersion cannot be ruled out (Carr and Stoiber 1990). In its present state Dominica is 16km at its widest point, by 45km long and has four (presumed dormant) volcanic peaks over 1000m running its length, the tallest of which, Morne Diablotin reaches an altitude of 1421m. These mountains represent a barrier to the passage of the prevailing moisture laden north-easterly trade winds and result in considerable precipitation along the Easterly aspect of Dominica as well as at altitude (Lang 1967). This is illustrated in figure 1.2. It is this combination of variance in precipitation and ranges in altitude that permits Dominica a broad distribution of habitats (Beard 1948).

Along the Caribbean coast of the West of Dominica, where precipitation levels are lowest and temperatures high, xeric woodland is the predominant habitat that experiences a pronounced dry season from February to July. The species assemblage

Figure 1.1 The Lesser Antilles

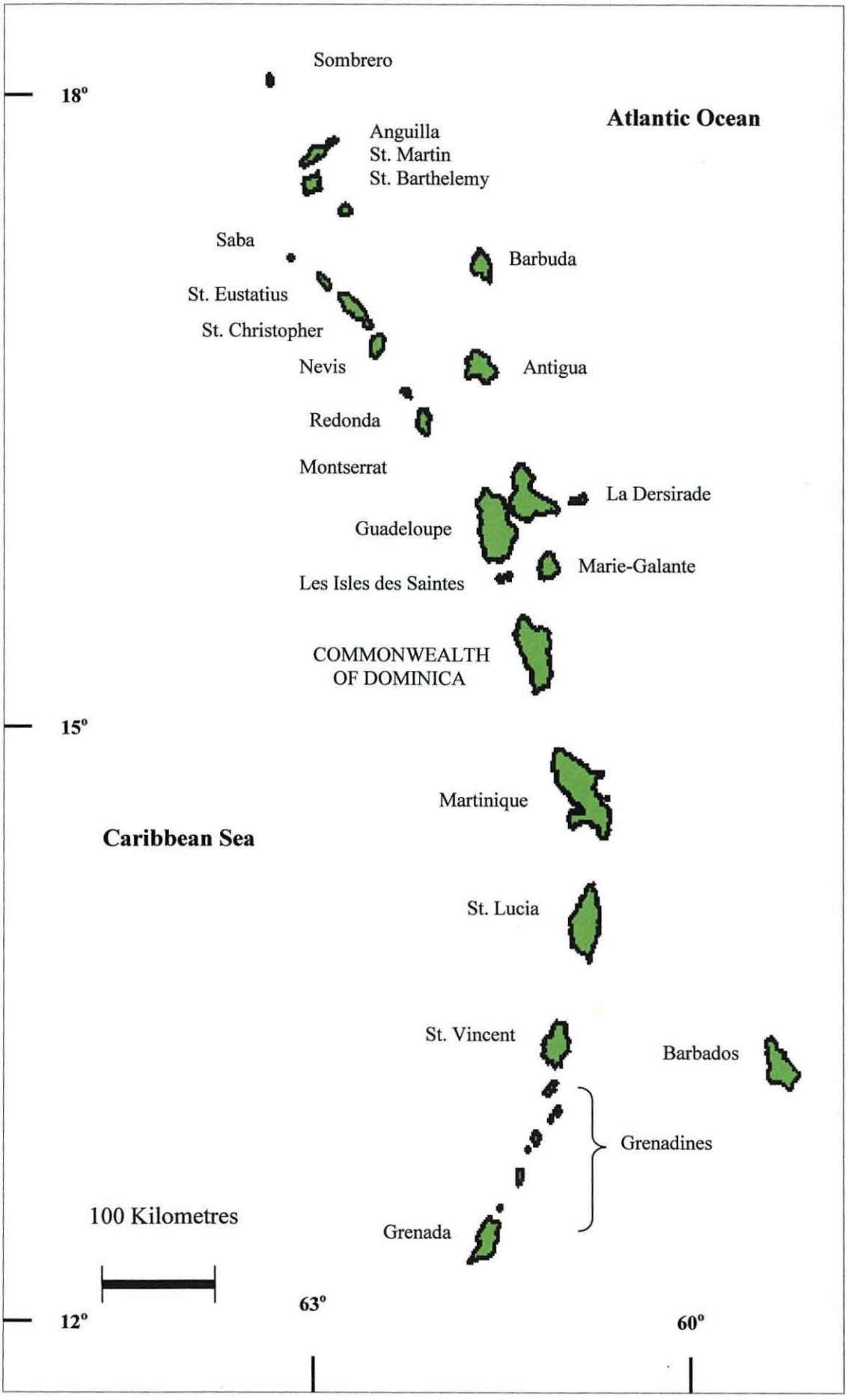


Figure 1.2. Topographic/Precipitation Cause of Ecotype Variability.

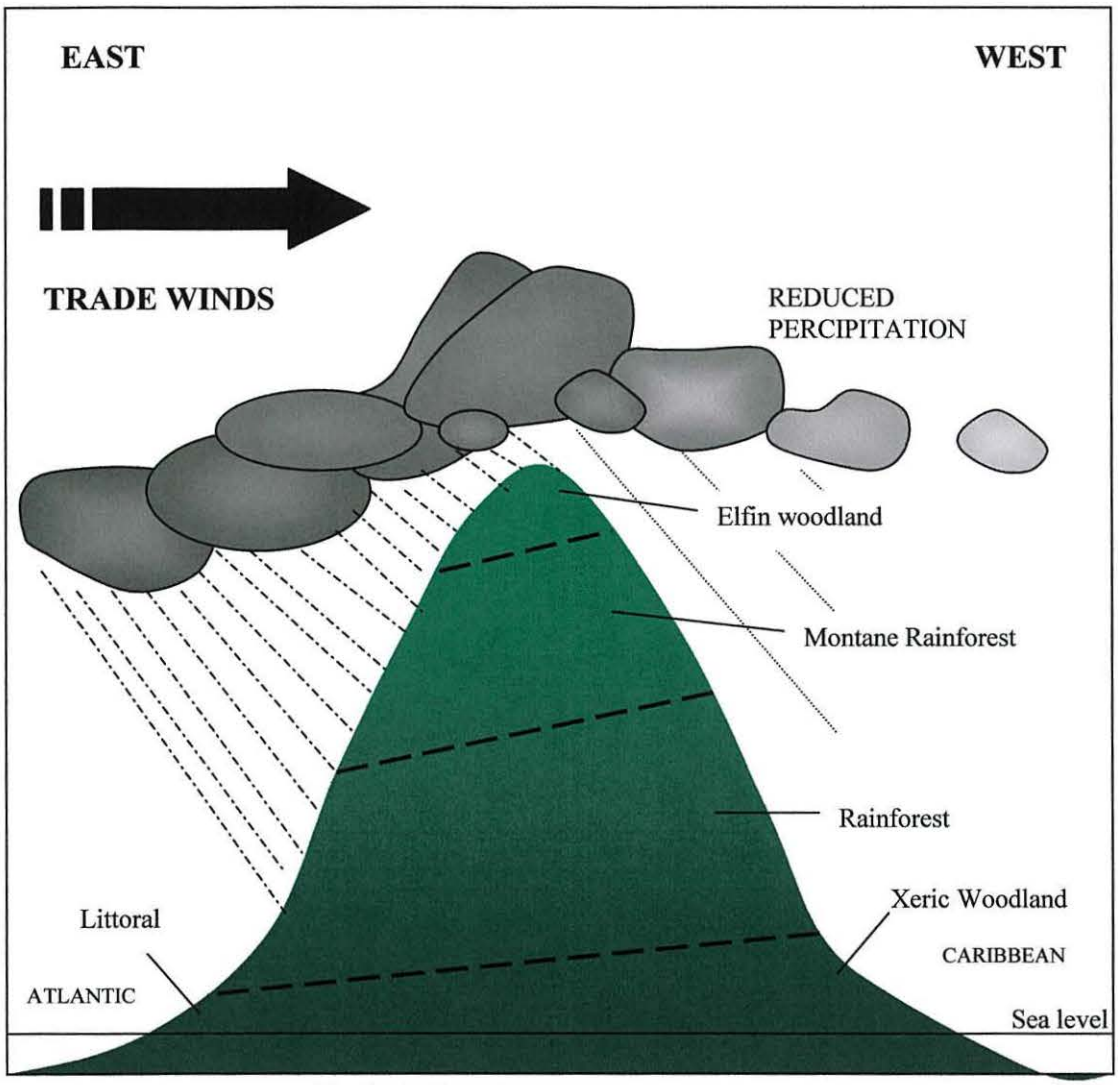


Figure 1.2 represents the altitudinal effect of precipitation distribution over Dominica (redrawn from Malhotra 1993)

here is characterised by savonette, *Lonchocarpus pentaphyllus*; *Pisonia spp* and the campeche tree, *Haematoxylon campechianum*. The Eastern Atlantic coast possesses a distinct vegetation type known as littoral woodland and consists of a mixture of xeric woodland and rainforest species with a bias to halophytic species, a consequence of the salt laden onshore winds. The species assemblage here is characterised by white cedar, *Tabebuia pallida;* sea grape, *Coccoloba uvifera;* and West Indian almond, *Terminalia catappa*. As altitude is gained, both these vegetational ecotypes give way to low altitude rain forest that becomes high altitude montane rain forest at approximately 800m, the two being distinguishes by a subtle change in tree species assemblage. This is characterised by the dominant species of kaklin, *Clusia plukenetii*; Bois diable, *Licania ternatensis*; carapite, *Amanoa caribaea*, at rainforest altitudes, and the two montane rain forest giants, the chataignier, *Sloanea spp*. and the gommier, *Dacryodes excelsa* higher montane elevations. Throughout the rain forest environments creating an under-canopy is the tree fern, *Cyathea spp*. Emerging above 1000m in altitude is stunted forest of epiphytes and bryophyte covered kaklin trees and gumbo montagne, *Hibiscus tulipiflorus* that is known as elfin woodland (Edwards and Dunn 1991). In the north of Dominica a small area of mangrove swamp persists, but its restricted range makes it of little ecological importance to the island as a whole except for migratory waders. Hodge (1943) also characterised the vegetational zones of Dominica, but did not distinguish rainforest from montane rainforest. These five major ecotypes are illustrated in plates 1.1 to 1.5 and have their distributions depicted in figure 1.3.

Plate 1.1 Caribbean Coastal Xeric Woodland

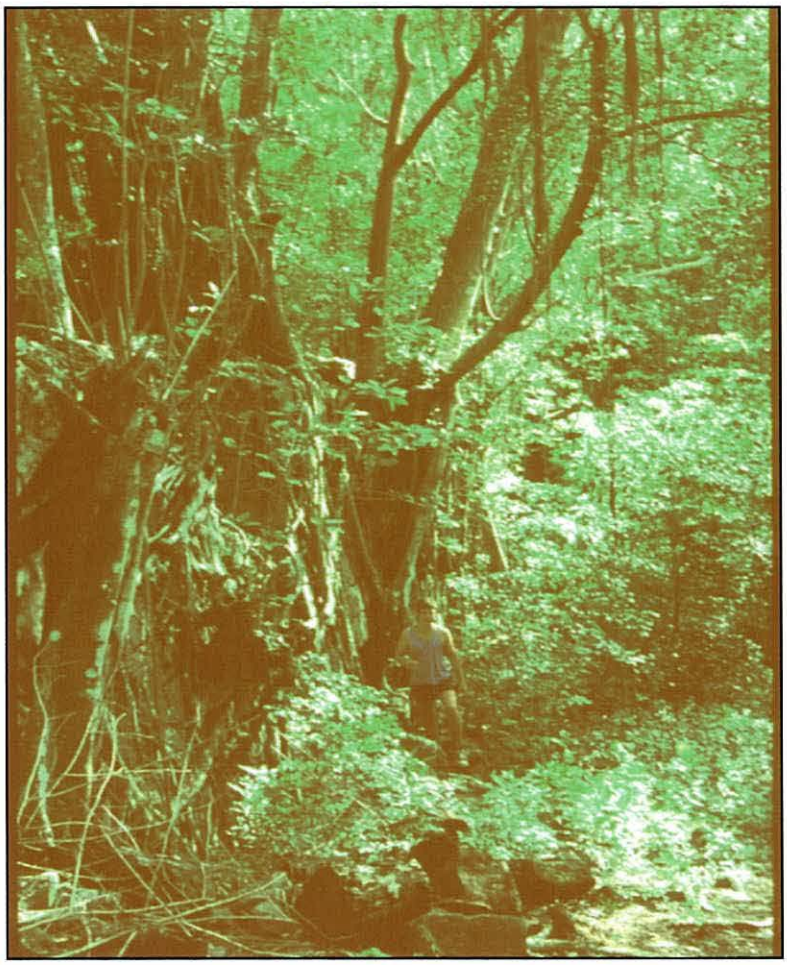


Plate 1.1 illustrates Caribbean coastal xeric woodland, dominated by *Ficus citrifolia* (left); *Bursera simarouba* (centre), and other sapling hardwoods, such as *Ceiba occidentalis*, and *Hura crepitans*.

Plate 1.2 Atlantic Coastal Littoral Woodland

Plate 1.2 illustrates the exposed nature of littoral woodland on the Atlantic coast of Dominica. The salt laden winds give the West Indian Almond and others, the distinctive 'hedged' appearance. Pictured is Womabati Bay.

Plate 1.3 Rain Forest

Plate 1.3 illustrates the lush understory and canopy of rainforest, the dominant vegetational community on Dominica. *Cyathea spp.* and *Eugenia spp.* in the understory with *Tapura latifolia* and *Sterculia caribae* common amongst the canopy. Pictured is the beautiful forest slopes of Morne aux Diables.

Plate 1.4 Montane Rain Forest.

Plate 1.4 illustrates the diverse forest floor of montane rainforest, dominated by *Dacrylodes excelsa* (centre), and *Sloanea spp* where the canopy height may reach 27-30 metres. Epiphitic plants and lianas adorn the buttressed trunks in this facinating environment. The forest pictured is on Rose Ridge, leading up Morne Diablotins.

Plate 1.5 Elfin Woodland

Plate 1.5 illustrates elfin woodland surrounding the high altitude (3000ft) Boeri Lake. Although *Cyathea spp.* tree ferns can survive in sheltered areas, Kaklin, *Clusia venosa* is the dominant tree species, stunted to a canopy height of 2 to 5 metres.

Figure 1.3. Major Habitat Classification.

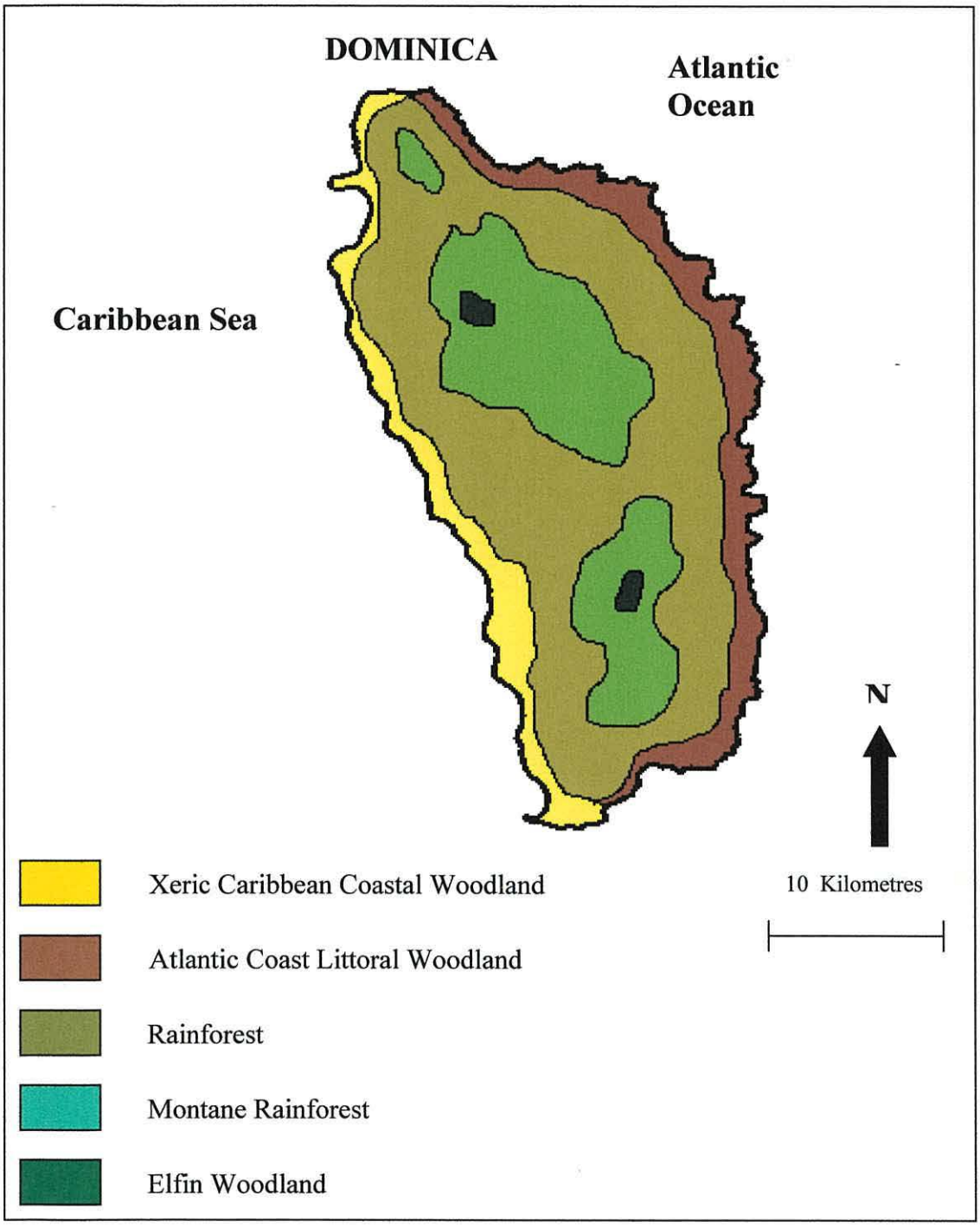


Figure 1.1 represents the distribution of major ecotypes over Dominica (Edwards and Dunn 1991).

1.5 ANOLES, AND *Anolis oculatus,* AS A MODEL.

Anoles represent a highly successful genus of lizards (Iguanidae) present throughout the islands of the Caribbean and Central South America. Consisting of over 300 species, *Anolis* are one of the most specious terrestrial vertebrate genera (Swartz and Henderson 1995). The islands of the Caribbean Sea contain over 150 of these species where they represent one of the most abundant vertebrates after the *Eluthero*dactylus *spp*. frogs of the region (Williams 1969). In general, anoles are small (<60mm snout to vent length) semi arboreal insectivores, capable of occupying a wide range of niches (Williams 1983). It is the study of this wide range of niche occupation by anoles that have led to the development of an understanding for the complex structured spatial communities. Generally these exist on the larger islands of the Greater Antilles where up to twelve species of anoles may exist in sympatry (Rand and Williams 1969).

This spatial microhabitat partitioning between species results in a predicable pattern in phenotype, specifically morphometric dimensions of the anoles concerned. These have been termed 'ecomorphs' and represent adaptation specific to the microhabitats they inhabit (Williams 1972; Losos 1995). Losos (1996) has demonstrated that these patterns of ecomorph adaptation have evolved independently at least three times on different islands in the Greater Antilles. Such a complex system doesn't exist between species in the Lesser Antilles, the subject of this study. This is probably due to the considerably smaller nature of the Lesser Antilles, being simply too small for multi-species complexes to arise. None of the Lesser Antillean islands (or island banks) naturally contain more than two endemic species of anole (Schoener 1970),

and most islands possess only one species. The species distribution of Anolis spp. across the Lesser Antilles is illustrated in figure 1.4.

The Commonwealth of Dominica, situated in the centre of the Lesser Antilles and demonstrates a typical single endemic species, *Anolis oculatus* (Cope) characterised by subrectangular prenasal scale. It is a member of the *bimaculatus* group, identifiable by the presence of two enlarged postanal scales in the males. All the anole species of the Lesser Antilles, including and north of Dominica, are members of the *bimaculatus* group. All anole species to the south of Dominica in the Lesser Antilles are members of the *roquet* group. *Anolis oculatus* is a medium sized anole with maximum snout to vent lengths ranging from 61 to 98mm across its range (Malhotra and Thorpe 1992). It is a highly phenotypically variable species and the variance in phenotype shows strong congruence to environmental variation in ecotype (Malhotra and Thorpe1991b). In previous studies this variability in phenotype and its correlation to habitat type led to the presumption of sub-species within *Anolis oculatus* (Lazell 1962). Lazell (1962) proposed four ecotype specific sub-species within *A. oculatus*; these being *A. oculatus oculatus*, ranging over the southern Caribbean coast; *A. oculatus cabritensis*, ranging over the northern Caribbean coast; *A. oculatus winstoni*, extending the full length of the Atlantic coast of Dominica and *A. oculatus montanus* occurring throughout the montane rain forest. An undefined large range of intermediates between these sub-species was also noted. The range of these sub-species is illustrated in figure 1.5 and can be seen to largely reflect the patterns of vegetation type distribution as discussed in chapter 1.5. Sub-species classification is of considerable question and a legitimate study in itself (Thorpe 1987). A lack of congruence to the proposed pattern of sub-species distribution

Figure 1.4 Distribution of the Genus *Anolis* over the Lesser Antilles.

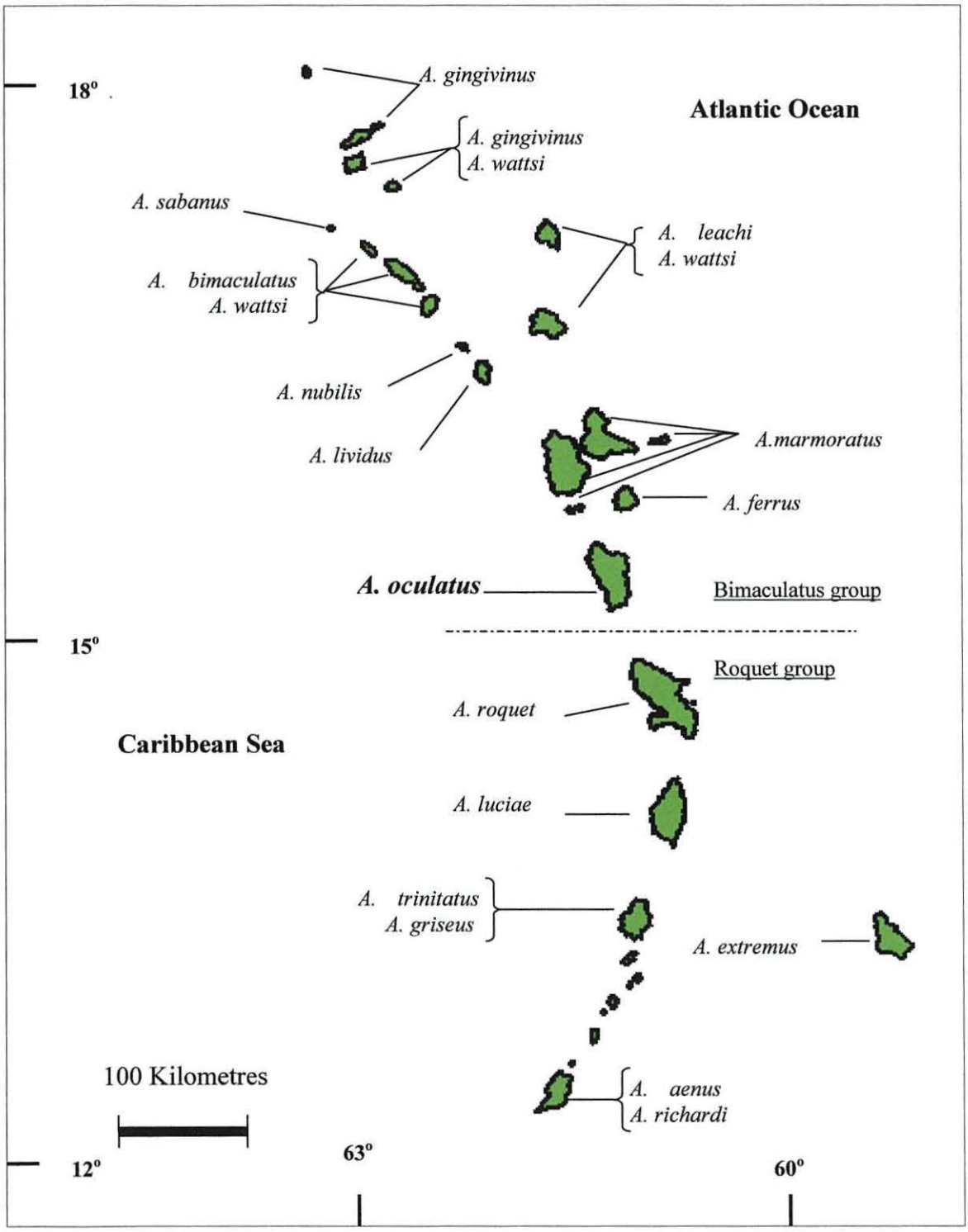


Figure 1.5. Subspecies Classification of *Anolis oculatus* by Lazell, 1962.

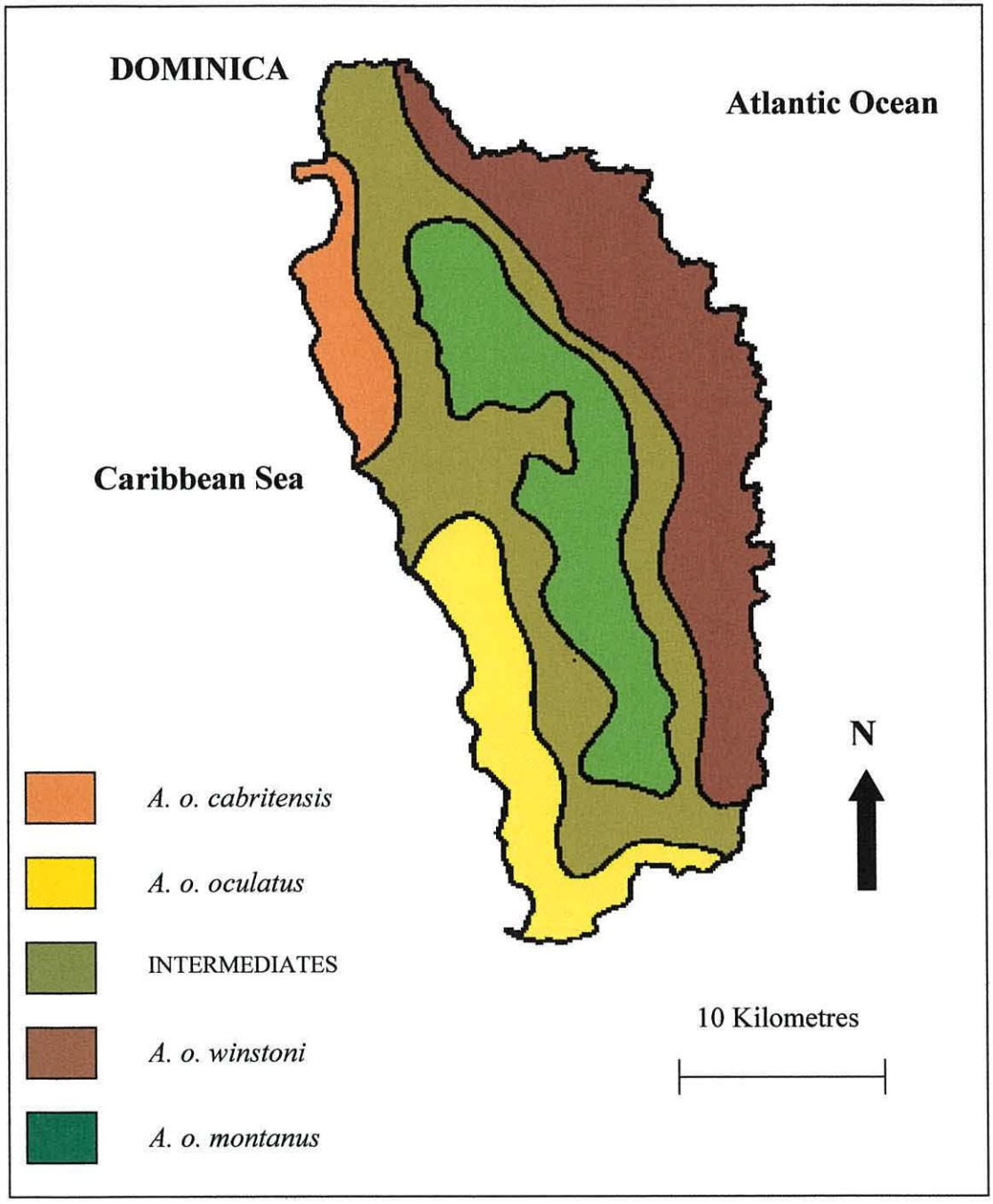


Figure 1.5 illustrates the range of the four sub-species described by Lazell (1962). The congruence with habitat ecotypes is clearly seem when considered against figure 1.3.

between a selection of variables, led to the dismissal of lazells sub-specific classification (Malhotra and Thorpe 1991b). Brooks (1968), and Ruibal and Philibosian (1970), state *Anolis oculatus* as a eurytherm, with no observations of heliothermy often associated with Squamata. *A. oculatus* is generally regarded as an insectivore with a relationship between body size and insect abundance (Roughgraden and Fuentes 1977; Andrews 1976, 1979).

Anolis oculatus also offers itself as an ideal experimental model, by virtue of the research already conducted on various aspects of its biology. The geographic variation in *Anolis oculatus* has been exhaustively studied, and the research illustrates the strong congruence in general colour pattern, body proportion, and squamous character traits to environmental variables (Malhotra 1992; Malhotra and Thorpe 1991b; Malhotra and Thorpe 1992; Malhotra and Thorpe 1992b, and Malhotra and Thorpe 1997).

Anolis oculatus has also been the subject of the study of natural selection (Malhotra and Thorpe 1991). In this study, geographically distinct populations of *Anolis oculatus* were translocated to enclosures to test for the action of current selection forces on natural populations. Multivariate morphometric profiles revealed that certain populations underwent a significant shift in mean character states over a selection event (translocation), indicating selection intensity. Such selection intensity was found to correlate with the magnitude of the difference between the ecological conditions of the enclosure site, and the original habitats of the translocated populations. These results suggest that ecogenesis, the adaptation to present

ecological conditions, plays a significant role in influencing the phenotype of *Anolis oculatus*.

The molecular phylogenetics of *Anolis oculatus* have also been addressed. Malhotra and Thorpe (1999), reconstructed the phylogenetic interrelationships of 33 populations of *Anolis oculatus* from across its range, using mitochondrial DNA. Microsatalite studies of *Anolis oculatus* are also in progress in the Bangor reptile research group, and have identified an anomalous area of its range in the Southwest of Dominica, where a significant barrier to geneflow appears to exist (Stenson, Malhotra and Thorpe pers. com.).

1.6 GENERAL AIMS.

The general aims of this study were; first to observe and test for selection operating on translocated populations of *Anolis oculatus*, while including assessing selection intensity and the relative fitness in the populations (chapter 2, chapter 3). Second, to observe and test the observed trends in sexual size dimorphism in *Anolis oculatus*, against both ecological and phylogenetic variables to gain some insight into the nature and interrelationships of evolutionary ecology, and sexual selection (chapter 4). Finally phenotypic plasticity in *Anolis oculatus* was tested to substantiate the conclusions drawn from the natural selection experiments, and other studies of geographic variation in this species (chapter 5).

CHAPTER 2:

TESTING FOR NATURAL SELECTION: EXPERIMENTAL TRANSLOCATION.

The Cabrits peninsula, north Caribbean coast, Dominica. Location of the translocation experiment enclosures, situated in the characteristic Caribbean coastal xeric woodland.

2.0 INTRODUCTION.

Despite great interest in the processes of evolution, field experimentation into the cause and effect of natural selection on wild populations are still uncommon. By the very nature of isolating a wild population of organisms from their conspecifers, enclosure experiments are ambitious. The potential results however, may be sufficiently rewarding to justify the efforts involved.

2.1.1 FIELD TRANSLOCATION EXPERIMENTS.

Natural selection may be viewed as a response of the phenotype and genotype to environmental variables resulting in a level of 'fitness' of an organism. It is, therefore, these variables that are employed to measure the fitness of an individual, or population, within a specific environmental context (Schluter 1988). Downhower et al (1987) use number of matings, number of mates, mortality, offspring and/or clutch size as a measure of fitness. One must not lose sight of the fact that all these variables do indeed provide a measurable indication of fitness, but they are inadequate in assessing lifetime fecundity, which is the ultimate factor of an organism's fitness. Thus, to fully demonstrate natural selection as operating on individuals in a population, experimental analyses must be carried out on natural populations. These analyses, to be valid, will often demand a natural habitat. Such situations, when manipulated, can provide quantitative measures of natural selection. It is this premise that has lead to the practice of analysing isolated natural populations of organisms to test for natural

selection (Halkka, Halkka and Raatikainen 1975; Breden and Wade 1989; Endler 1991; Malhotra and Thorpe 1992; Roughgarden 1995).

Experiments studying natural selection in the wild include Via (1991) and Bell (1991). Both tested locality specific natural selection, where selection intensity and/or direction appeared to be environmentally influenced. Malhotra and Thorpe (1991), Hughes (1992) and Johanesson et al (1990) have tested differential selection between classified habitat ecotypes. Hoffermann (1981) investigated natural selection along a cline. The use of vertebrate models in such studies was pioneered by Endler (1973) in his studies of natural selection operating on isolated populations of *Poecilia reticulata* fish in the streams of Trinidad.

Because of the logistics involved, terrestrial vertebrate studies into the effects of natural selection acting on wild populations, are rare. Terrestrial vertebrates are generally characterised by their K (carrying capacity optimisation) selected reproductive strategies, with often considerable generation times. As vertebrates are generally larger than invertebrates, they will usually require a large area of habitat to sustain a viable experimental population. This is in strong contrast to traditional model species of invertebrates such as *Drosophila melanogaster*, or microbial models. In such models reproductive strategies are strongly R selected. With minimal generation times and organism size and density perimeters are such that the populations may be laboratory maintained and manipulated.

Experiments capable of indicating direction and intensity of selection make such studies invaluable to a further understanding of natural selection and evolutionary

processes. By the use of statistics that detect the degree of difference in variables between group means, and the selection coefficients of those variables, one can elucidate both intensity and direction of selection pressures with some statistical confidence. To focus only on easily manipulated invertebrate models is to overlook the equally complex role of natural selection acting on 'higher' organisms in their natural environments (Ayre 1985, Malhotra and Thorpe 1992, Losos et al 1997).

2.1.2 DIRECTIONAL SELECTION.

In *Anolis oculatus* geographic variation has been shown to reflect patterns in the environment (Thorpe and Malhotra 1992). Correlation between phenotypic character sets and such environmental variables can be taken as evidence that strong environmental influences are driving, to some degree, phenotypic variation in the model (Endler 1980). If such adaptation to environmental conditions exist in a species then the translocation of an experimental population into a quantifiably different environment within the species range should yield further evidence for natural selection in action. This should demonstrate itself in an increase in the intensity of directional selection, and significant coefficients of selection that are the targets of selection. Such results would suggest current selection operating on the translocated population.

Therefore, one may predict that the translocation of a population into a sub-optimal habitat, will lead to an increase in the intensity of directional natural selection on the translocate phenotype (Wright 1935). Thus, it could be anticipated that the direction

of selection acting on the translocated population may lead to a convergence of phenotype in the translocated population, towards that of the control population, resident in the translocation environment. However, this is not necessarily the case. Because phenotypically, the closest ecological optima to the translocated population source phenotype, in the translocated environment, may not necessarily be the same phenotypic ecological optima occupied by the control experimental population (Coyne et al 1997). It is possible that over many generations a degree of convergence between the two populations would be observed in phenotype, but the selection acting on the translocated experimental population may not be expected to do so in the short term.

2.1.3 THE *Anolis oculatus* MODEL.

Anolis oculatus is an exemplary model for such a study due to its generally high population density over the majority of its range of the island of Dominica (pers. obs.). *A. oculatus* is a highly fecund species capable of oviposition at intervals of around 12 days on average across its range (pers. obs.), reaching sexual maturity at six to nine months (Bullock 1988, pers obs). This is rapid by vertebrate standards in general; making it a relatively R selected subject in terms of terrestrial vertebrate reproduction. Its density in the three dimensional habitat of the natural range means that a relatively small and manageable area of habitat will be sufficient to sustain a viable experimental population.

Due to the arboreal nature of *A. oculatus*, a trunk-ground anole (Losos 1993, pers obs), enclosure design and maintenance must be assiduous. Digital lamellae and saltatory ability in *A. oculatus* mean that a robust enclosure design is important.

2.1.4 SEASONAL REPLICATION.

The seasonal climate of the Caribbean basin is characterised by a wet season from July to November, punctuated by the hurricane season in September and October and a dry season which reaches its highest temperatures from January to May.

Stabilising natural selection may be presumed in a population existing within a homogenous, stable habitat, but this may not necessarily be so (Fleming and Hooker 1975). Directional selection may operate on a population occurring within a single habitat ecotype due to seasonal fluctuations in the environment and climate. We may therefore anticipate that the direction and intensity of natural selection will vary accordingly with these seasonal trends in climate. These should be expressed in the selection coefficients where both intensity and direction of selection will be indicated. To test for such patterns it would be necessary to conduct both a wet and dry season translocation experiments.

2.1.5 CONDITION AND FITNESS.

Simple progressive mortality during experimental analysis within experimental populations may yield valid results, but the subtleties of selection pressure may also be detected by a measure of condition fitness of experimental animals. In male experimental animals this may be achieved easily from measures of growth. Such measures are invalidated in female specimens due to the physiological stresses of reproductive effort. This may be overcome by assessing the gravid state of an animal. However, personal observations reveal that re-absorption of an egg may allow *Anolis oculatus* to utilise yolk development as a lipid store and so some measure of actual oviposition is necessary.

2.1.6 RELEVANCE TO CONSERVATION.

The value of this study must also be considered with regard to conservation management techniques. Modern conservation programs often involve the introduction of translocated populations into reclaimed or protected habitat from which a species may have become rare or locally extinct (Tudge 1992). In considering the translocation techniques involved in this study, one may attempt to gauge some of the effects of translocation on mortality, condition and reproductive success of a translocated population of lizards both within and between seasons. The value of such knowledge is evident in Bloxam (1982), where the reintroduction of the Round Island herpetofauna is described.

2.1.7 AIMS.

It is intended to address the following topics: -

i). Is there greater selection intensity acting on a translocated experimental population, compared to a control experimental population?

ii). Using condition as an estimate of a component of fitness, in the male experimental population, and reproductive frequency as an estimate of fitness in the female experimental population, do experimental translocated populations have lower fitness than control experimental populations?

iii). Does seasonal variance in environment result in seasonal differences in fitness, selection intensity and directional selection, in translocated and control experimental populations?

2.2 METHODS AND MATERIALS.

2.2.1 HABITAT SELECTION.

To test for environmentally induced natural selection, by means of a translocation experiment, it is essential to identify the environmental gradient along which adaptation may have occurred. Malhotra and Thorpe (1992) found that the phenotype in *A. oculatus* co-varied with habitat, and that the habitat was classifiable into five climatically and altitudinally determined ecotypes (Lang 1961; Edwards and Dunn 1991). These habitats are i). Caribbean coastal xeric woodland; ii). Atlantic coastal littoral woodland; iii). Low altitude rain forest; iv). Montane rain forest; v). Elfin woodland. Details and illustration of these habitats are given in chapter 1, the general introduction.

To test for adaptation to environmental difference between sites (environmental distance), it is intuitive to translocate a population from a habitat with a maximal ecotypic distance from that of the translocate enclosure site. However, one must be cautious not to translocate a population from a habitat so environmentally different that the stress of translocation will be so great that any selective direction in mortality will be obscured by the sheer degree and rapidity of environmentally induced mortality. One must also consider the logistics and ethics, of obtaining a sufficient experimental population, as certain habitats are inaccessible and/or have a low population densities of *A. oculatus.*

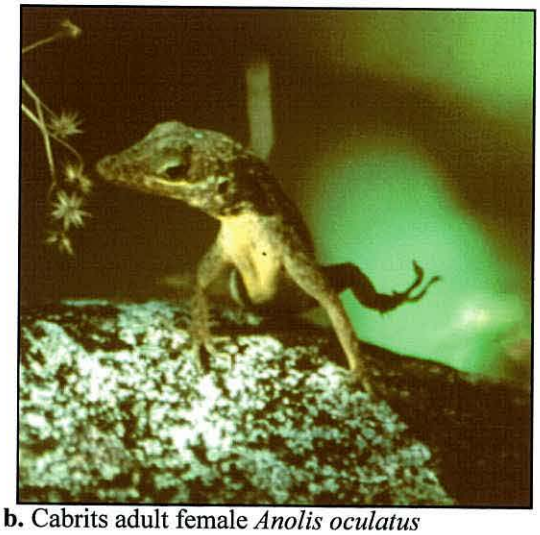
The choice of control population, and therefore, the site of experimental enclosure construction were the Cabrits National Park, a 2.2km peninsula on the north-west Caribbean coast of Dominica. This site was chosen for several vitally important reasons. It has ease of access, as such an experiment will require considerable man hours; its exceedingly high native density of *Anolis oculatus*; the extreme nature of its habitat, being one of the most xeric environs present on Dominica (Lang 1961), the fact that previous enclosure experiments had been conducted on the site, and so some enclosure construction persisted. This allowed for some time saving in construction from new, and confidence in the enclosure population sizes, due to previous successful experimental use (Malhotra and Thorpe 1991) . The final vital factor making the Cabrits locality ideal for enclosure construction and maintenance, is the presence of a competent member of Forestry staff who safeguarded the enclosures against tree fall and theft of materials.

Choice of a translocate population is also challenging for many of the reasons stated above. On consideration of ease of access and logistic distance from experimental site, adequate capture rate of experimental population, and significant ecological distance from the experimental enclosure site, the Syndicate montane rainforest reserve population of *Anolis oculatus* was chosen as the experimental translocate population. This population had also yielded a significant degree of differential mortality in a previous translocation experiment (Malhotra and Thorpe 1991). Male and female representatives of these populations are illustrated in plate 2.0

Thus, the control experimental population was selected from Cabrits at 10 to 25 meters above sea level in xeric woodland, and the translocate experimental population

Plate 2.0

a. Cabrits adult male *Anolis oculatus*



b. Cabrits adult female *Anolis oculatus*

c. Syndicate adult male *Anolis oculatus*

d. Syndicate adult female *Anolis oculatus*

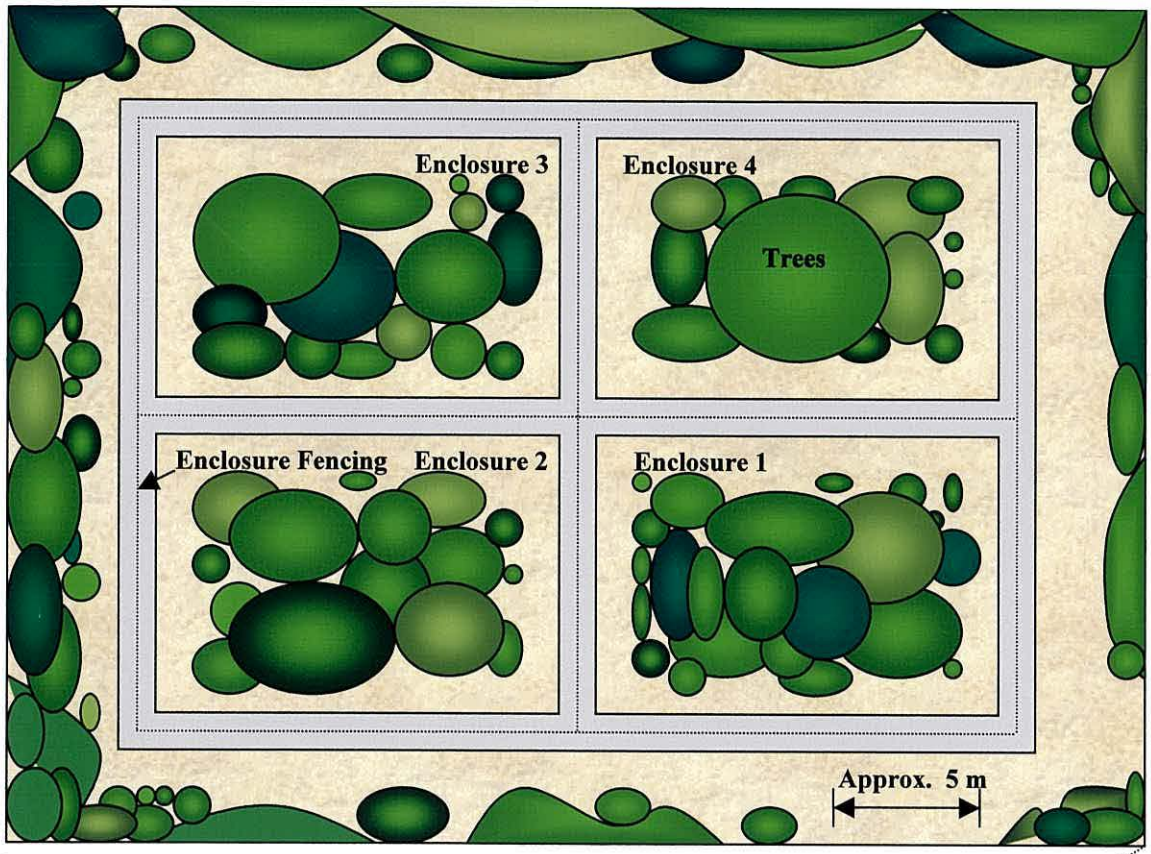
Plate 2.0 illustrates the extreme geographic variation in morphology and colour pattern exhibited between the two experimental populations of *Anolis oculatus*. Plates a and b depict the Cabrits control population. The female in plate b is engaged in a submissive leg raising gesture, a behaviour, observed by the author in other members of the genus, previously undocumented in anoles. Plates c and d illustrate the montane translocated population from the Syndicate montane rainforest. The male illustrated in plate c is engaged in the characteristic dewlap display, used in territory defence and mate attraction.

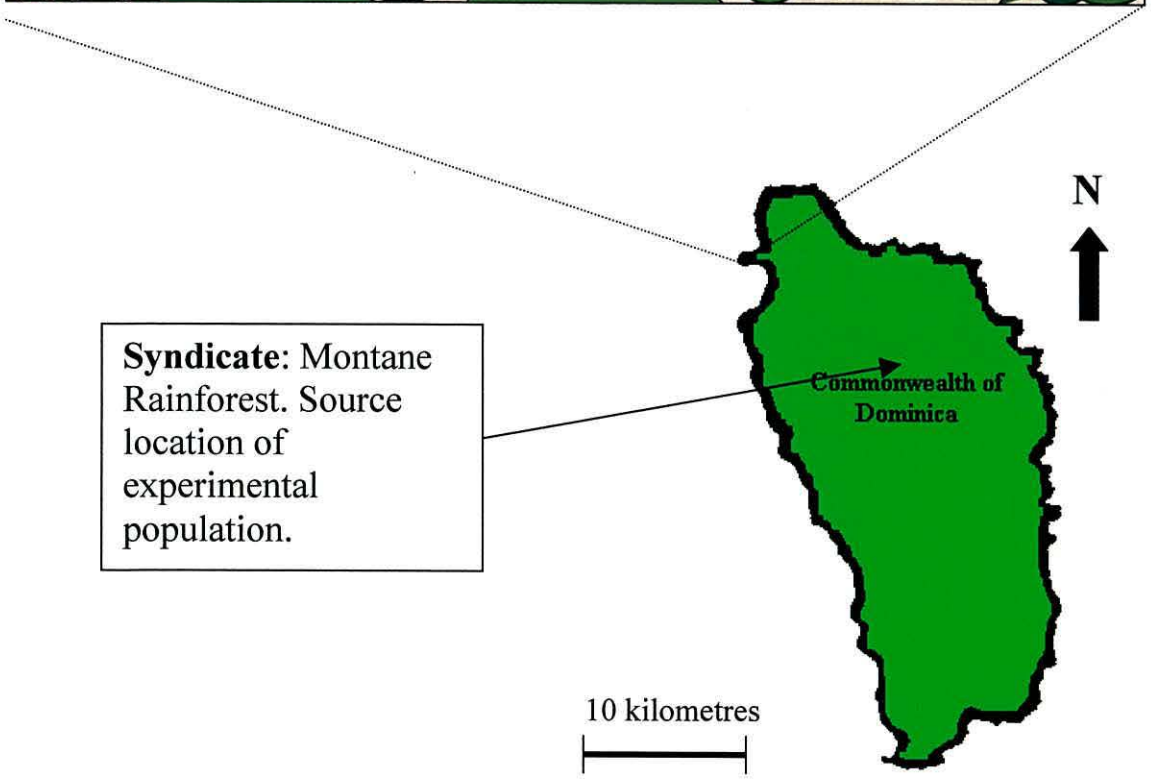
from Syndicate montane rainforest reserve at 820 meters above sea level in primary montane rainforest.

2.2.2 ENCLOSURE CONSTRUCTION.

Due to the high population densities, and three dimensional nature of *Anolis oculatus* habitat, viable experimental populations were able to be enclosed in an area of approximately twelve meters squared to the height of the canopy. As the experiment was necessarily replicated to allow statistical testing of results, four independent enclosures were required in close proximity for this experiment. They were designed and constructed in a manner to minimise materials, area over which the enclosures are constructed and to optimise the strength and durability of the structure. The basic design is illustrated in figure 2.1. Initial enclosure construction involved measuring out appropriate areas of forest considering the topology and existing vegetative structure to maintain the maximum viable natural structural complexity of the forest environment. A trench to the depth of 30 centimetres was then dug into which the perimeter fence would be constructed to allow for the burying of the lower portion of the fence netting. This was supported at regular intervals by eight centimetre by eight centimetre wooden posts of 125 centimetres in height, insecticidally, and fungicidally treated (this is essential in such a tropical environment to guard against the effects of termite damage and fungal rot). Fencing material consisted of 2 millimetre ultra violet light resistant (to prevent photodegredation) knitted polythene netting (Tildenets LS, Kerrypak Ltd.). Netting specification was high as it needed to retain flexibility and durability in an environment of intense heat, direct sunlight, frequent high winds,

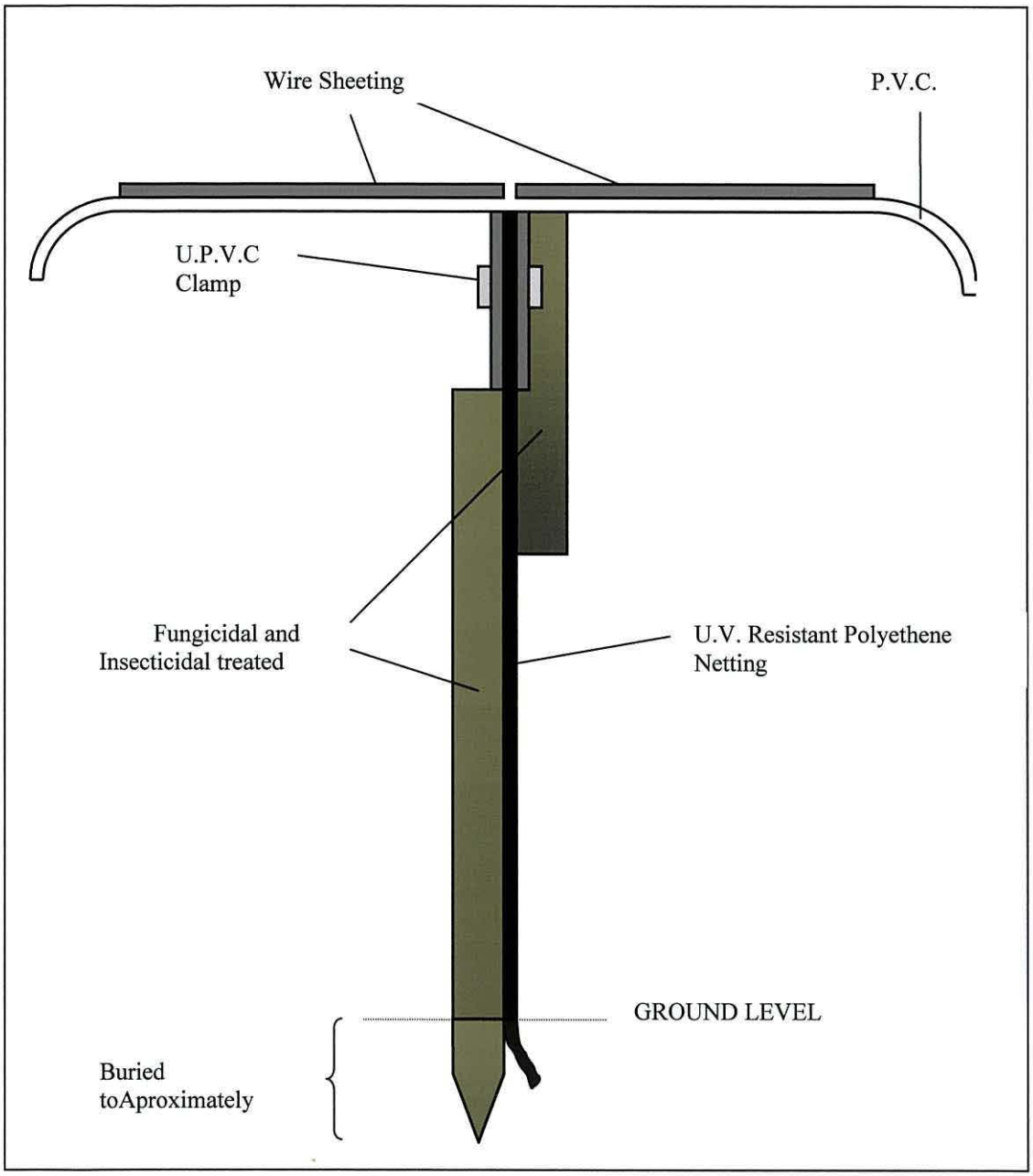
Figure 2.1. Schematic Arial View of Translocation Experiment Enclosure.





Syndicate: Montane Rainforest. Source location of experimental population.

Figure 2.2. Schematic Transverse Section of Enclosure Fencing.



including hurricanes, and regular precipitation. Horizontal struts supported a horizontal flexible PVC sheet (DIY Plastics plc.) of 45 centimetres diameter at the top of the netting. Fence structure is diagramatised in figure 2.2 and is a modification of the design used by Malhotra and Thorpe (1991).

The enclosure design is intended to retain translocated experimental *Anolis oculatus* within the enclosures and maintain non-experimental animals outside the enclosures. This is achieved by clearing all vegetation within one and a half meters of the fencing to prevent anoles from jumping onto the horizontal PVC sheet. Special attention must be given to vegetation overhanging the perimeter fencing to prevent anoles from dropping onto the horizontal plastic. Maintaining enclosure integrity at canopy height must also be assiduously pursued considering the arboreal nature of *Anolis oculatus*, as although largely a trunk-ground anole, its habitat extends to the canopy limits. This involves skilled tree surgery, as illustrated in Plate 2.1.

Enclosures previously utilised by Thorpe and Malhotra were used, but in reconstructing the enclosures, and much of the netting, an additional 25 centimetres in height of the netting was added, as was the entire horizontal PVC sheet at the top of the netting. The integrity of the horizontal PVC sheet is paramount to the function of the enclosures as anoles are equipped with lamellae pads on the toes that enable them to easily traverse smooth vertical surfaces. However, the clean underside of the horizontal PVC sheet proved to be beyond anole adhesive capability. The PVC sheeting was supported by a vertical extension of the wooden posts and clamped wire horizontal supports of the PVC. Wire supports replaced previously wooden supports to achieve increased flexibility in the structure, necessary in such an environment of

Plate 2.1

Plate 2.1 illustrates Mr Percy Pierre engaged in delicate tree surgery, in an attempt to maintain the enclosure integrity by preventing anole escape via the tree canopy.

high wind and precipitation. The wire struts are glued with contact adhesive to the upper surface of the PVC sheeting so as not to compromise the non-blemished under surface and stapled to the wooden posts then firmly secured with non-corroding 'u' nails. The replaced netting and all minor repairs were carried out using 12 grade oiled and treated Waxon sail thread. The enclosures are illustrated in plate 2.2 and 2.3.

2.2.3 EXPERIMENTAL POPULATION SIZE AND STRUCTURE.

Once the integrity of the enclosures was ensured it was necessary to remove all native anoles from within each enclosure. This is a highly time consuming and labour intensive task as the cryptic lizards utilise all elements of their three dimensional environment and spend a large proportion of their time motionless. Experience proved that collecting times are best restricted to morning and evening when anole foraging and territorial behaviour is at its peak (pers obs). Although nylon nooses affixed to the end of a telescopic fishing pole are effective and often necessary for the capture of animals perched at great height, capture by hand with sufficient technique proved more efficient. Where animals were perched at inaccessible heights in the canopy, the simple procedure of capturing another anole and holding the specimen gently by the leg at a lower elevation of the perch usually elicited a territorial response that brought the required animal into a suitable position for capture, such is the territorial and sexual ethology of *Anolis oculatus*. All anoles collected from each enclosure were sexed, recorded as being removed, weighed and marked with a permanent marker (ethanol

Plate 2.2

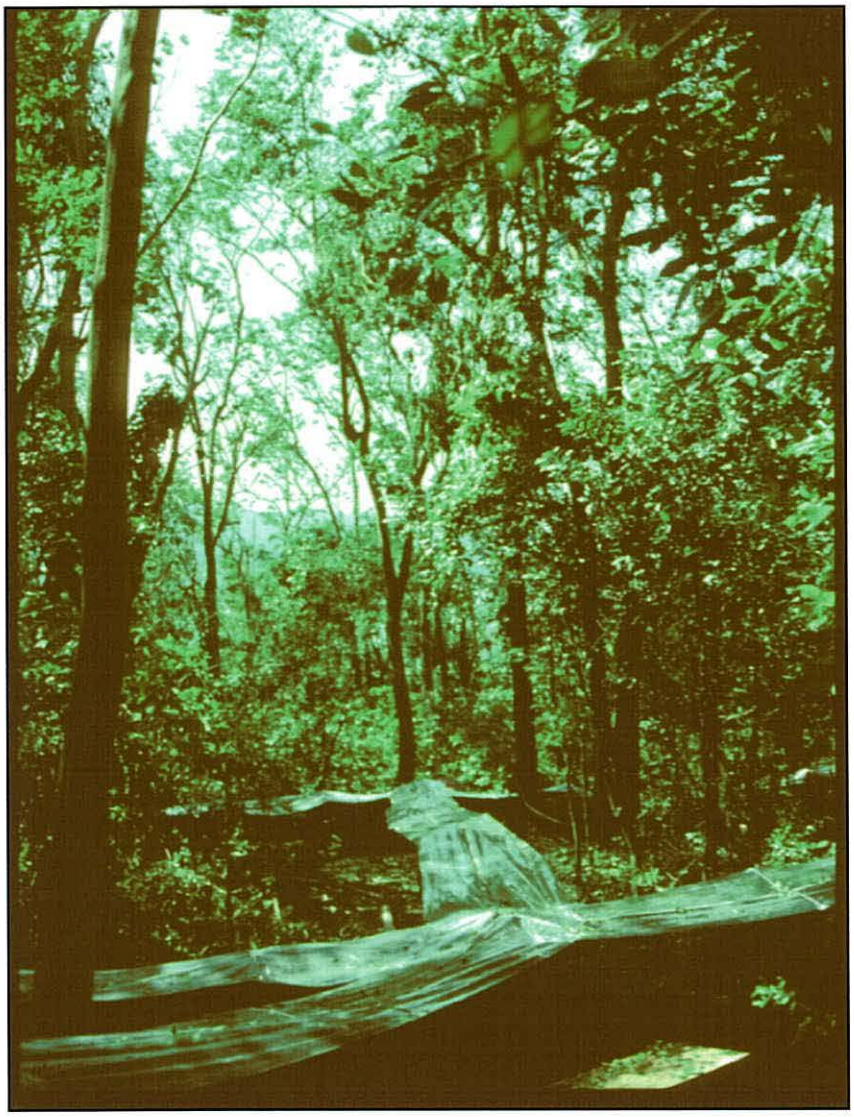


Plate 2.2 illustrates the interlocking nature of the four enclosure areas at the Cabrits National Park. The enclosures are pictured recovering from the ravages of Hurricane Louis (20/9/95) where a substantial proportion of the canopy vegetation was removed by the 200mph winds and torrential rain.

Plate 2.3

Plate 2.3 illustrates the construction of the enclosure fencing consisting of UV resistant netting and clear polyethene sheeting to prevent escape by the agile experimental anoles. An anole is pictured in the lower left of the picture, on the netting, for scale.

based black ink dye) to ascertain whether they were re-entering the enclosures. Data of biomass and sexual ratios from the removal of specimens from enclosures were used together with data from a population density estimate to calculate a stocking density for the enclosures based on biomass and sexual ratios. The population density estimate was achieved by a 'triple catch' technique applied to the Petersen estimate of population density (Begon 1979), which also provides standard errors in estimates and a quotient of growth and survival in the population.

2.2.4 PROCESSING EXPERIMENTAL POPULATIONS.

A biometric multivariate profile of phenotype was generated for each individual *Anolis oculatus*. The data recording consisted of a morphometric recording of body proportions, the recording of certain aspects of squamation, and colour pattern and hue analysis, carried out remotely from colour transparency analysis. Following photographing each specimen, all experimental specimens underwent the biometric data recording under anaesthesia. Full details of the biometric analysis are given below.

Both control and translocate populations of *Anolis oculatus* underwent exactly the same procedures of capture and treatment. Captured specimens were placed in a damp cloth sack of 60 by 30 centimetres that contained foliage to maintain humidity, thus avoiding heat stress in the specimens and to reduce visual contact between captives which leads to psychological stress and physical conflict. Approximately 25 specimens

were collected at a time, as this is the maximum number of specimens from which data can be recorded in a day. The specimens in the sacks spent a night in total darkness (this reduces stress and conflict) prior to analysis and release into enclosures.

2.2.5 BIOMETRIC RECORDING OF EXPERIMENTAL INDIVIDUALS.

Photographic analysis: On removal from the collecting sack, specimens were placed individually into a grey cloth photographic 'tent' of 60 centimetres square mounted on a tubular plastic frame with a draw-string entrance. Specimens were then permitted 15 minutes to settle in the tent to allow their colour hues to return to an unstressed norm. As all members of the genus *Anolis* have a dermal chromatophore response to physiological and behavioural stress usually leading to a darkening in specimen colouration. This is caused by melanin reorientation within dermal cells resulting from increased epidermal blood pressure (Bagnara and Hadley 1973).

A colour transparency was then taken of the lateral view of the Anole specimen onto Kodachrome ISO 64 unpushed transparency film. Standardised photographic conditions were achieved by recording all specimens at an aperture of f16 and a shutter speed of $1/90^{th}$ of a second, illuminated by a GN16 ML-3 Canon macro ring flash dictated by TTL evaluative metering at zero. All transparencies were made through a 100mm f2.8 Canon auto focus macro lens set to manual focus at a ratio of 1:4. For the wet season experiment a Canon EOS1000F SLR camera body was used

and a Canon EOS1 SLR camera body used for the dry season experiment. Transparencies were later analysed under constant lighting conditions using a Leica Wild M8 binocular microscope.

Colour hue was recorded as a trinomial value of percentage cyan, magenta and yellow obtained from printed colour charts (Campbell 1983). Below is a description of colour hue and pattern markings (figure 2.3).

1). Colour hue of lateral surface : Background colouration of the lateral surface calculated by the median value of four readings taken from a vertical transect of the lateral surface half way between the fore and hind limbs, recorded as three unit characters, i.e. percentage cyan, magenta and yellow.

2). Eye ring colouration : Colouration hue of the peri-ocular scales surrounding the eye, recorded as a three unit characters, i.e. percentage cyan, magenta and yellow.

3). Black patch width : Scale count at maximum width of black patch (if present) on lateral surface.

4). Anterior transect percentage white markings : The percentage cover of white markings against the back ground hue taken from a vertical transect of the lateral surface immediately posterior to the fore limb.

5). Central transect percentage white markings : The percentage cover of white markings against the background hue taken from a vertical transect of the lateral surface at the mid point between the fore and hind limbs.

6). Posterior transect percentage white markings : The percentage cover of white markings against the background colour hue taken from a vertical transect of the lateral surface immediately anterior to the hind limbs.

Figure 2.3 Colour Hue and Markings Characters

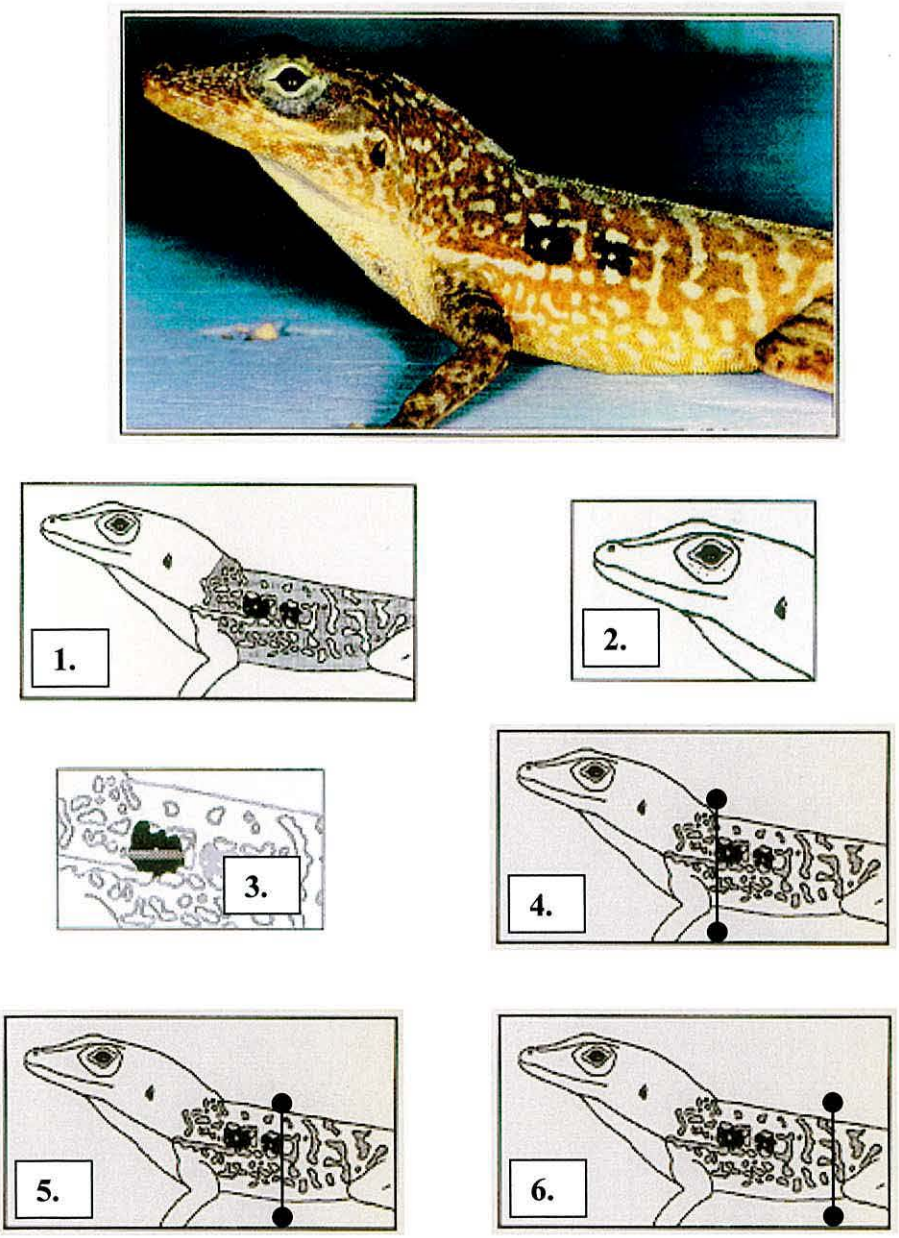


Figure 2.3 illustrates the six colour hue and marking character traits recorded for analysis.

They are: 1. Colour hue of lateral surface.
2. Eye ring colour hue.
3. Black patch width.
4. Anterior transect % white markings.
5. Central transect % white markings.
6. Posterior transect % white markings.

Redrawn from Malhotra (1992).

Anaesthesia : The photographed specimen was then removed from the photographic tent and the snout to vent length (SVL) measured with a plastic rule in millimetres This measurement must be taken prior to anaesthesia as it is a measurement that is repeated during the field experiment where anaesthesia is not administered. The reason for this is that the two types of recording are not comparable. The relaxed skeletal muscle state of an anaesthetised specimen yields a greater SVL measurement than that of a conscious restrained animal. Once done, the specimen is placed in a plastic zip lock bag that has been pre-tared. This is then weighed on an electronic balance (RS components) to 0.01 grams. Body weight is then recorded.

Using a 0.001 millilitre per gram body weight dosage of sodium penta-barbitone BP (100mg/kg) (Sagital™) diluted down to 1:20 in H_2O, an intra-coelomic injection is administered ventrally approximately three scale rows anterior of the pelvic ridge in males and approximately eight to ten scale rows anterior to the pelvic ridge in females. The specimen is then placed back into the plastic zip lock bag and monitored for anaesthetic effect. Taking between five and ten minutes to become fully anaesthetised, the dose permits a 15 minute window of anaesthesia in which to record morphometric data. All measurements except for the SVL (as explained above), are taken using an electronic vernier callipers (RS components) that recorded to 0. 01 of a millimetre.

Body proportions :

7). Snout to vent length : As defined above.

8). Lower hind leg length : Measured from the intercept of the metatarsals with the calcaneum to the intercept of the femur with the patella on the anterior surface of the limb.

9). Upper hind leg length : Measured from the patella to the intercept of the femur with the torso on the anterior surface of the hind limb.

10). Rear fourth toe length : Measured from the intercept of the tarsals with the metatarsals to the tip of the lamella.

11). Rear fourth toe width : Measured at the widest transverse point on the fourth toe.

12). Tail depth : measured at ½ SVL along the tail on the vertical aspect (see diagram).

13). Head length : measured from the tip of the rostral scale to the front of the tympanic membrane.

14). Head width : Measured at the widest horizontal point of the head usually at a point anterior of the tympanum.

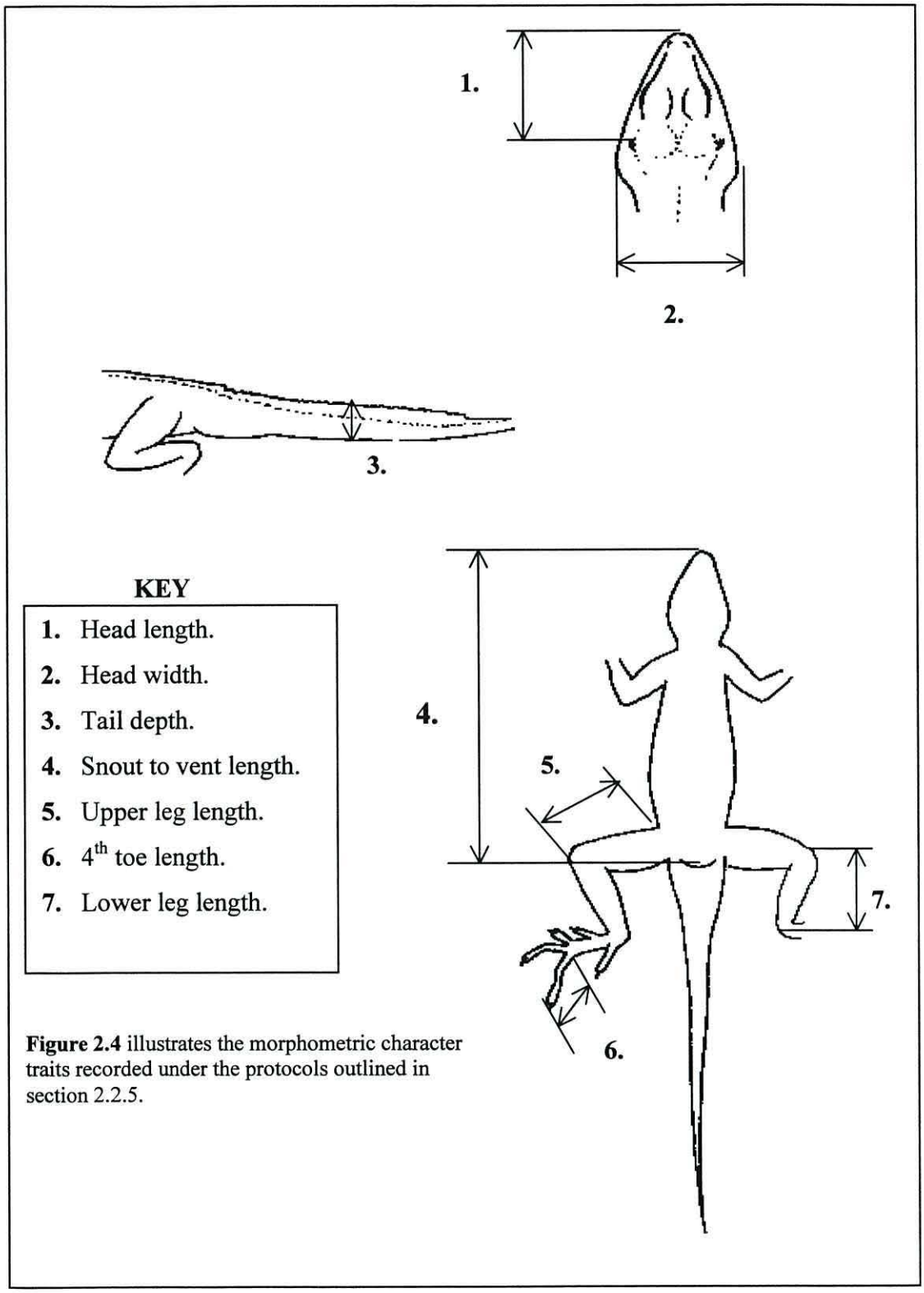
The systematics of recording body proportions are illustrated in figure 2.4.

Squamation : These dimensional scale counts are taken along an axis under a x20 magnification binocular microscope. During counts, scales were marked with a permanent marker every twenty scales to maintain accuracy.

15). Around body scale count : A ventral mark is made at ½ SVL and all scales counted around the circumference of the torso at that point.

16). Ventral scale count : All scales are counted in a line on the ventral surface between the axis of the fore and hind limbs.

Figure 2.4. Morphometric Body Proportions



KEY

1. Head length.
2. Head width.
3. Tail depth.
4. Snout to vent length.
5. Upper leg length.
6. 4^{th} toe length.
7. Lower leg length.

Figure 2.4 illustrates the morphometric character traits recorded under the protocols outlined in section 2.2.5.

17). Between supra ocular scale count : The minimum number of frontal scales between the supra ocular scales.

18). Fourth toe lamellar scale count : The number of scale rows possessing lamellar pads present on the digital process of the fourth toe.

19). Scale size index : Index of relative scale size of tuberculide scale of the lateral surface. Classified into : 0, same size as normal lateral surface scales; 1, less than twice as large as normal lateral surface scales; 2, less than three times as large as normal lateral surface scales and 4, larger than three times the size of normal lateral surface scales.

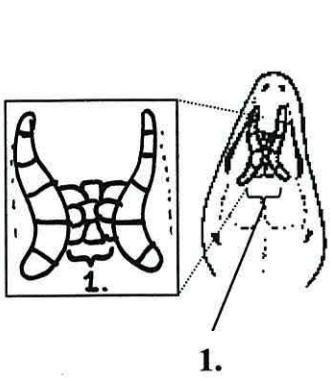
Figure 2.5 illustrates the recording perimeters of all squamation variables.

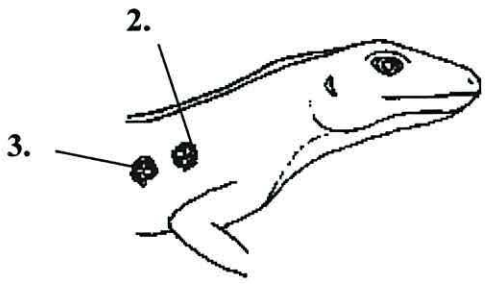
In total, 23 character traits are recorded per experimental specimen, as all colour hue recordings consist of three values representing percentage cyan, magenta and yellow. On completion of the character recording, each specimen was individually identified by terminal phalangial amputation (toe clipping), considering the digits of the forelimbs as the 'tens' and the digits of the hind limbs as the 'units'.

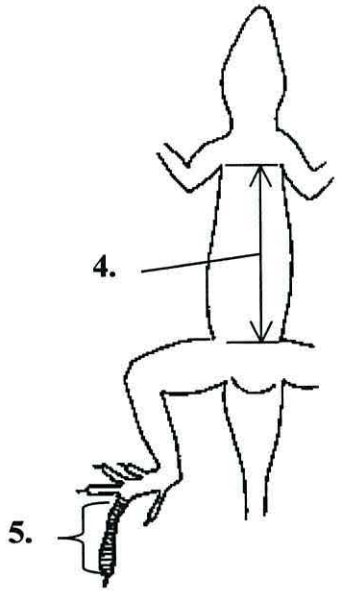
2.2.6 ENCLOSURE STOCKING.

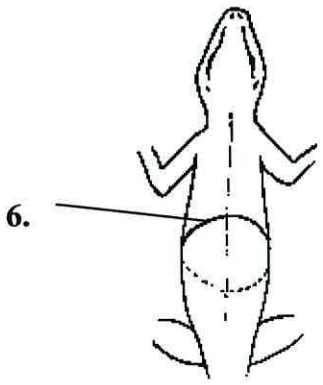
The biomass and sexual ratios of the translocated populations were designed to correspond to those of the *Anolis oculatus* removed from the enclosures following

Figure 2.5. Squamation.









KEY

1. Between supra-ocular scale count.
2. Black patch width.
3. White spot scale size index.
4. Ventral scale count.
5. 4th toe lamellar scale count.
6. Around body scale count.

Figure 2.4 illustrates the squamous character traits recorded according to the protocol outlined in section 2.2.5.

construction and must be supported by the results of the triple catch technique applied to the Petersen measure of population density (Begon 1979). During the stocking of the enclosures it is essential that experimental populations of *A. oculatus* are processed through the biometric character recording and released into the enclosures as quickly as possible. Experimental analysis cannot begin until all translocated and control specimens are in situ in the enclosures. Selection may act rapidly (Halkka, Halkka and Raatikainen 1975). An unduly long enclosure stocking process may 'blur' results as selective pressures will act on some individuals already released into enclosures and not on the others, yet to be biometrically analysed and released. All four enclosures were stocked simultaneously. An effort was made to release specimens into the enclosures either at dawn or at dusk as these are peak activity periods for *Anolis oculatus.* This would aid dispersal into enclosures and territory acquisition.

Once the enclosures were fully stocked they were allowed to settle for ten days before the first experimental analysis commenced. This was necessary in order to prevent loss of condition or even mortality in experimental specimens induced by excessive capture and handling. It would also to permit territory establishment unhindered by capture and inappropriate release. However, due to the dynamic nature of the environment, the enclosures were checked daily for structural breeches.

2.2.7 EXPERIMENTAL RECORDING AND ASSESSMENT OF FITNESS.

After an initial ten day settling in period of the experimental populations within the enclosures the first experimental analysis was carried out.

Each enclosure was searched initially all day for experimental specimens. Later, during subsequent analysis searching for experimental specimens was limited to morning and evening periods as these are times of maximum Anole activity. On capture, experimental specimens were placed into a clear plastic zip-lock bag. The identification number of the specimen (taken from toe clipping) was recorded and the specimen weighed on the electronic balance to 0.01 of a gram. The specimen was then removed from the zip-lock bag and a snout to vent measurement taken with a plastic rule along the ventral surface. Female specimens were also examined for gravidity. In the latter stages of egg development in anoles, gravidity is obvious. The large egg mass is evident through the shape and colour of the ventral surface of the posterior abdomen. However, in the early stages of egg development a gentle amount of pressure on the lower anterio-pelvic spinal region and the dorsum of the pelvis will cause any egg development to protrude ventrally allowing an assessment of gravidity to be made. Any indication of gravidity is recorded as positive. Once all such inspection of specimens was complete, a mark was made with a permanent marker on a limb of the specimen to signal that the anole had all ready been captured during the present analysis. Such marks are obviously lost during ecdysis, which occurs every two to three weeks (pers. obs.) and so would not cause confusion during subsequent experimental analysis. The specimen was then released in the exact location that it was captured in. This was done to minimise territory disruption and maintain the physical population structure within the enclosures as spatial relationships are

important factors of survival to anole lizards (Stamps 1994a; 1994b). Such surveys were only terminated after two consecutive days of recording no new specimens.

As previously stated, a simple measure of gravidity within experimental populations is not necessarily an accurate assessment of reproductive success in the experimental populations. To account for successful oviposition within the experimental populations transect counts were carried out over two days during each analysis to assess the number of hatchling juveniles within the four enclosure populations. Hatchling specimens were identified as those specimens with an estimated snout to vent length of less than 3 centimetres, a judgement made without capture of the specimen. Transects diagonally across the enclosures of fifteen meters were carried out during morning, midday and evening over both days to account for the activity patterns of the populations. Field observations suggest that anole eggs take 11 to 19 days to hatch in the xeric woodland environment. During the repair, emptying and stocking of the enclosures, which took over a month to complete, all hatchlings were removed, so it is presumed that those recorded during surveying would represent the reproductive efforts of the experimental populations.

For loose comparison, similar transects of fifteen meters were carried out in the control environment outside the enclosures and at the montane rainforest location from where the translocated experimental population was sourced. These were also carried out during the period of experimental analysis in an attempt to standardise climatic factors in hatchling presence in the environment and to the same system of morning, midday and evening transects.

Such analyses were carried out at two weekly intervals throughout the duration of both the wet and dry season enclosure experiments.

2.2.8 STATISTICAL ANALYSIS OF SURVIVORSHIP AND PHENOTYPE.

Data was recorded onto a Toshiba 486 lap-top computer in the field. Data sets were prepared and entered in ASCII format (7.2) into Word Perfect 5.1 (DOS). Colour and marking analysis data was then added to this after lab analysis of the transparencies. Analyses were run on BMDP-DYNAMIC (BMDP Statistical Software,Inc.)

2.2.9 CONSIDERING ONTOGENETIC CHARACTER SETS.

Due to considerable within and between group variance in overall specimen size, it was important to consider characters under the influence of size ontogeny within the phenotypic character set and adjust for them accordingly. This was achieved by using the pooled within-group slope against snout to vent length within each ecotype of experimental lizards. Size dependent characters of head length, head width, toe length, toe width, upper leg length, lower leg length and tail depth (illustrated in fig.2.4), were

then regressed against the slope of snout to vent length, considered separately for both sexes and seasons.

2.2.10 MULTIVARIATE ANALYSIS OF VARIANCE AND COVARIANCE IN SURVIVAL PHENOTYPES.

The multivariate profile (colour, body dimensions, squamation) was used in a three way MANOVA, with survival, ecotype and enclosure as the three dimensions. The survival dimension had two categories, survival and non-survival at stage three in the experiment. The ecotype dimension had two categories, montane and control xeric woodland; and the enclosure category had four categories, one for each enclosure replicate. To achieve a complete block design in the analysis, both wet and dry season data was pooled so that each enclosure possessed data representing both control and montane populations, i.e. for the dry season experiment enclosures 1 and 3 had control ecotypes and 2 and 4 had montane ecotypes while in the wet season experiment, the allocations of ecotype to enclosure was the opposite.

A significant difference between groups along the survival dimension indicates a significant selection intensity and a significant interaction between survival and ecotype. Interaction between survival and ecotype indicates that the selection intensity varies with ecotype. The program was instructed to model interactions between the enclosure an individual specimen was maintained in, survival to an

identified stage in the experiment, and the source ecotype of the specimen. An orthogonal interaction was also specified between survivorship and ecotype. This interaction was designed to detect any significant differences in the phenotypic characters of experimental specimens between surviving and non-surviving groups when regarding their ecological origins. The analysis was duplicated separately for males and females.

2.2.11 DIFFERENTIAL PHENOTYPE BETWEEN SURVIVORS AND NON-SURVIVORS.

Canonical variates analysis (CVA), was then employed to assess selection intensity, measured as the Mahalonobis Distance (D), in phenotype between surviving and non surviving groups in both the control and translocated experimental populations. This was chosen over a euclidean taxonomic distance, as it allows within-group character covariance to be taken into account, which is preferable (Thorpe 1987). The analysis was performed separately on both the translocate and control experimental populations, considering the sexes separately. Each chronological step in the translocation experiment was also considered individually as described above. The CVA F matrix also provided a measure of significance of the selection intensity (D), between survivors and non-survivors. The multivariate distances between group means were obtained via the formula below calculated from the F matrix values and is a measure of selection intensity.

$$D^2_{ij} = [NV \times (NC - NG)/NC - NG - (NV + 1)]\ [n_i + n_j / n_i \times n_j]\ F_{ij}$$

D^2 is the Mahalonobis distance when NV is the number of variables; NC is the number of cases; NG is the number of groups; n_i is the number of cases in the group, and n_j, is the number of cases in the group.

The stepwise CVA was then allowed to run to step 12 for all analyses. This is necessitated by the fact that after a point the Mahalonobis distance asymptotes with the addition of character traits into the analysis, while it diminishes with the addition of the characters. The analysis was carried out considering the chronological data in both an accumulative and sequential manner.

2.2.12 TESTING FOR TRAIT SPECIFIC SELECTION COEFFICIENTS.

To observe differential selection at a character trait level between surviving and non surviving groups it was possible to perform a partial regression of character states in experimental individuals against an ordinal of survival. This measure took into account the status of the experimental specimen at each chronological stage in the analysis and produced a parametric measure of survival. To carry out such a regression analysis it is necessary to standardise the data (zero mean, unit standard deviation), and Grant (1993) and Grant and Grant (1993) argue that a logistical regression should be employed when using a non-parametric binary measure of survival (Grant and Grant 1993). However, in this study, survival was assessed at five (temporally equal) stages resulting in the ordinal value of survival being represented by 0 for no survival; 0.25

for survival to the first experimental interval; 0.5 for survival to the second experimental interval; 0.75 for survival to the third survival interval and 1.0 to the fourth and final experimental interval. Such an ordinal measure of survival is less likely to offend against the assumptions of bivariate normal data analysis than a binary measure of survival. Therefor, partial regressions were used to measure selection coefficients.

2.3RESULTS.

2.3.1 REPLICATION.

A simple chi squared contingency table (tables 2.1 and 2.2) shows that there was no significant difference in survivorship between enclosure replicates within experimental groups.

Table 2.1

	Wet Season Replicate Survival Chi Squared Contingency Table							
Ecotype & sex	Control males		Control females		Translocate males		Translocate females	
Enc.	Enc. A	Enc. C	Enc. A	Enc. C	Enc. B	Enc. D	Enc. B	Enc. D
Surv	11	14	18	15	25	25	26	24
Non-surv	17	17	12	16	12	14	17	13
total	28	31	30	31	9	11	15	12
	χ^2= 0.709		χ^2= 0.358		χ^2= 0.268		χ^2= 0.506	
	P = 0.950		**P = 0.986**		**P = 0.992**		**P = 0.973**	

Table 2.2

	Dry Season Replicate Survival Chi Squared Contingency Table							
Ecotype & sex	Control males		Control females		Translocate males		Translocate females	
Enc.	Enc. B	Enc. D	Enc. B	Enc. D	Enc. A	Enc. C	Enc. A	Enc. C
surv	29	58	52	54	17	19	21	23
nonsurv	31	31	21	18	11	12	14	13
Input	60	58	52	54	17	19	21	23
	χ^2= 0.057		χ^2= 0.156		χ^2= 0.117		χ^2= 0.333	
	P = 1.00		**P = 0.997**		**P = 0.998**		**P = 0.998**	

2.3.2 MANOVA RESULTS.

The MANOVA (Appendix 2.1 and 2.2) indicates a significant difference (significant selection intensity) between the morphology of survivors and non-survivors, and ecotype dimensions for both males (P = <0.05, for snout to vent length) and females (P = <0.05 for head length and eye ring magenta), indicating that the extent of selection intensity is dependent on ecotype. Whilst expressing significant differential selection intensity between ecotypes, results do not show if xeric (control) or montane (translocated) populations are subjected to greater selection intensity. For this, a direct measure of selection intensity operating on specific populations is required.

2.3.3 SELECTION INTENSITY.

Selection intensity between survivors and non-survivors were calculated for both experimental replicates, for both ecotypes, and both sexes, over both seasonal experiments at each chronological experimental period (0, 14, 42, 68, and 96 days). The accumulative results are tabulated in table 2.3 and graphically represented in the following graphs.

2.3.3.1 WET SEASON SELECTION INTENSITY.

Figure 2.6 illustrates the accumulated selection intensity (D), for male control and translocated montane populations during the wet season experiment. The montane population has a consistently higher selection than the control population of males. A significant difference in phenotype was also shown at the first three experimental intervals for the translocated montane groups. At no stage during the experiment was a significant selection intensity for the control male population recorded. At all stages both montane replicates had a greater selection intensity than both control replicates.

Figure 2.7 illustrates the accumulated selection intensity (D), for female control and translocated montane populations during the wet season experiment. Except for the first experimental interval, selection intensity is greater for the translocated females than the control females. The selection intensity for montane females is consistently significant throughout the experiment while at no stage is the selection intensity for

Table 2.3

Wet Season Selection Intensity						
Experimental Pop^{n}.	**days**	**Mahalonobis D**	**Replicate 1 D**	**Replicate 2 D**	**Survivor/ Nonsurv.**	**F-Stat.**
Cmw 0-1	14	1.324	1.556	1.076	39:20	1.95
Cmw 0-2	42	1.323	1.395	1.253	35:24	1.82
Cmw 0-3	68	1.116	1.346	1.178	30:29	1.54
Cmw 0-4	96	0.948	0.672	1.139	27:32	1.11
Smw 0-1	**14**	**1.727**	**1.567**	**1.913**	**26:24**	**3.02****
Smw 0-2	**42**	**1.909**	**1.553**	**2.179**	**20:30**	**3.52****
Smw 0-3	**68**	**1.942**	**1.899**	**2.017**	**17:33**	**3.43****
Smw 0-4	96	1.621	1.522	1.734	13:37	2.05
Cfw 0-1	14	2.659	2.594	0.204	58:30	1.71
Cfw 0-2	42	1.586	2.323	0.533	53:80	1.48
Cfw 0-3	68	1.422	1.442	1.356	46:15	1.93
Cfw 0-4	96	1.165	1.117	1.258	35:36	1.71
Sfw 0-1	**14**	**1.969**	**1.795**	**2.139**	**30:20**	**3.78****
Sfw 0-2	**42**	**1.980**	**2.157**	**1.900**	**27:23**	**3.95****
Sfw 0-3	**68**	**1.892**	**1.986**	**1.827**	**24:26**	**3.63****
Sfw 0-4	**96**	**1.787**	**1.622**	**1.938**	**20:30**	**3.11****

Key – Cmw = Cabrits Male Wet season population; Smw = Syndicate Male Wet season population; Cfw = Cabrits Female Wet season population; Sfw = Syndicate Female Wet season population.
** = Significant to 0.05.

Dry Season Selection Intensity						
Experimental Pop^{n}.	**days**	**Mahalonobis D**	**Replicate 1 D**	**Replicate 2 D**	**Survivor/ Nonsurv.**	**F-Stat.**
Cmd 0-1	**14**	**0.889**	**0.981**	**0.796**	**66:52**	**2.12****
Cmd 0-2	42	0.917	1.015	0.822	65:53	1.93
Cmd 0-3	68	0.857	0.934	0.779	64:54	1.98
Cmd 0-4	96	0.857	0.934	0.779	64:54	1.98
Smd 0-1	**14**	**2.290**	**2.308**	**1.529**	**17:19**	**3.46****
Smd 0-2	**42**	**2.398**	**2.263**	**1.875**	**16:20**	**3.76****
Smd 0-3	**68**	**2.427**	**2.340**	**1.940**	**14:22**	**3.70****
Smd 0-4	**96**	**2.046**	**2.092**	**1.501**	**13:23**	**2.55****
Cfd 0-1	14	1.001	1.560	0.456	69:37	1.82
Cfd 0-2	42	1.001	1.560	0.456	69:37	1.82
Cfd 0-3	68	1.086	1.560	0.226	67:39	1.85
Cfd 0-4	96	1.086	1.560	0.226	67:39	1.85
Sfd 0-1	**14**	**1.690**	**1.795**	**1.415**	**20:24**	**2.45****
Sfd 0-2	**42**	**1.690**	**2.157**	**1.415**	**20:24**	**2.45****
Sfd 0-3	**68**	**2.133**	**1.986**	**2.236**	**17:27**	**3.73****
Sfd 0-4	**96**	**2.133**	**1.622**	**2.236**	**17:27**	**3.73****

Key – Cmd = Cabrits Male Dry season population; Smd = Syndicate Male Dry season population; Cfd = Cabrits Female Dry season population; Sfd = Syndicate Female Dry season population.
** = Significant to 0.05.

Figure 2.6

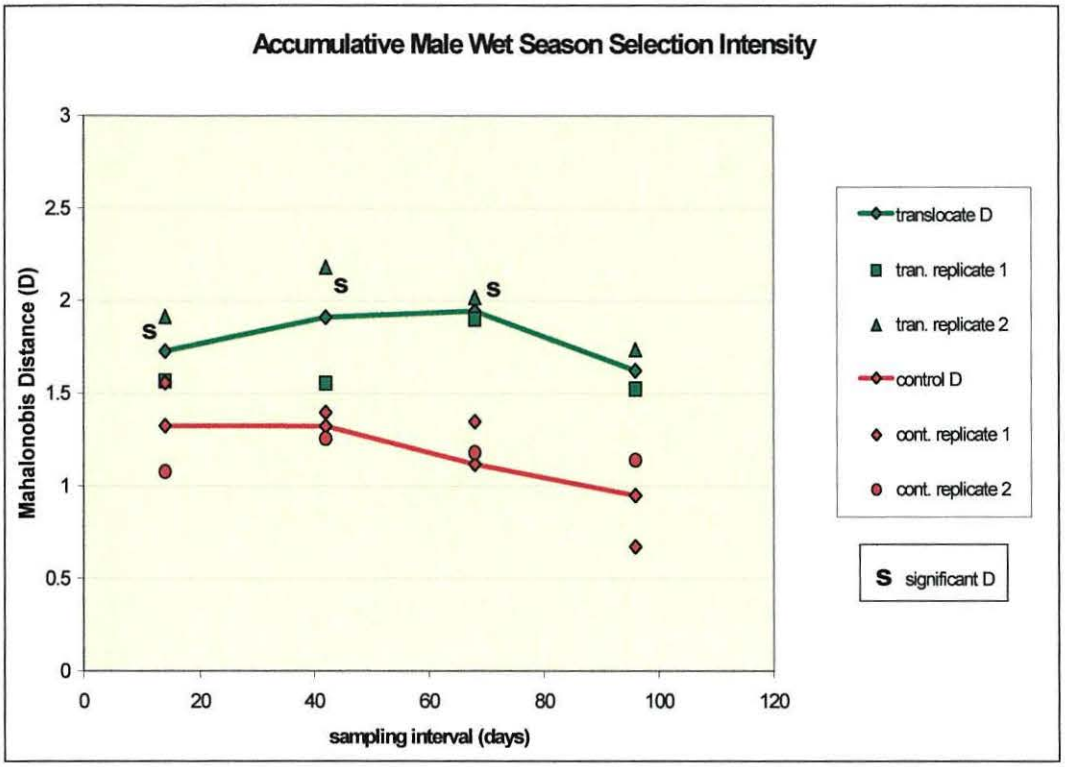


Figure 2.6 illustrates the selection intensity acting on male control and translocate populations during the wet season experiment.

Figure 2.7

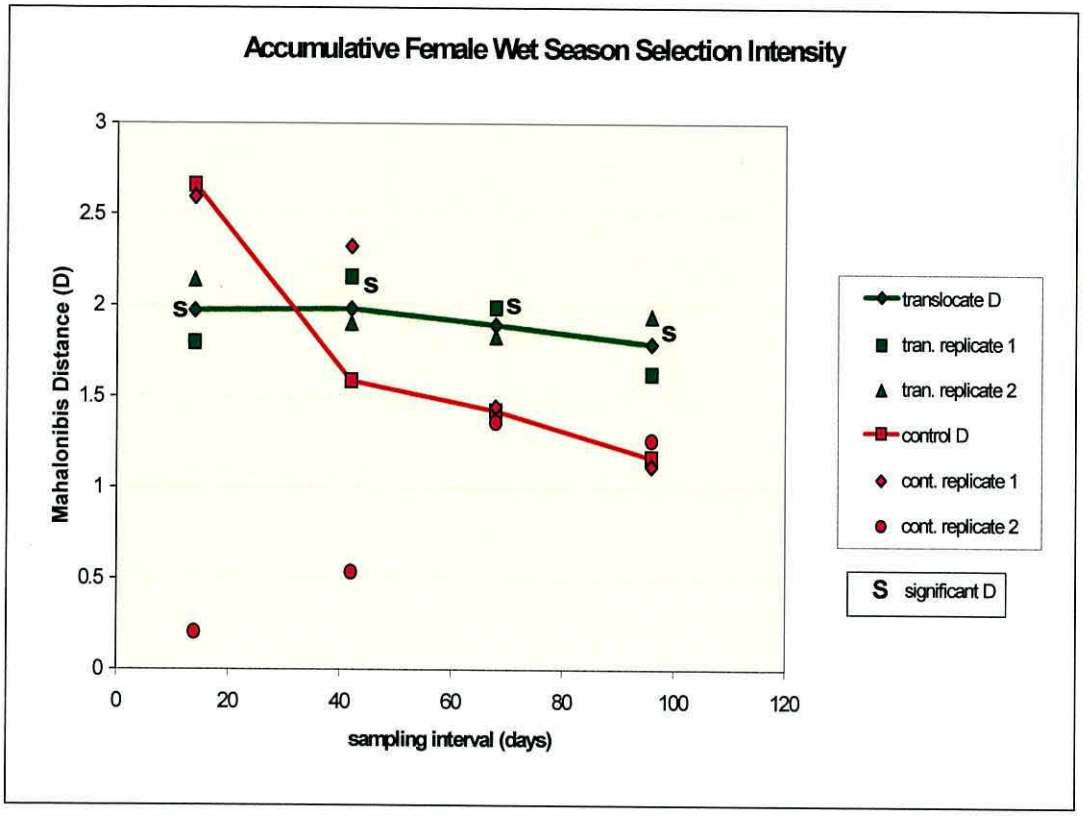


Figure 2.7 illustrates the accumulated selection intensity acting on female control and translocated populations during the wet season experiment.

control females significant, even when the Mahalonobis distance was greater than the translocate population at the first experimental interval.

2.3.3.2 DRY SEASON SELECTION INTENSITY.

Dry season accumulated male selection intensities (D), are illustrated in figure 2.8. Here one observes a consistently greater selection intensity in the translocated montane groups throughout the experiment, also significant at each stage in the translocated population. Only the first interval shows any significance in the selection intensity in control males. Moreover, at all stages both montane replicates had greater selection intensity than both control replicates.

Figure 2.9 illustrates the consistently significant, and high selection intensity in the translocated montane female populations in the dry season compared to Cabrits control female experimental populations.

A sequential analysis was also carried out on the change in Mahalonobis distance between survivor and non-survivor groups for males and females during both the wet and dry season translocation experiments. However, due to the constricted sample sizes in survivor and non-survivor groups only the wet season experiment yielded results of any worth. In general they reflect the results of the accumulated analysis detailed above and can be seen in appendix 2.3.

Figure 2.8

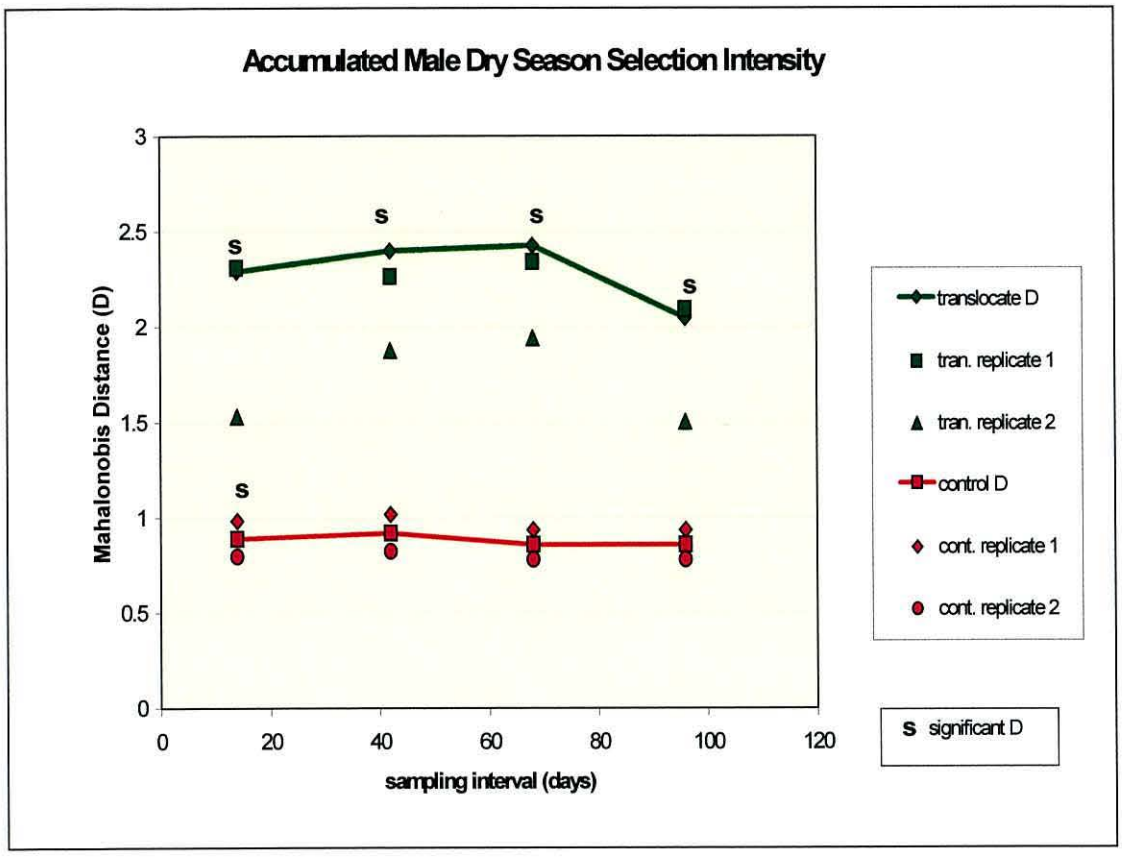


Figure 2.8 illustrates a consistently greater selection intensity operating on experimental translocated individuals throughout the experiment in the dry season.

Figure 2.9

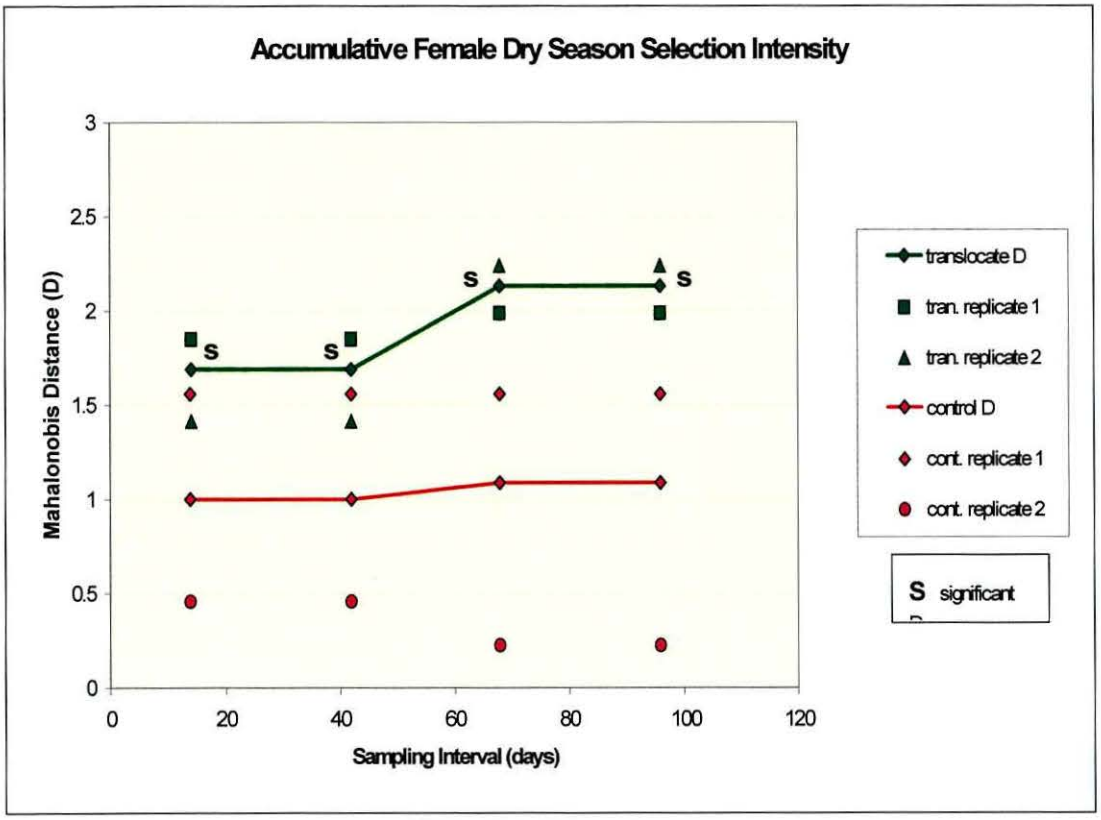


Figure 2.9 illustrates the consistently significant and greater selection intensity acting on the translocated female population in the dry season female experimental populations.

2.3.4 FITNESS AND CONDITION.

Table 2.4a, and b, illustrates the pattern of significant difference in condition between Cabrits control, and Montane translocated males, for both the wet (a), and dry (b), season experiments calculated by an ANOVA. For both the wet and dry season experiments, tables 2.4a and b show that the enclosure groups of control and translocated male anoles give consistently significantly different measures of condition. This is clearly illustrated by graphical representation in figure 2.10a and b, illustrating wet season condition, and in figure 2.11a and b, illustrating dry season condition of experimental males. By comparing the change in condition between the enclosure groups and native populations, it is evident that the translocated montane experimental populations fail to improve their condition through both the wet and dry seasons, whereas the control populations within the wet season do improve in condition.

A Tukey studentized range test (Dixon 1992) on condition consistently showed no significant difference between enclosure replicates of the same ecotype but a significant difference between ecotypes. The interaction table below illustrates this result:

Tukey Studentized Range Method Test of Difference between Replicates				
Group Label	Control rep. 1	Montane rep. 1	Control rep. 2	Montane rep. 2
Control rep. 1	Not Significant	**	Not Significant	**
Montane rep. 1	**	Not Significant	**	Not Significant
Control rep. 2	Not Significant	**	Not Significant	**
Montane rep. 2	**	Not Significant	**	Not Significant

Key - ** = significance to <0.01.

Table 2.4a, b.

Table 2.4a illustrates the significant difference in male condition that the enclosure control populations exhibit when tested against the translocated montane populations in the enclosures during the wet season. A comparison is also made between native and enclosure population of both experimental ecotypes.

WET SEASON ANOVA RESULTS OF CONDITION			
Experimental interval	Experimental populations	F - Value	Probability
14 days	Enc. Control – Enc. Montane	990.64	0.0000**
	Native Control – Native Montane	970.44	0.0000**
	Native Control – Enc. Control	3.45	0.7332
	Native Montane – Enc. Montane	7.71	0.4733
42 days	Enc. Control – Enc. Montane	304.97	0.0000**
	Native Control – Native Montane	1058.73	0.0000**
	Native Control – Enc. Control	102.44	0.0000**
	Native Montane – Enc. Montane	24.88	0.0391*
68 days	Enc. Control – Enc. Montane	923.18	0.0000**
	Native Control – Native Montane	58.06	0.0000**
	Native Control – Enc. Control	5.62	0.7554
	Native Montane – Enc. Montane	66.34	0.0000**
96 days	Enc. Control – Enc. Montane	141.76	0.0000**
	Native Control – Native Montane	30.14	0.0000**
	Native Control – Enc. Control	6.18	0.8046
	Native Montane – Enc. Montane	119.21	0.0000**

Key – Enc. = enclosure groups; * = significance to 0.05; ** = significance to 0.0001.

Table 2.4b illustrates the significant difference in male condition that the enclosure control populations exhibit when tested against the translocated montane populations in the enclosures during the dry season. A comparison is also made between native and enclosure population of both experimental ecotypes.

DRY SEASON ANOVA RESULTS OF CONDITION			
Experimental interval	Experimental populations	F - Value	Probability
14 days	Enc. Control – Enc. Montane	25.70	0.0000**
	Native Control – Native Montane	614.53	0.0000**
	Native Control – Enc. Control	33.42	0.0245*
	Native Montane – Enc. Montane	2.98	0.3665
42 days	Enc. Control – Enc. Montane	1356.26	0.0000**
	Native Control – Native Montane	471.75	0.0000**
	Native Control – Enc. Control	807.91	0.0000**
	Native Montane – Enc. Montane	56.63	0.0027*
68 days	Enc. Control – Enc. Montane	795.97	0.0000**
	Native Control – Native Montane	247.14	0.0000**
	Native Control – Enc. Control	24.71	0.0844
	Native Montane – Enc. Montane	1055.76	0.0000**
96 days	Enc. Control – Enc. Montane	4089.17	0.0000**
	Native Control – Native Montane	67.85	0.0000**
	Native Control – Enc. Control	7.66	0.0569
	Native Montane – Enc. Montane	992.42	0.0000**

Key – Enc. = enclosure groups; * = significance to 0.05; ** = significance to 0.0001.

Figure 2.10a, 2.10b.

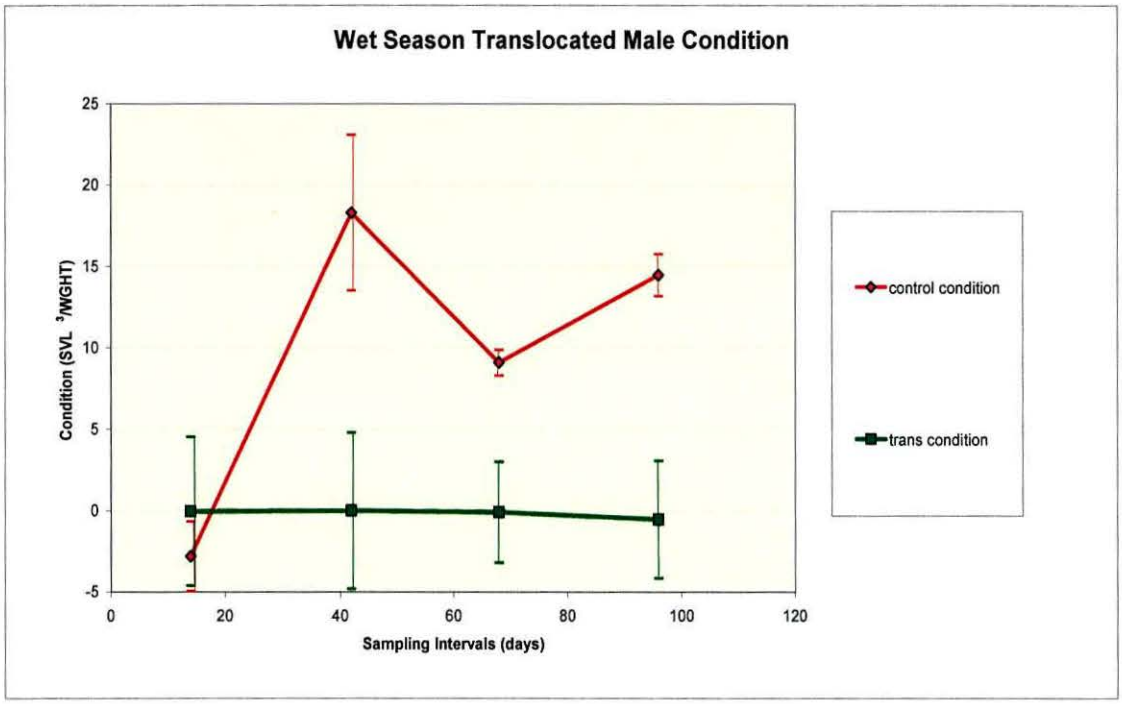


Figure 2.10a illustrates the change in condition, as described in section 2.2.5, in wet season experimental males. Error bars represent the confidence interval from the population mean.

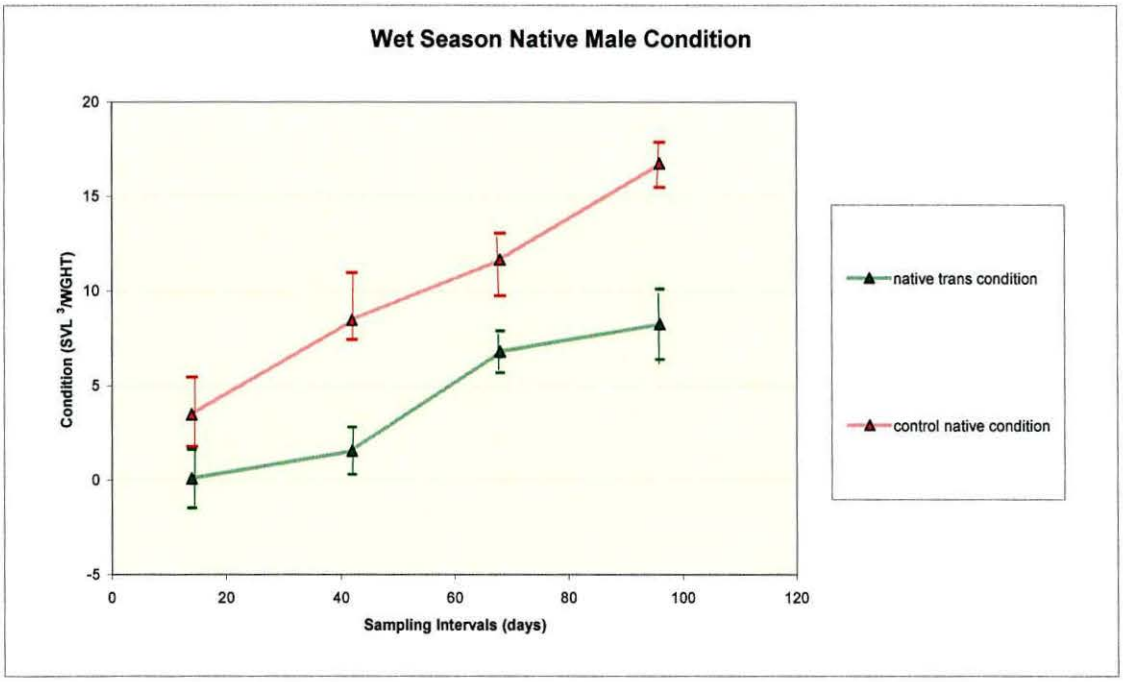


Figure 2.10b illustrates the change in condition in native populations from Cabrits and Syndicate over the wet season experimental period. The data is intended for an approximate comparison to the enclosure population data of fig.2.10b. Error bars represent the confidence interval from the population mean.

Figure 2.11a, 2.11b.

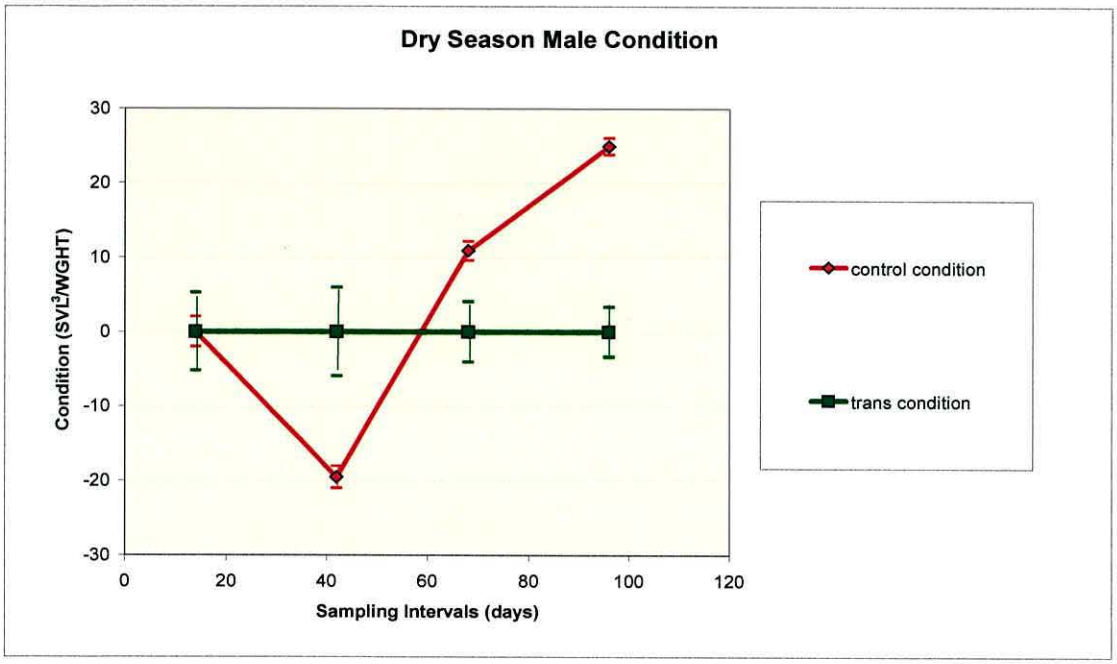


Figure 2.11a illustrates the change in condition, as described in section 2.2.5, in dry season experimental males. Error bars represent the confidence interval from the population mean.

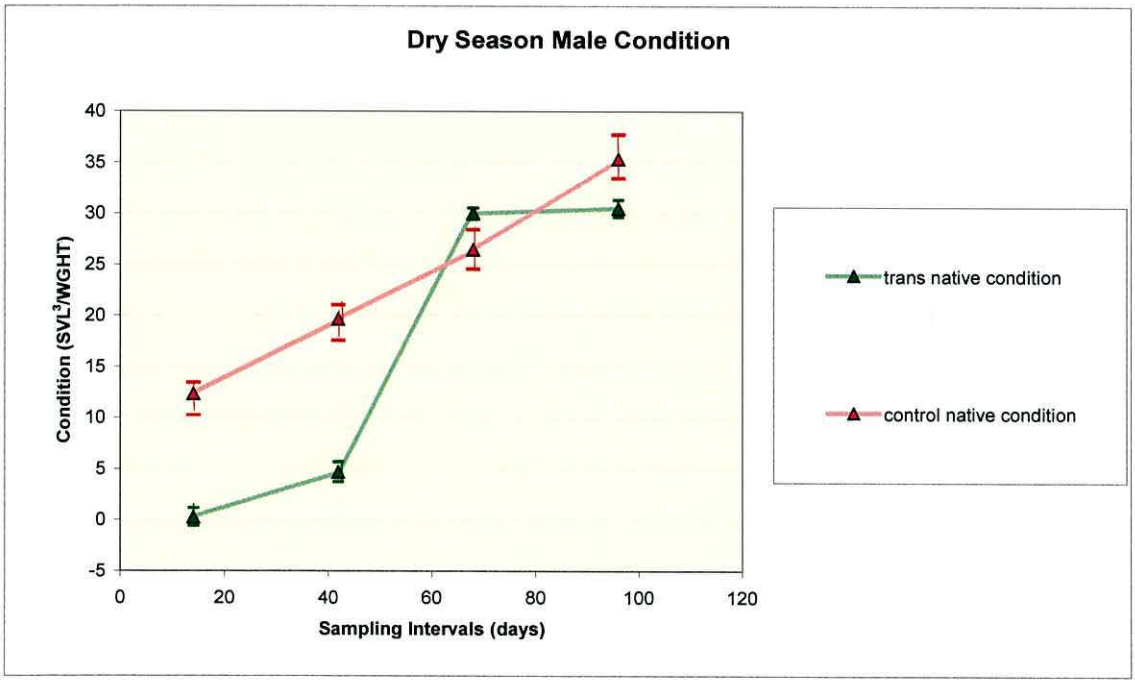


Figure 2.11b illustrates the change in condition in native populations from Cabrits and Syndicate over the dry season experimental period. The data is intended for an approximate comparison to the enclosure population data of fig.2.10b. Error bars represent the confidence interval from the population mean.

Figure 2.12a, 2.12b.

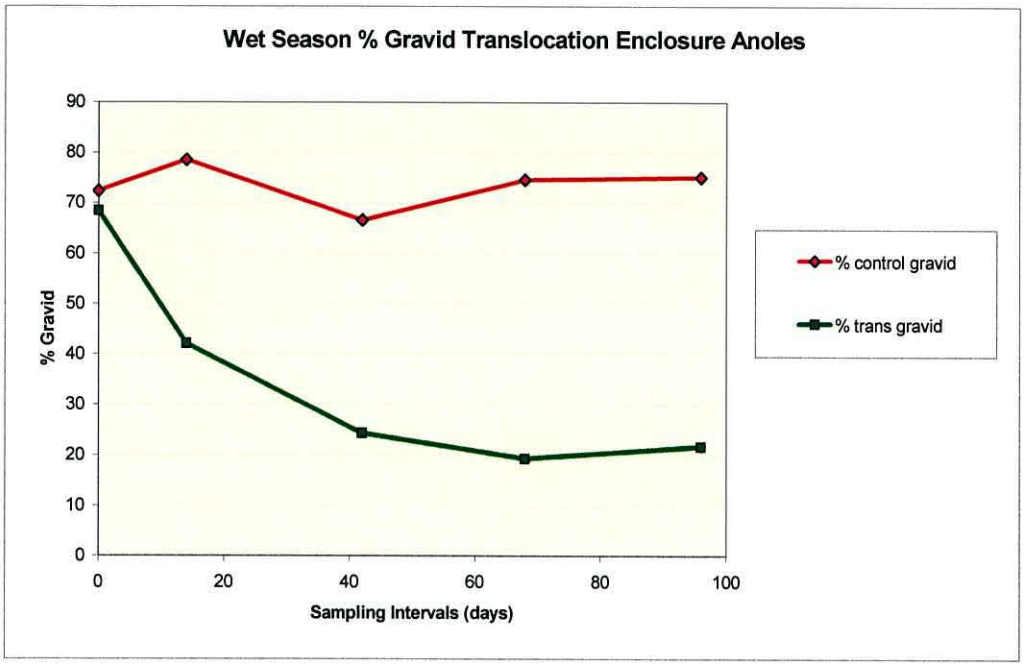


Figure 2.12a illustrates the change in % of observed gravidity in both control and translocate populations during the wet season experiment.

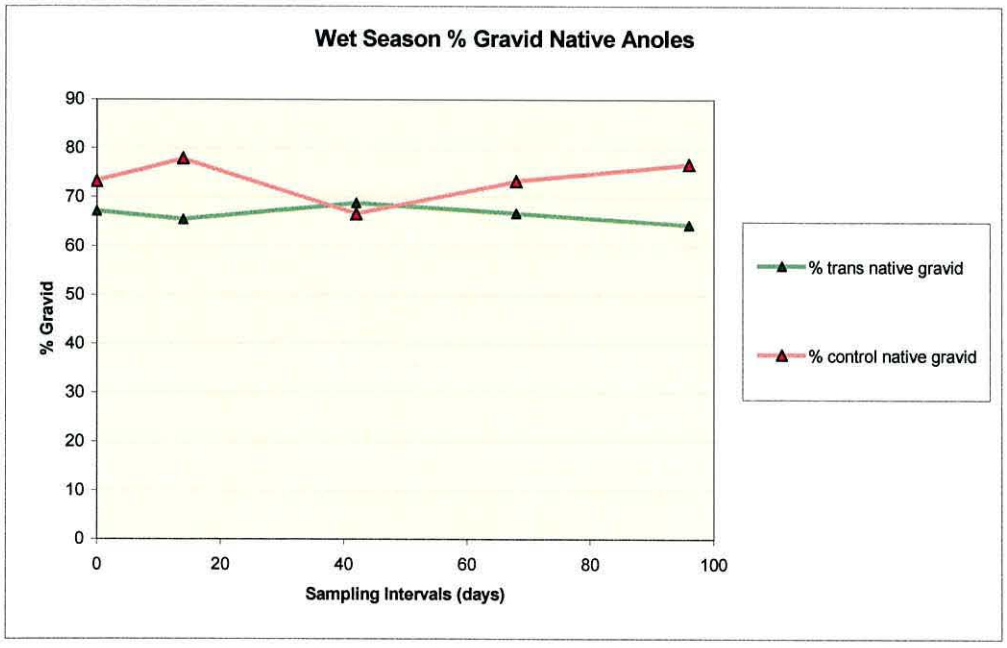


Figure 2.12b illustrates the change in % of observed gravidity in both control and translocate populations in their native habitat, during the wet season experiment.

Figure 2.13

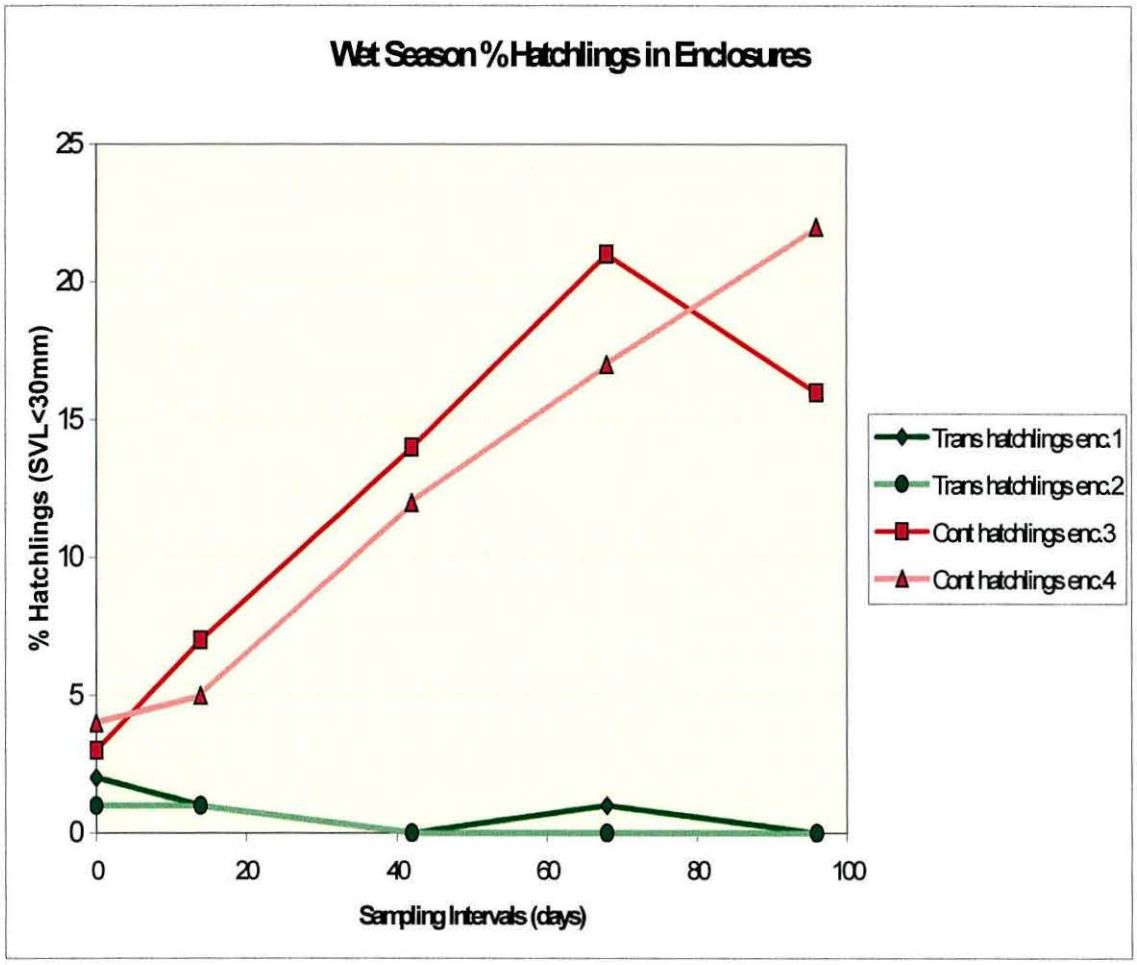


Figure 2.13 illustrates the % of hatchlings in the population in both replicates of the control (Cont.)and Translocate (Trans) populations during the wet season experiment.

Figure 2.14

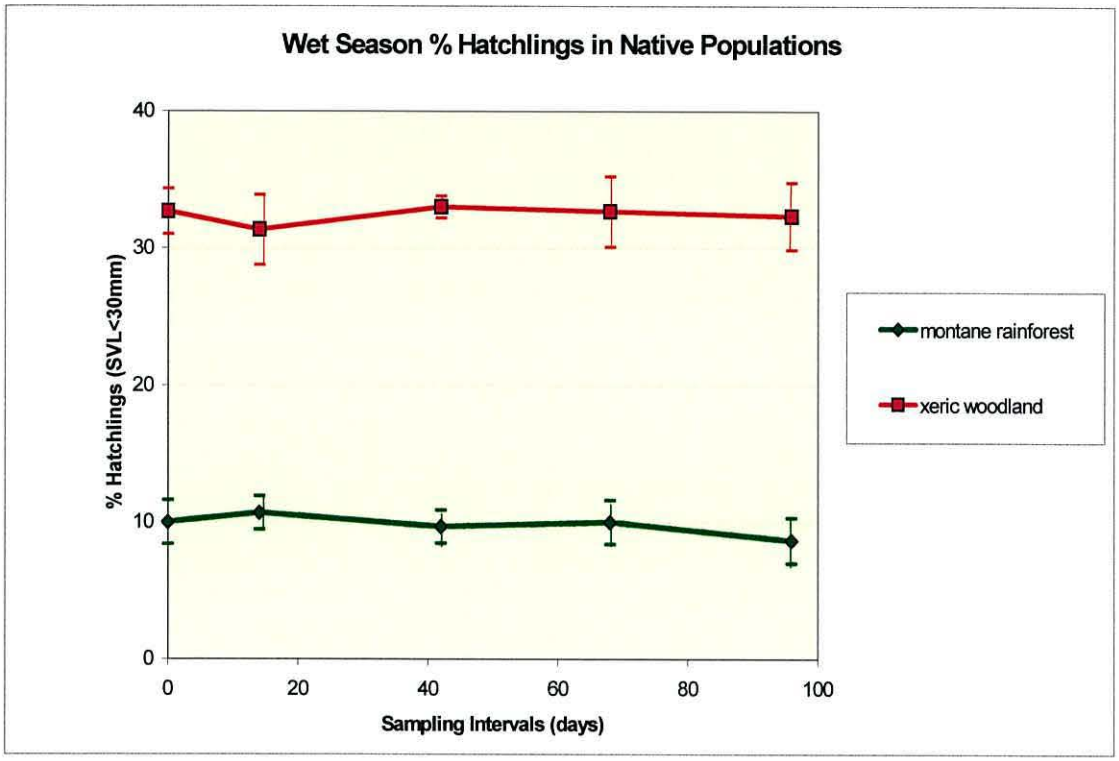


Figure 2.14 illustrates the % hatchlings in the experimental populations in their native environments.

Error bars represent the confidence interval from the population mean.

As stated in section 2.1.5, female condition cannot be assessed in the same manner as that of male experimental anoles. In assessing a component of fitness in females, attention is paid to the level of reproduction. Figure 2.12a and b, illustrate the level of gravidity in the wet season enclosures (a), and in the native populations (b). Figure 2.12a clearly shows that the level of gravidity rapidly drops in the translocated montane females, whereas it remains largely constant in the Cabrits control populations, and in both control and montane native populations. This is supported by the significant difference in gravidity between the control and montane groups tested by Chi-squared analysis portrayed in appendix table 2.9a. These trends in gravidity are supported by the observed levels of hatchlings in the populations, illustrated for both the enclosure populations and the native populations, in figure2.13 and figure 2.14, and proved to be significant by a Chi-square analysis (Appendix table 2.10a).

Again, during the dry season experiment, the translocated montane females exhibited a significant reduction in gravidity when compared to the control enclosure populations and both the native populations. Figure 2.15a and b, illustrate the level of gravidity in the dry season enclosures (a), and in the native populations (b). This is supported by the significant difference in gravidity between the control and montane groups tested by Chi-squared analysis portrayed in appendix table 2.9b. These trends in gravidity are supported by the observed levels of hatchlings in the populations, illustrated for both the enclosure populations and the native populations, in figure2.16 and figure 2.17. Hatchling levels are proved to be significantly different between controls and montane translocates, by a Chi-square analysis (Appendix table 2.10b).

Figure 2.15a, 2.15b.

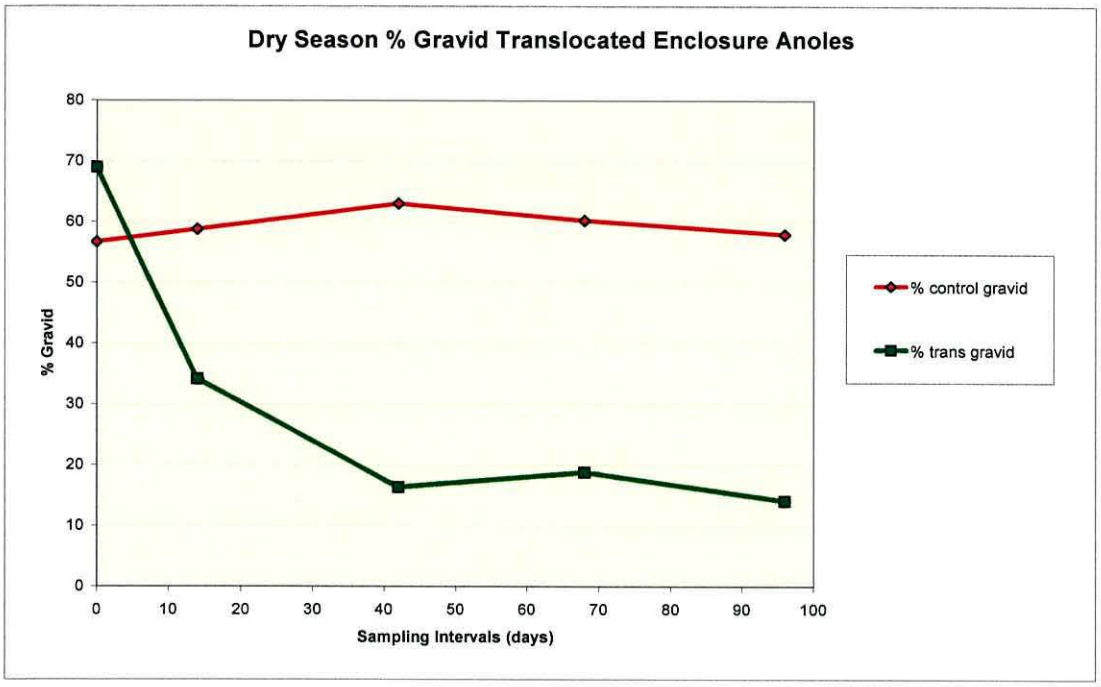


Figure 2.15a illustrates the level of gravidity observed in both control and translocated experimental populations in the translocation experimental enclosures, during the dry season.

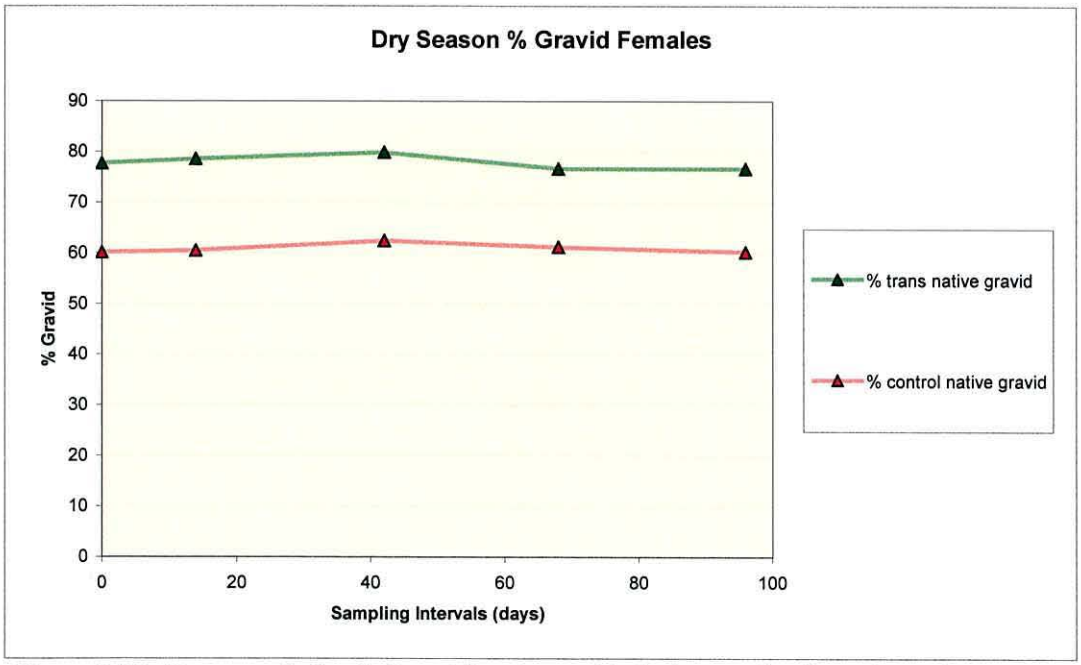


Figure 2.15b illustrates the level of gravidity observed in both control and translocated experimental populations in their native environment during the dry season.

Figure 2.16

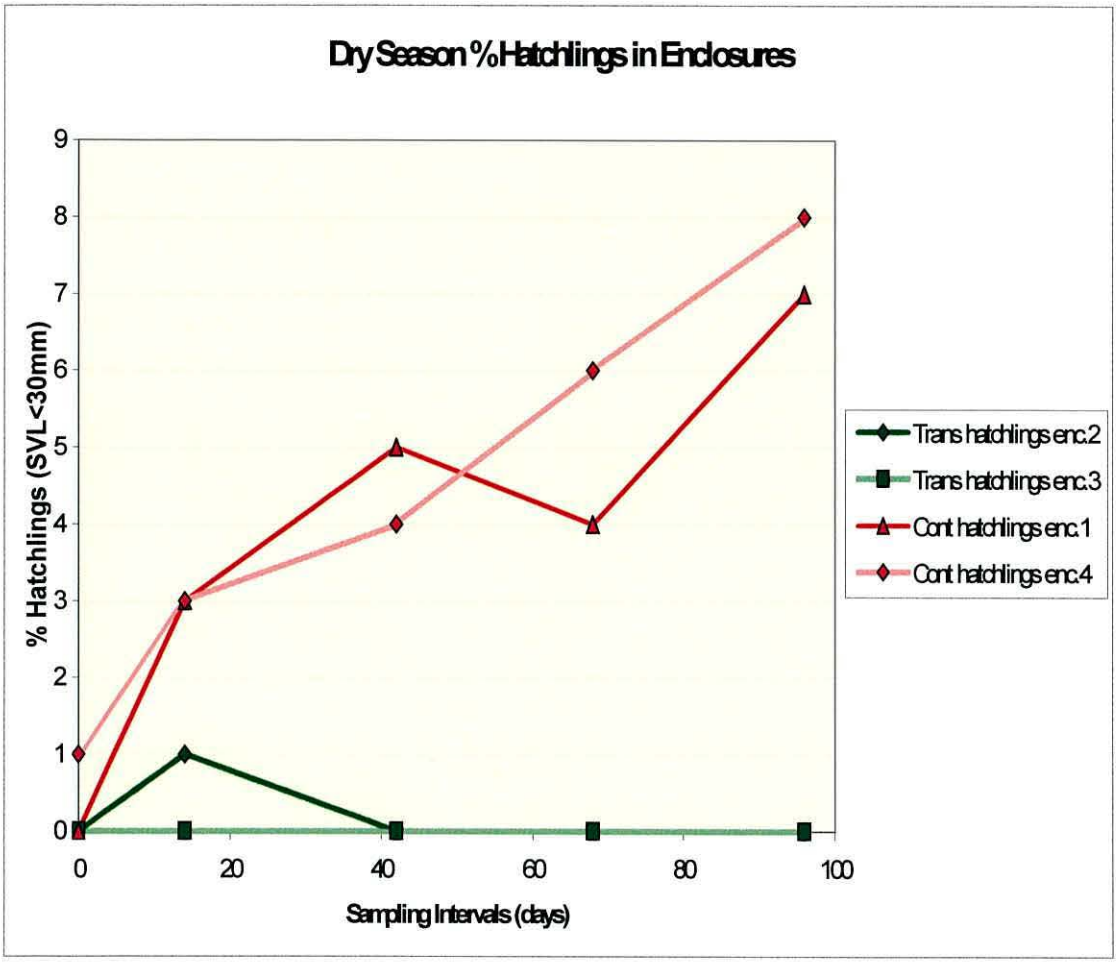


Figure 2.16 illustrates the % of hatchlings in the populations of experimental anoles in the dry season translocation experiment.

Figure 2.17

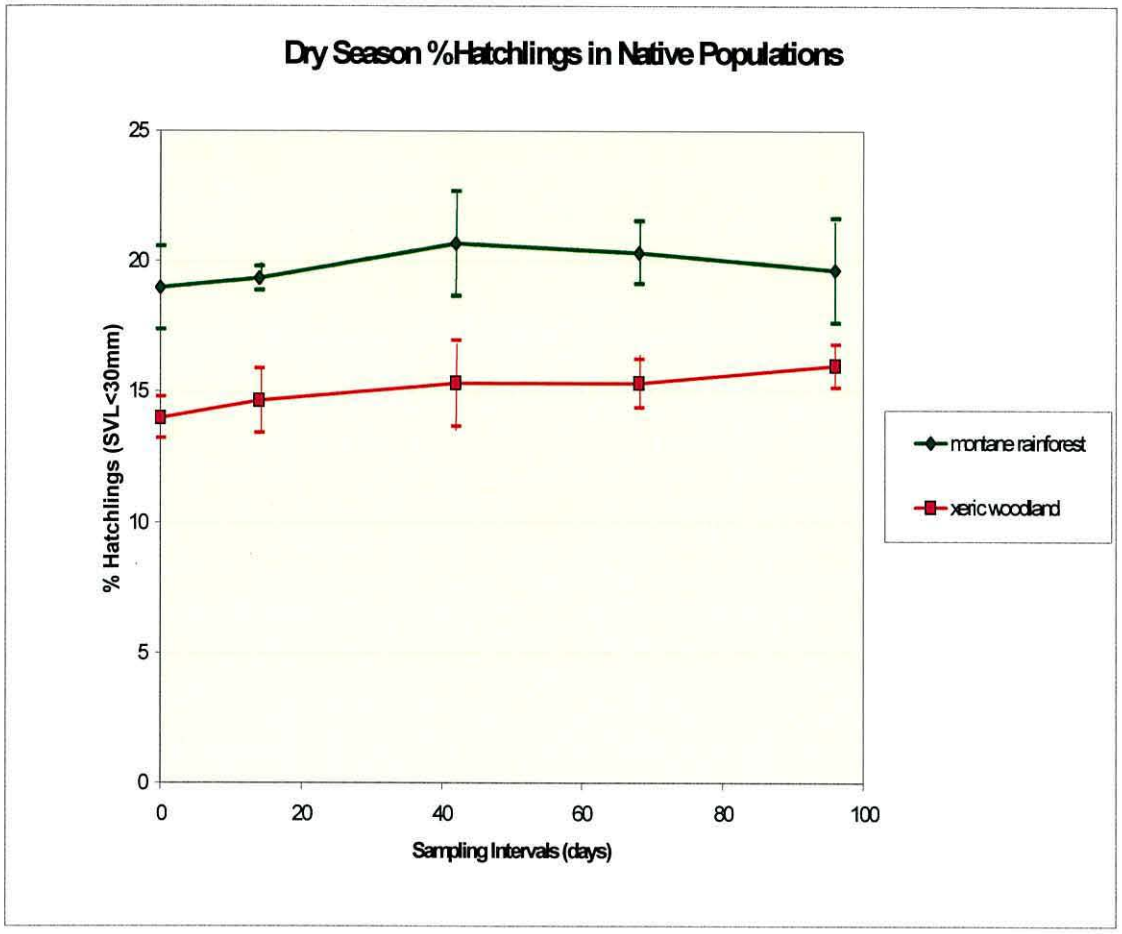


Figure 2.17 illustrates the hatchling % in population in the native environments of both populations during the dry season. Error bars represent confidence interval.

Finally, in the investigation of change in condition in experimental populations included in the translocation experiment one may consider the role of mortality. Figures 2.18 and 2.19 illustrate the percentage mortality observed in control and translocated populations of *Anolis oculatus* in the wet season experiment in males and females respectively. Appendix 2.11a illustrates a Chi-square analysis of accumulating mortality, and describes the largely significant difference between control and translocated montane populations.

Similarly, figures 2.20 an 2.21 illustrate the percentage mortality observed in control and translocated populations of *Anolis oculatus* in the dry season experiment in males and females respectively. Appendix 2.11b illustrates a Chi-square analysis of accumulating mortality, and describes the significant difference between control and translocated montane female populations throughout the dry season experiment. No significant difference was detected for levels of accumulating mortality between control and montane males in the dry season, but the general trend may still be observed in figure 2.20.

2.3.5 SELECTION COEFFICIENTS.

Selection coefficients were calculated from partial regressions and detailed in 2.2.12. The results of these partial regression analyses are illustrated in table 2.5 for the wet season experiment and in table 2.6 for the dry season experiment.

There are few significant selection coefficients for the control groups; in the wet season only posterior white markings in females provided a significant selection coefficient and female lower leg length in the dry season, and neither coefficients are

Figure 2.18

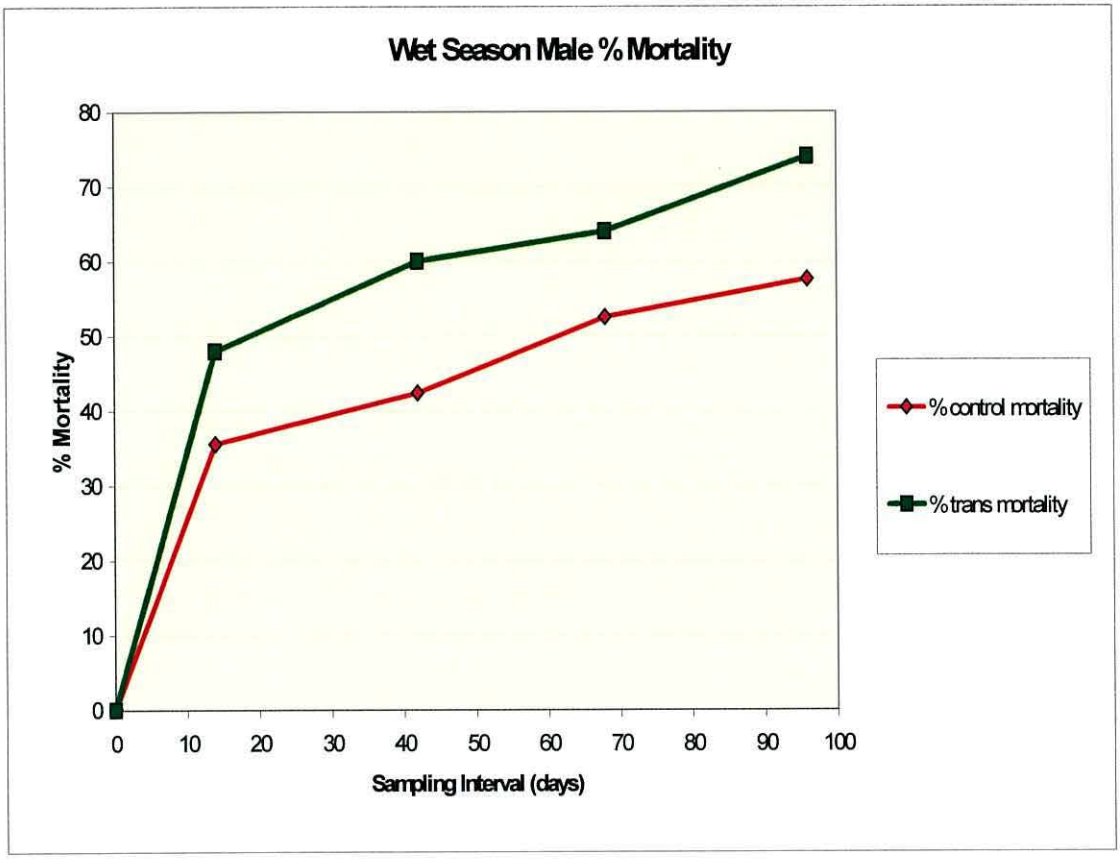


Figure 2.18 illustrates the % mortality observed in male control and translocated populations of *Anolis oculatus* in the wet season.

Figure 2.19

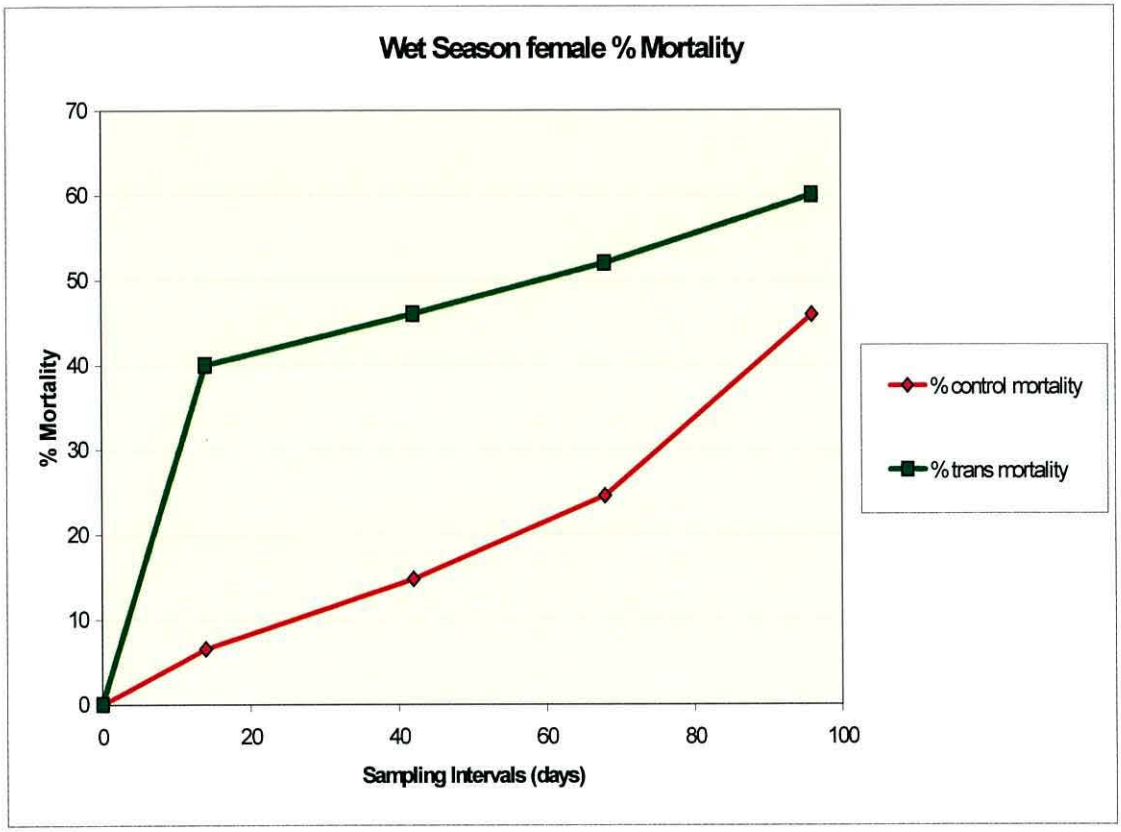


Figure 2.19 illustrates the % mortality observed in female control and translocated populations of *Anolis oculatus* in the wet season.

Figure 2.20

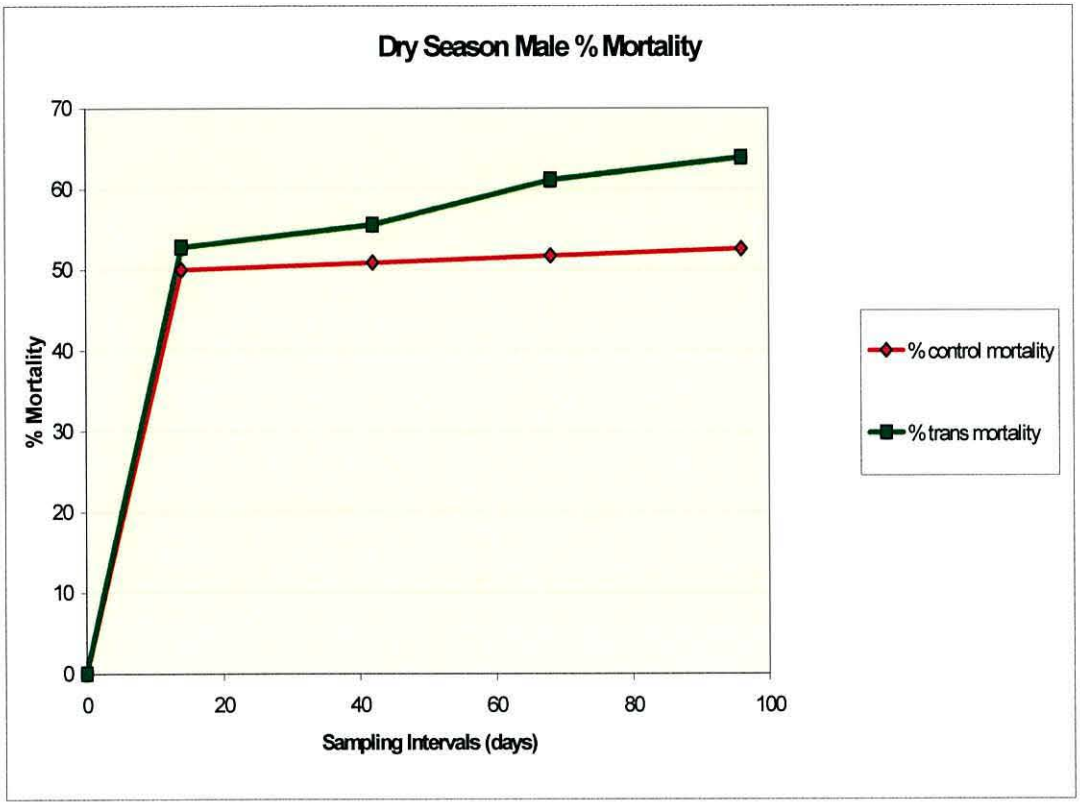


Figure 2.20 illustrates the % mortality observed in male control and translocated populations of *Anolis oculatus* in the dry season.

Figure 2.21

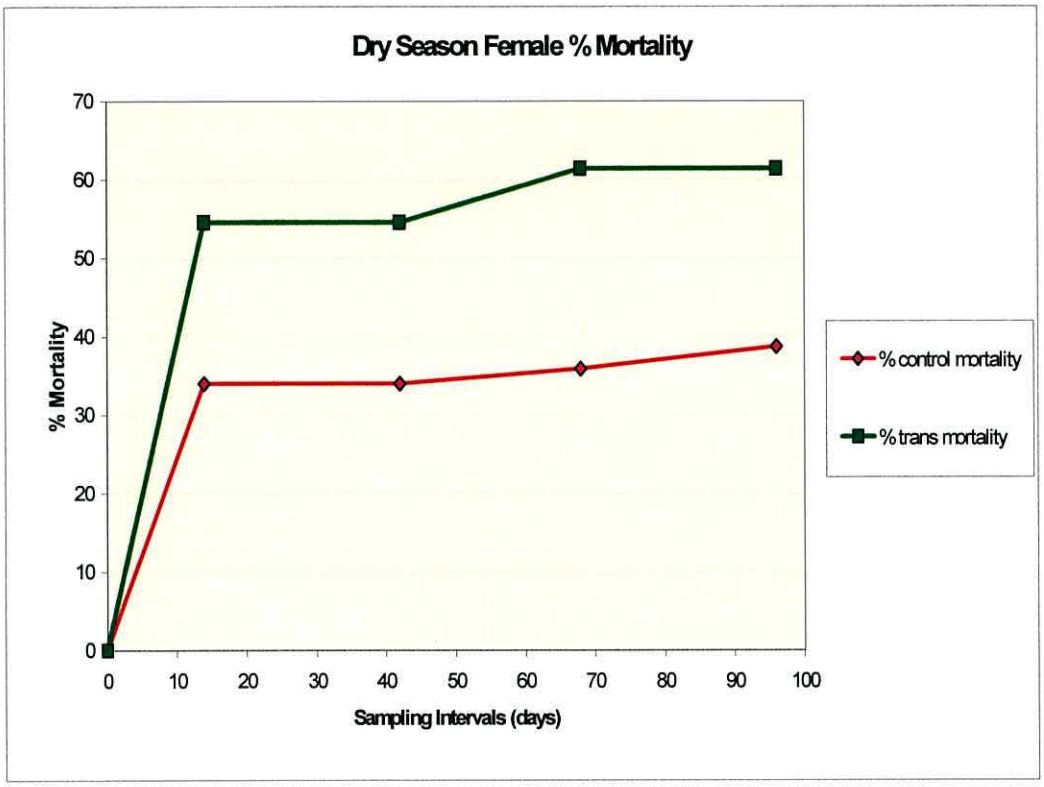


Figure 2.21 illustrates the % mortality observed in female control and translocated populations of *Anolis oculatus* in the dry season.

Table 2.5

Wet Season Character Selection Coefficients				
Character set	Control Males	Control Female	Translocated Males	Translocated Females
Snout to vent length	-0.0399	0.0105	**0.3789**	-0.0693
Upper leg length	0.0779	0.0334	-0.1299	**0.3283**
Lower leg length	0.0843	-0.0086	0.1706	-0.2272
Toe length	0.2087	-0.1433	0.0752	0.0010
Toe width	-0.1827	-0.1127	**-0.3957**	0.1886
Head width	-0.0089	0.1450	0.0212	-0.0449
Head length	-0.1018	0.1440	-0.2298	-0.0947
Around body scale count	0.1128	-0.1966	-0.1564	-0.1133
Lamellar scale count	-0.1081	-0.1361	-0.1011	-0.0779
Scale size	-0.2077	0.0322	0.2025	0.2632
Ventral scale count	-0.0748	0.2448	0.1321	0.2095
% eye yellow	0.1464	-0.1220	-0.0097	0.1337
% eye magenta	-0.1805	-0.1124	**0.2717**	**-0.3753**
% eye cyan	-0.0657	0.0892	0.1045	-0.0772
% dorsal yellow	0.1391	-0.0352	**0.3932**	-0.0423
% dorsal magenta	-0.0741	-0.0943	**-0.3122**	0.0596
% dorsal cyan	0.0940	0.1570	-0.2241	0.0499
Black marking width	-0.2283	----	-0.0657	----
% anterior white marking width	-0.0762	-0.0386	**-0.3681**	-0.0813
% mid-body white marking width	0.2280	-0.0688	0.1328	**0.3474**
% posterior white marking width	0.1170	**-0.2578**	0.0763	-0.1294
Degrees of freedom	55	61	48	50
Critical value at 0.05	**0.263**	**0.250**	**0.279**	**0.273**

Table 2.5 illustrates the selection coefficients exhibited by each recorded character trait and their significance for the wet season experiment.

Table 2.6

Dry Season Character Selection Coefficients				
Charater set	Control Males	Control Female	Translocated Males	Translocated Females
Snout to vent length	-0.0072	0.1157	-0.0220	**0.4996**
Upper leg length	0.0569	-0.1250	**0.4206**	-0.2233
Lower leg length	0.0107	**0.19**	0.2295	0.2027
Toe length	0.0697	-0.1349	-0.0640	0.0240
Toe width	-0.1258	0.1066	**-0.6456**	0.1476
Head width	0.1587	-0.1160	0.1533	0.2404
Head length	-0.1443	0.0626	-0.2306	**-0.5454**
Around body scale count	0.0863	-0.0681	**0.5611**	0.1954
Lamellar scale count	-0.2724	0.0134	0.0572	0.0243
Scale size	-0.0167	0.0157	-0.1877	0.0479
Ventral scale count	0.1202	0.0633	0.3071	-0.1626
% eye yellow	0.0457	0.1298	0.1514	-0.0416
% eye magenta	0.0561	-0.0198	0.1049	0.1705
% eye cyan	0.0098	0.0263	**-0.3390**	-0.1540
% dorsal yellow	0.1198	-0.1587	-0.0229	-0.0566
% dorsal magenta	-0.0568	-0.1350	**0.4585**	**0.3797**
% dorsal cyan	-0.0212	0.0679	-0.0324	-0.1160
Black marking width	0.0336	----	**-0.5938**	----
% anterior white marking width	-0.1722	0.1669	-0.0351	-0.0097
% mid-body white marking width	0.1769	-0.0458	0.2592	0.2320
% posterior white marking width	-0.1278	-0.0058	-0.0161	-0.2954
Degrees of freedom	114	102	33	42
Critical value at 0.05	**0.182**	**0.190**	**0.325**	**0.297**

Table 2.6 illustrates the selection coefficients exhibited by each recorded character trait and their significance during the dry season experiment.

particularly high. In the montane translocate groups several characters yield significant selection coefficients, with an emphasis on snout to vent length, toe width, eye and dorsal colour hue. Nevertheless, there are no strong trends and little consistency between sexes and seasons.

Character trait regression coefficients were also calculated from logistical regressions despite their binary limitation in the consideration of survival, using a comparative (survivor Vs non-survivor) measure at each chronological stage of the experiment. The logistical analysis were carried out for both sexes over both seasonal experiments and are illustrated in appendices 2.4 to 2.7.

2.4 CONCLUSIONS AND DISCUSSION.

2.4.1 SELECTION INDICATORS.

The MANOVA results for both males and females, support those of earlier studies (Malhotra and Thorpe 1991; Thorpe and Malhotra 1996), which show a significant selection intensity (multivariate difference between survivors and non-survivors) and that the extent of this difference is dependent on ecotype.

2.4.2 SELECTION INTENSITY.

Figures 2.6 to 2.9 illustrate the multivariate morphological difference between survivors and non-survivors in both wet and dry season experiments. This difference in phenotype between the groups is interpreted as a measure of selection intensity (Brodie et al 1995).

Considering the wet season experiment first, one observes that within the male populations a consistently greater selection intensity (i.e. greater difference exists between the morphology of survivors and non-survivors) in the translocated montane population than in the control population. This is supported by the fact that the first three experimental intervals also exhibit significance in difference between survivor/non-survivor phenotype. It may be suggested that this represent evidence for the fact that the phenotypic variation observed in *Anolis oculatus* is maintained by selection pressures emanating from the environment and ecology. A loss of significance in the difference between survivor and non-survivor phenotype over time, in the translocated population is not incomprehensible. It is likely that by the latter

stage in the experiment, selection resulting in mortality will have reduced the frequency of the maladapted phenotype to an insignificant level. In addition, one must remember that due to mortality, the sample size of the survivor category is significantly reduced by the fourth experimental interval.

This general trend is repeated for the wet season experimental female populations seen in figure 2.7. A greater selection intensity is observed in the control population at the first experimental interval but it is not significant, and at all other stages in the experiment it is the translocated montane female population that exhibits the greatest selection intensity. Throughout the experiment, the translocated females demonstrated a significant difference between survivors and non-survivors and no significance is observed in the control females.

Thus, when considering the wet season experiment as a whole, it is the translocated montane populations that exhibit the greater, and significant, selection intensity for both males and females.

When observing the results of the dry season translocation experiment, in figure 2.8 and 2.9, we observe an even greater selection intensity in both males and female translocated populations when compared to the wet season experiment (figures 2.6 and 2.7). In the male populations of the dry season experiment significance is observed in the first experimental interval in the control population. This is not entirely unexpected and is discussed further in chapter 2.4.2.1. However, the translocated males show consistent significant difference between survivors and non survivors throughout the experiment and this pattern is seen again in the dry season female translocated

population (figure 2.9), where no significance is observed in the controls. This again may be suggested as evidence for ecological and environmental forces of selection operating to sustain phenotypic variation in *Anolis oculatus.*

In chapter 2.1.7, the question posed was 'Is their greater selection intensity acting on a translocated experimental populations compared to a control experimental population?' From the results illustrated in figures 2.6 to 2.9 and detailed in the appendix 2.8 it is possible to conclusively state that greater selection intensity is exerted on the translocated populations of *Anolis oculatus* in both males and females and over both wet and dry seasons. This conclusion can lead us to the postulation that such forces of selection, of ecological and environmental consequence, are at least in part, the cause of observed geographic variation in phenotype in *Anolis oculatus* over its range.

2.4.2.1 A SEASONAL COMPARISON.

Seasonal replication of the translocation experiment allows a valuable comparison to demonstrate overall replicability of the translocation and a confirmation of the general trend of results. Indeed, similar patterns of selection intensity are observed in both wet and dry season experiments, but they are not identical. The singular occurrence of significance between survivor and non-survivor phenotype in the control dry season males may not necessarily be the result of sample size limitations or experimental error. The selection intensity observed in the montane rain forest translocated population is

undoubtedly directional, but such strong directional selection intensity was not expected in the control populations. However, given the degree of seasonal fluctuation in environment in the translocation experiment site location, some seasonal variance in selection intensity and direction may be considered as likely to be acting on the control population as well. This is especially the case when considering the degree of micro geographic adaptation demonstrated in *Anolis oculatus* (Malhotra 1993) and the apparent rapidity of selection acting on *Anolis oculatus* populations as illustrated and described above. One may also note that the difference in selection intensity between the Cabrits control and montane translocated groups is less during the wet season, than in the dry season. This result supports the hypothesis of environmentally driven selection intensity, as the environmental (temperature and humidity) difference between the source habitat and translocation habitat for the Syndicate montane groups is greater during the hotter and less humid 'dry season' than it generally is during the cooler and more humid 'wet season'.

2.4.3 CONDITION AS A MEASURE OF FITNESS.

For males condition was assessed throughout the experiments from a calculation of weight and snout to vent length change and is illustrated in figures 2.10a,b and 2.11a,b for wet and dry season experiments respectively. The results include a comparison with a measure of condition in the native habitats for both control and translocated

populations. For the wet season experiment, montane translocated males were the only population to exhibit no increase in condition over the experiment. This is in strong contrast to both native montane male condition and the control condition, all of which increased over the course of the experiment. The same pattern is reflected for the dry season male condition except for the fact that the control experimental population at the second interval demonstrated a considerable loss of condition over the other populations. This could be the result of the seasonal flux in selection pressures being brought to bear on the control population as a consequence of their territory disruption in being moved into the enclosures. The seasonality of reproductive effort or any cyclical nature to the intensity of territory defence may vary between populations of different ecological origin. This seems especially likely given that the native control population included for comparison maintains a consistent improvement in condition. The trend across the two experiments for males is however clear in that the only male populations to exhibit no increase in condition are the translocated montane males.

As detailed in chapter 2.2.7, female condition cannot be evaluated by the same criterion as male condition as reproductive effort may lead to weight loss and growth reduction. Therefore a measure of reproductive effort is essential to an assessment of female condition. Figure 2.12a,b illustrates the clear reduction in gravidity in translocated montane females in the wet season when compared to both control and both native populations. This trend is strongly supported by the population percentage of hatchlings observed in the enclosures illustrated in figure 2.13. If reproductive effort is regarded as a measure of female condition then the wet season translocated

females demonstrate significantly reduced condition when compared to the control population.

A similar pattern of shift in gravidity and population hatchling percentages is observed over the dry season experiment where an even greater reduction in gravidity in the translocated montane rain forest *Anolis oculatus* females is observed (figure 2.15a,b). This is again supported by the measure of hatchlings within the populations of each enclosure replicate.

In chapter 2.1.7 the question was posed, 'Using condition as an estimate of fitness in the male populations, and reproductive effort as an estimate of female fitness, do experimental translocated montane populations have lower fitness in comparison to control experimental populations?' From these results it may be concluded that the condition and fecundity of the translocated rainforest populations was reduced significantly both when compared to the control populations and the native population levels of gravidity. This reduction in condition is interpreted as an indication of the loss of fitness in the translocated populations as a direct result of their shift in ecology and environment.

A product of the observations of the relative measures of fecundity between the control and translocated populations from Caribbean xeric woodland and montane rain forest, has been that a seasonal fluctuation in reproductive effort has been observed between the ecotypes. Figure 2.14 and figure 2.17 illustrate the opposing fluctuations in hatchling numbers where, during the wet season xeric woodland *Anolis oculatus* have a large (av.33%) return of hatchlings into the population and montane rainforest

populations of *Anolis oculatus* contain approximately only 10% hatchlings. These trends are supported by the percentage gravid females recorded in both xeric woodland and montane rain forest environments (figure 2.12a,b). However, in the dry season the montane rain forest population averages nearly 20% hatchling content in the anole population and in the xeric woodland hatchling percentages have dropped to approximately 15% from their 33% average during the wet season. Again, these figures are supported by the illustration of native percentage gravidity seen in figure 2.15a,b. These fluctuations are quite understandable given that the wet season in the xeric woodland not only provides more suitable environments for oviposition in anoles but also experiences an increase in invertebrate prey abundance (pers. obs.). It must be stressed, however, that this apparent trend has been observed over only two seasons, and although likely to be a true reflection of the trend described above, would need further seasonal analysis to replicate and provide statistical significance of the trend.

2.4.4 TARGETS OF SELECTION.

Selection on specific character traits and the direction in which they have been selected has been tested for with the use of selection coefficients, generated from partial regressions. Selection coefficients were generated for both males and females, in both control and translocated populations, and over both wet and dry season experiments (table 2.5 and 2.6).

The results of the selection coefficients must be met with extreme caution in their interpretation, for a number of reasons. As explained in the chapter 1.2, only when all character traits are included in an analysis can any correlation in selection acting on linked traits be fully accounted for. In a complex organism such as *Anolis oculatus*, such a complete account of character traits is logistically impossible. One must also remain cautious of the selection coefficient results of the translocated population. Any direction of selection observed in a trait may be a short-term response to the shift in ecology and environment. An example is the selection for larger body size observed in wet season male translocated individuals and in dry season female translocated individuals. It is likely that the selection for greater body is attributable to a variety of factors, possibly including, an immediate response to optimal territory acquisition, and differential desiccation rates between smaller and larger individuals in the translocation xeric environment. This a reflection of a movement in the translocated population towards a local short term phenotypic optima (Wright 1935). Worthy of note is the fact that for both wet and dry season, a considerable number of colour hue character traits of dorsal and eye ring colour provide significant selection coefficients. Again, it is possible to speculate on the potential causes. Thermoregulation is significantly effected by dermal colouration as documented by Sherbrooke et al (1994), and such thermal stresses were likely to have been operating on the translocated populations.

One must be conscious of the fact that the phenotype of the translocated population is not representative of the ancestral morphology of the xeric woodland anoles and so converging selection on character traits cannot necessarily be anticipated. However, over several generations, it would be intriguing to discover if convergence in

phenotype occurred or if another phenotypic optimum, that offered similar adaptation to the environment and ecology, was located by the translocated population.

Selection coefficients observed in the control populations may offer a more reliable measure of selection direction resulting from the seasonal fluctuation in selection pressures discussed above. Unfortunately, the two significant selection coefficients demonstrated in the control populations, selection for smaller % white posterior marking width in wet season females (table 2.5) and selection for longer lower leg length in dry season females (table 2.6) offer little obvious ecological significance without unreliable speculation on various elements of their ecology. However, reflecting the greater selection intensity experienced by the montane translocates over the control groups and the greater loss of fitness through condition and reproductive effort, is the fact that over both seasonal experiments, only two character traits in the control groups yielded significant selection coefficients, where as eighteen significant selection coefficients were detected in the montane translocated populations.

In chapter 2.1.7 the question was posed, 'Does seasonal variance in environment result in seasonal differences in fitness in both translocated and control experimental populations?' Although certain character traits such as translocated male dorsal magenta colouration provide significant and opposing selection coefficient, results are neither clear nor categorical enough to prove or disprove the existence of seasonal difference fitness.

2.4.5 DISCUSSION

By translocating a population of *Anolis oculatus* from a montane rain forest environment into a xeric woodland environment, these two seasonal experiments have conclusively demonstrated increased within generation selection intensity and a reduction in fitness in the translocation population as a whole. This is suggested to have resulted from a shift in ecology and environment. A control population undergoing the same experimental treatment as the translocated population but without a shift in their ecology or environment demonstrated a negligible degree of significant selection intensity or overall loss of fitness.

Thus, one may conclude that in the absence of barriers to gene flow between populations, the observed variability in phenotype exhibited by *Anolis oculatus* is maintained by natural selection.

To better assess the maintenance of phenotype variability and the environmental role in natural selection pressure it is a logical step to conduct a translocation experiment using populations sourced from an environmental cline, where ecological distance between translocate population and translocation enclosure site can be assessed and a prediction of order in selection intensity acting on the populations under translocation can be made. This is the aim of chapter 3.

The results of this set of wet and dry season experiments, translocating experimental populations from the montane Syndicate environment to xeric woodland, together with a control population, provides complimentary results to the translocation experiments

of Malhotra and Thorpe (1991; 1992). Significant selection intensities were detected in montane translocated populations by Malhotra and Thorpe (1991), but failed to replicate the results of selection within ecotype groups from the same habitat. The synchronous replication carried out in both wet and dry season experiments, provides sound and repeatable evidence that natural selection pressures act differently on spatially differentiated populations of *Anolis oculatus*. Repeating the experiment during wet and dry seasons also illustrates the general continuity of selection intensity and pressures expressed in the montane translocated groups, and supplies additional chronological replication. It must be stressed that the results of these translocation experiments illustrate the response to short term pressures of natural selection, operating within generation times, and on experimental populations that, with regard to the montane populations, are significantly maladapted to the translocation enclosure environment. However, the nature in which the processes of natural selection have been studied in this analysis, compliment well, the long term research into the processes of natural selection operating on anoles, as investigated by Losos et al (1997). Losos et al (1997) describe how, *Anolis sagrei* introduced onto previously uninhabited (by anoles) islands in the Bahamas. Over a ten to fourteen year period after introduction, the anoles show significant morphological differentiation from their source populations. The result of the wet and dry season translocation experiment suggests that the differentiating selection event may have occurred far more rapidly than may be expected. In certain montane translocated groups, significant selection intensities were being recorded fourteen days into the experiment.

The translocation of individuals or populations has become a widely used and much publicised technique employed within many conservation strategies. Griffiths et al

(1989) sites over 700 incidences of manipulated animal translocations annually, for conservation purposes, in the United States of America and Canada during the late 1980s'.

For the purposes of this discussion, translocation may be assumed to mean the movement of individuals or a population of organisms to an area of the species natural range even if the species is locally extinct in that area.

In the majority of circumstances the movement of animals is undertaken in an attempt to reduce the probability of extinction in a population or species from a specific area of natural habitat, within the species natural or historical range, by either increasing the number of individuals or the number of populations (Scott and Carpenter 1987). In spite of this increasing use of translocation programs in conservation management, serious doubts have been expressed concerning the theory and effectiveness of such programs (Mlot 1989; Tasse 1989; Griffiths et al 1989 and Dodd and Seigel 1991). From the literature, it appears that translocations are perceived as a quick fix, and often the cause of species or population decline in the first instance has been addressed only in a cursory fashion (Burke 1991). However, when an area with a species or population that is under threat of extinction, has been returned to an adequately natural habitat or where other extraneous causes of population decline have been alleviated, allowing for natural recolonisation may be impractical or impossible. In such instances, the translocation of individuals or populations from other sources to the area of conservation interest is the only option.

According to Dodd and Seigel (1991), only 5 of 26 translocations of herptiles were deemed as successful. Success is gauged as the establishment of a self sustaining population that does not suffer from inbreeding depression (Tudge 1992). Failure of translocation programs seems largely to be the result of a lack of knowledge of the logistics and long term ecology of translocated organisms; Dodd and Seigel (1991) also state that "we cannot over emphasise the need to publish the results of RRT [translocation] experiments in appropriate journals."

This study offers a unique opportunity to assess the effects of translocation due to the inclusion of a control population. Due to this experimental design it is possible to assess the effects of translocation regarding the movement of a population less than 5 miles within the continuous range of the species. It is also possible to assess the impact not only on survival but also fecundity and condition. Due to the inclusion of a control population the effects of territory disruption can also be gauged.

This study is seen as pertinent to the field of herptile conservation as although *Anolis oculatus* and indeed other members of the *Anolis* genus as a whole not under threat of extinction, they offer an excellent model of an island endemic lizard and it is a well accepted fact that island endemics tend to be most at threat from extinction. The classical case of the Round Island herpetofauna exemplify this, and also provide valuable data on the relative success of translocations as opposed to natural recolonisation from residual populations (Bloxam 1982). Bloxam (1982) also emphasises the need for more data pertaining to the translocation of Squamata. It would also be entirely unethical to conduct such an experiment with an endangered species and so the results may provide valuable information for the formulation of

conservation strategies of Squamata that are considering translocations as part of a program.

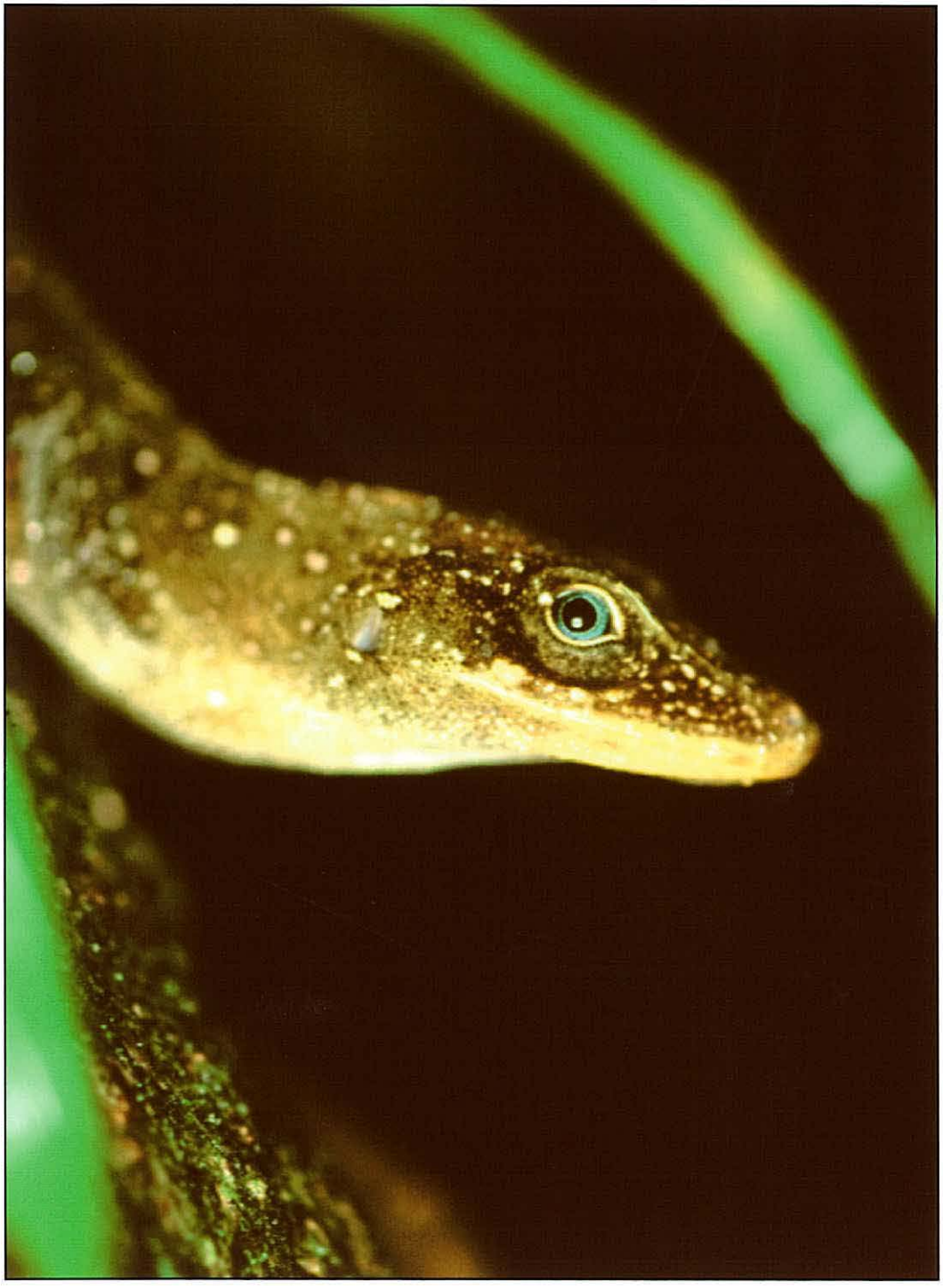
It is acknowledged that in practice it is unlikely that the translocation of smaller herpetofauna for conservation purposes is unlikely to involve anaesthesia as in this case, but all experimental animals were subjected to the same treatment and so even if an increase in mortality or loss of condition is the result of analytical treatment of specimens, the comparison between control and translocated populations should remain valid.

Thus, the results, as detailed in section 2.3 of this chapter provide a clear picture of significant condition loss in males and reduction in fecundity in females during both wet and dry seasons. As stated above, the essence of a successful translocation program is the establishment of a viable and self-sustaining population and the measure of fecundity from percentage gravidity (Figures 2.16 and 2.19) and percentage hatchlings within the experimental populations (Figures 2.17 and 2.20) are a useful measure of this. Figures 2.16 and 2.19 also contain a comparative representation of the levels of gravidity observed in the native experimental populations illustrating the negligible effect on gravidity in the control population. However the loss of gravidity and the supporting results of the number of hatchlings in the enclosure populations illustrates the devastating effect on the population demographics experienced by the translocated montane populations over both wet and dry seasons. There are virtually no hatchlings observed from the montane translocated populations where as the control population hatchling percentage rapidly approach the levels observed in the native populations.

If this translocation had been conducted for conservation purposes it is highly unlikely that a viable population would have been established from the montane translocated populations. Due to the degree of reduction in fecundity in the translocated montane population, even a large increase in the translocated population size is not predicted to significantly improve the opportunity of the successful establishment of a viable population. The experimental populations were also maintained in large enclosures, which would aid in the maintenance of cohesive territorial structure. The results of releasing a translocated population into non confined area of habitat is suggested to result in a further reduction of the opportunity to establish a viable population. As the conclusions of chapter 2 indicate this is most likely the result of shift in environment and ecology. However, it must be borne in mind that this translocation uses an experimental population sourced less than seven kilometres from the translocation enclosure site within the continuous and natural range of the species *Anolis oculatus*. Therefore great emphasis should be made on the identification of habitat ecotypes of source and translocation site locations regardless of geographic proximity or the continuous nature of the range of the species or population under management.

CHAPTER 3:

TESTING FOR A SELECTION GRADIENT.



A male *Anolis oculatus,* from the Syndicate montane rainforest reserve.

3.0 INTRODUCTION.

In chapter 2, both wet and dry season translocation experiments provided strong evidence for an increase in selection intensity acting on a translocated populations of *Anolis oculatus.* In that experiment, the translocated population was collected from a montane rainforest environment and translocated to a Caribbean coast xeric woodland.

To assess the causes of the observed increase in selection intensity, and in an attempt to reinforce the evidence that a significant factor of natural selection intensity are physical and biotic variables, a translocation of 12 populations of *Anolis oculatus* was conducted. These populations were sourced from an ecological gradient of environmental variability, from the xeric woodland translocation environment to elfin woodland, and were translocated to the xeric woodland enclosure site. The aim is to test to see if the increasing environmental and ecological distance moved, is reflected in increasing selection intensity. An account of enclosure experiments for natural selection, the nature of directional selection, and the model organism, *Anolis oculatus*, are given in chapter 2.

3.0.1 SELECTION ALONG A GRADIENT.

When differential selection pressures are exerted along an environmental gradient, the result in phenotypic variation in inherited traits may be interpreted as a cline. Such clines in inherited traits are generally observed in species of limited dispersal ability

(Endler 1977; Hedrick 1986), but have also been observed in highly dispersive species (Struhsaker 1986).

When observing a gradient in phenotypic traits, and regarding them as a reflection of genotype, it is necessary to determine whether the observed pattern is the result of secondary contact, or natural selection in response to an environmental gradient.

Such clines in environment, and in the selection of differing phenotypic traits, may also be suggested as the origin of hybrid zones (Moore and Price 1993). These may be between defined populations, sub-species or species, resulting from adaptation to the variability of selection resulting from the cline. This occurs when genetically distinct populations with adaptation to specific environmental criteria are maintained by the fact that hybrids are less fit and therefore reproductively disadvantaged over the adapted populations. However, this is not always the case. Moore and Price (1993) demonstrate hybrids that are as fit and in some circumstances fitter than the parental morphs within the hybrid zone.

This maintenance of defined populations may be the result of genetically less fit hybrids where endogenous (intrinsic) selection may be seen to maintain the hybrid zone (Janson 1983), or by hybrids being phenotypically less well adapted to the environment or at a sexually selected disadvantage, when exogenous (extrinsic) selection is in play (Day and Schluter 1995).

Anolis oculatus has been shown to exhibit significant phenotypic variation across the environmental gradient in its range (Malhotra and Thorpe 1991b; 1992b). Except for

a defined region in the south western part of the island range, it does not express any significant barriers to gene flow other than geographic distance (Stenson pers. com.; Malhotra and Thorpe in press) or any delineated rapid shifts in phenotype, and therefor no identifiable zones of sub-speciation have been observed (Malhotra 1993). Malhotra (1992) states that, "the congruence between patterns of [phenotypic] variation both for characters within a character system, and for generalised character systems, is generally low. Because of the non-predictive patterns of variation, and the fact that variation is continuous (clinal) rather than categorical, it is suggested that the division of the species into formal subspecies is inappropriate. However, four loosely defined geographical groups do seem to exist. The incongruence of the patterns [outside the south western range of *Anolis oculatus*] also suggest that the variation is ecogenetic in nature."

Malhotra (1993) demonstrated that the geographic variation in *Anolis oculatus* was congruent to certain environmental factors and it was suggested that the observed variation in phenotype was the result of island wide natural selection resulting from physical (environmental), and also biotic (ecological) factors. If these environmental selection forces are responsible for the maintenance of geographic phenotype variation in *Anolis oculatus*, then by translocating populations taken from along an environmental gradient, a relationship between selection intensity and ecological distance should become apparent. Thus, the cause of phenotypic variation across the environmental cline will be further elucidated. Considering the increased selection intensity and loss of condition in translocated individuals illustrated in chapter 2, together with the evidence of Diaz et al (1996), and their study of Lacertid thermal ecology across an environmental cline, it becomes pertinent to consider the

translocation of individuals taken from an environmental cline in the anole model. Their study shows, using both correlation analyses and phylogenetically independent contrasts, that continuous among-species variations in mass-specific heating rates are negatively related to clinal differences in environmental temperatures. Temperature is a significant factor in the environmental variability observed between ecotypes on Dominica (Lang 1967).

The poikilothermic nature of reptiles means that any shift in thermal environment will elicit either a change in thermoregulatory behaviour, or reduced fitness as the critical thermal minimum, or maximum is approached. Such selection forces, and evolutionary consequences of environmental temperature change in the performance capacity of individual Squamata has been investigated by Bennett (1987), who showed a genotypic component to thermoregulation between individuals. Although *Anolis oculatus* has been classified as a eurytherm (Malhotra and Thorpe 1992, Roughgraden 1995), personal observations conducted throughout the wet and dry season experiments suggested the thermal niche may be an important factor in the fitness and survival of *Anolis oculatus* despite the absence of overt heliothermic behaviour. Hertz et al (1993) explains how, regardless of thermoregulatory mechanism, if the environmental temperature (T(e)), constitutes a narrow range, within which lies the optimal body temperature (T(b)), then thermoregulatory behaviour is unnecessary. However, even in eurythermic Squamata, if T(e) is outside the optimal range of T(b) then some response in the organism is required. This is supported by the work of Underwood (1981) who identified heliophilic responses in thermoregulation in *Anolis carolinensis*. Eurytherms, by definition have optimal T(b)s within the range of usual environmental temperatures (Roughgarden 1995), and

so, when considering *Anolis oculatus* populations sourced from environments of significantly different ambient temperatures, some thermal response in the lizards can be anticipated. This is because it is extremely unlikely that the environmental temperatures at the translocation environment will be within the optimal T(b)s for all translocated experimental populations. As Haily and Coulson (1996) point out, attempting to measure the 'effectiveness' of thermoregulation is a complex and often speculative matter. However standardised comparisons of thermoregulation between populations should identify any trends in thermoregulation between the experimental populations (Stevenson 1985). Therefore, attention to the thermal ecology of translocated *Anolis oculatus* may yield further details of environmentally linked selection pressures.

However, in some species, a response to differential selection regimes may be expressed through phenotypic plasticity rather than by genetic differentiation in the phenotypic traits under selection (Appleton and Palmer 1988; Palmer 1990; Gibbs 1993). This important issue is dealt with exclusively, in chapter 5.

3.0.2 AIMS.

The aim of this chapter is to:

i) Test the null hypothesis that selection intensity will not increase with the increasing ecological and environmental distance involved in the translocation to the xeric woodland enclosures.

ii) To attempt to assess whether thermal stress is not a contributory factor in the selection intensity observed.

3.1 METHODS AND MATERIALS.

As stated above the enclosure apparatus of the wet and dry season translocation experiments were maintained in serviceable condition and employed in the clinal translocation experiment. Therefore, for reference of enclosure design and construction, see chapter 2, section 2.2.2.

3.1.1 SEASONAL LOGISTICS.

From the results of the wet and dry season translocation experiments it is evident that selection intensity was less during the wet season experiment (chapter 2, section 2.3.4,). It was decided that this fact would aid the demonstration of differing selection intensities on a multiple population translocation, as the more rapid rate of selection observed in the dry season may condense the difference in selection intensity between populations to an insignificant level. Therefore it was decided to conduct the clinal translocation experiment during the wet season.

3.1.2 EXPERIMENTAL *Anolis oculatus* POPULATIONS.

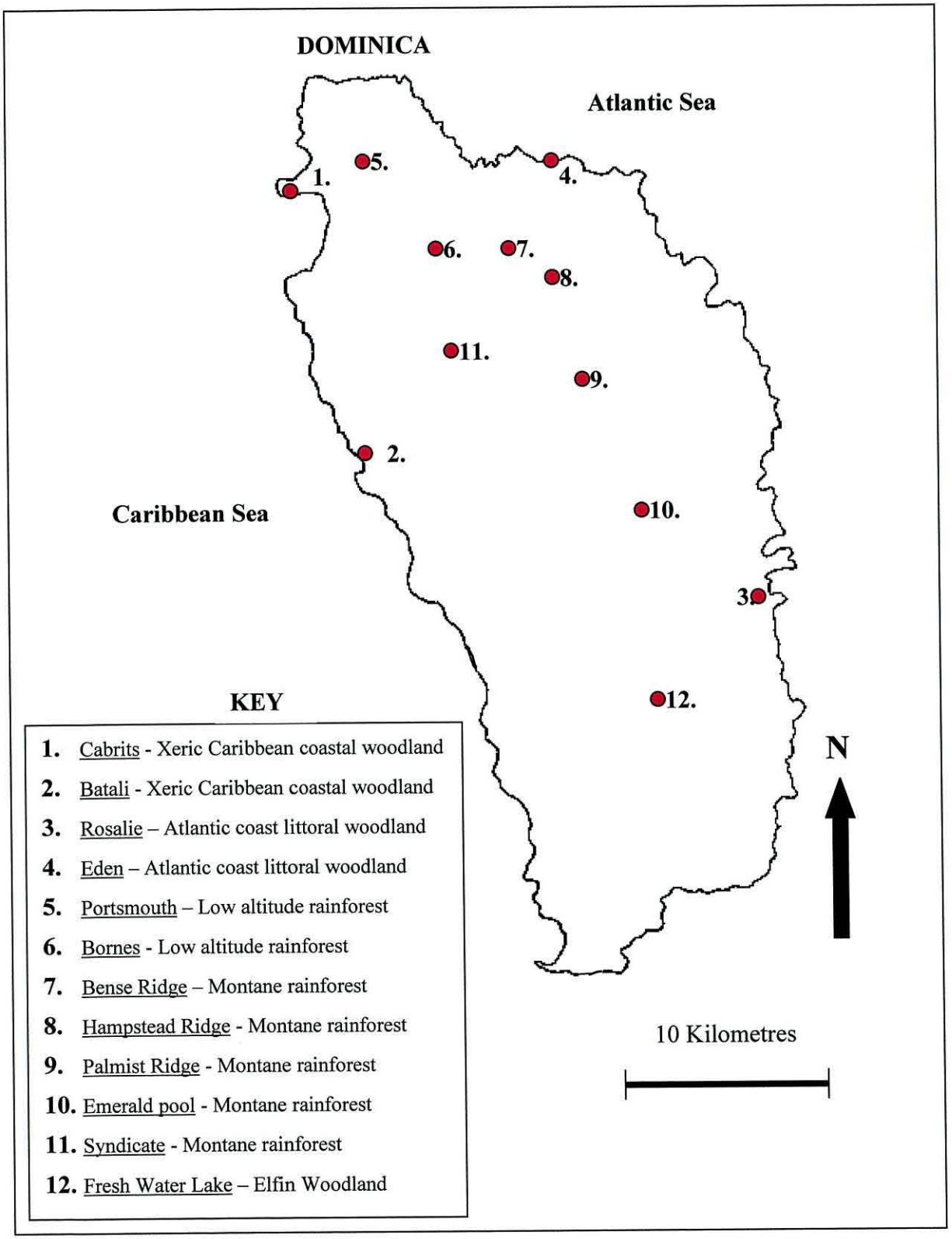
Anolis oculatus, contrary to previous published data (Bullock et al 1993; and Malhotra and Thorpe 1992b) is present at varying densities across the entire range of terrestrial vegetative habitats on Dominica (pers. obs). Therefore, selection of twelve populations of experimental anoles can be made from any sampled population of

appropriate environmental distance from the xeric Caribbean coast woodland translocation site without that risk of differential isolation in populations that would result from areas devoid of *Anolis oculatus*. Populations from the south western Caribbean region are excluded from the translocation experiment because of suspected barriers to gene flow (Stenson pers com. Mahotra and Thorpe in press). Using quantified vegetation classifications (Malhotra 1992), and measurements of altitude, floral assemblages, and topographic aspect, 12 populations including the control xeric woodland population from Cabrits, were selected. These are illustrated in figure 3.0.

A limiting factor in the analysis of both wet and dry season translocation experiments, as anticipated, was sample size. This is a logistically inevitable fact when considering enclosing viable populations of terrestrial vertebrates in enclosures to be maintained by a single field worker. Due to the sexual size dimorphism observed in *Anolis oculatus* (Malhotra and Thorpe 1991b), if experimental populations consisted of only female individuals, the smaller sex, then the numbers of individuals required to stock the enclosures to the necessary biomass would significantly increase. On the strength of Stamps (1998) it was decided that females were capable of maintaining a coherent territory structure in a sexually bias population and so such a strategy should not adversely effect the survival of individuals. In addition, as all experimental populations would similarly consist of females, any effect on the population would be consistent. Each of the four enclosure replicates, was stocked with an equal representation of experimental individuals from all twelve experimental populations. Approximately 40 individuals from each experimental locality were required to achieve the required enclosure biomass in each of all four enclosures. Therefor, in

Figure 3.0. Site Locations of Experiment *Anolis oculatus* Populations, in Environmental Gradient Translocation.

Figure 3.0 illustrates the site locations of all 12 experimental populations of *Anolis oculatus* translocated in the gradient translocation experiment. Their habitat ecotypes are given in the key below.



excess of four hundred experimental anoles were maintained, with approximately 100 individuals per each of the four experimental enclosures.

3.1.3 BIOMETRIC RECORDING.

Collection of specimens, anaesthesia, and the recording of morphometric and squamous character traits were all carried out using the same methodology as described in chapter 2, section 2.2.5, except for analysis of colour hues. Instead of using colour charts to read cyan, magenta and yellow percentage representation, the transparencies (taken using the same methodology outlined in chapter 2, section 2.2.5) were digitised using a Nikon Coolscan 400^{TM} and a digital interpretation of % representation of cyan, magenta and yellow provided by Adobe PhotoShop 4.0. Colour hue character trait variables remained the same as those described in chapter 2, section 2.2.5.

3.1.4 THERMOREGULATION.

An additional variable added to the character traits recorded in the clinal translocation experiment is the temperature differential between body temperature, T(b), of the experimental *Anolis oculatus*, and the temperature of the immediate environment, T(e). This differential measure of temperature was predicted to identify any trends in thermoregulatory behaviour in *Anolis oculatus*. Temperatures departing from the environmental ambient were not anticipated as *Anolis oculatus* is generally not

observed in direct sunlight over the majority of it's range (with the notable exception of high altitude elfin woodland – pers. obs.). However, niche selection observed over the wet and dry translocation experiments were interpreted as having a thermal component in the populations observed in the xeric woodland ecotype.

Therefor the following methodology was formulated to assess body temperature and immediate environmental temperatures to establish a temperature differential.

During each analysis period of the clinal translocation experiment individuals were collected and identified by their 'toe clip' number (chapter 2, section 2.2.5). On capture, using an Mtech™ paediatric thermometer, rectal body temperatures were recorded in degrees centigrade to 0.01°C (Avery 1982). This was done as rapidly as possible to minimise the heating effect of capture and handling, and any specimen not captured directly from natural behaviour (i.e., a specimen that was chased prior to capture) was excluded from the T(b) analysis. Upon recording rectal body temperature, (a beep is emitted from the thermometer when a stable temperature is achieved), the specimen was replaced at the precise location of capture to minimise the effects of territory disruption. Immediately after releasing the specimen the ambient environmental temperature was recorded as close as possible to the precise point of capture using a Vaisala™ HMI-31 temperature and relative humidity indicator fitted with a HMP-35 probe. For subsequent analysis, the differential between the two temperatures was calculated by subtracting the experimental specimens body temperature T(b) from the immediate environmental ambient temperature T(e). This provided the specimen specific temperature differential T(d) and a very simple equation expressing this is given below:

$$T(e) - T(b) = T(d)$$

This was recorded for each specimen on capture at each experimental interval throughout the clinal translocation experiment.

3.1.5 ENVIRONMENTAL VARIABLES.

To account for variation in climate, and ecotype of habitat at each experimental site locality, a range of environmental variables were recorded.

At each site altitude in meters was recorded using a Thomen Classic™ barometric altimeter. At each experimental site locality shaded ambient temperature and relative humidity was recorded between 1200hrs and 1400hrs using an Vaisala™ HMI-31 temperature and relative humidity indicator fitted with a HMP-35 probe. Recordings were made on each visit to site locations throughout the experimental period. The mean average temperature and relative humidity were then calculated for each location. An indices of vegetation classification was also used as an environmental variable, adapted from Malhotra (1992).

3.1.6 STATISTICAL ANALYSIS.

Statistical analysis followed the same basic framework as the analysis of both the wet and dry season translocation experiments. Data was recorded onto a Toshiba 486 laptop computer in the field. Data sets were prepared and entered in ASCII format

(7.2) into Word Perfect 5.1 (DOS). Colour and marking analysis data was then added to this after lab analysis of the transparencies. Analyses were run on BMDP-DYNAMIC (BMDP Statistical Software,Inc.).

3.1.6.1 REPLICATION.

To test bias in the replication of the experiment over the four enclosures, a Chi-squared test for independence of survival between the experimental replicates was carried out (Langley 1970). Although mortality is not the focus of this study, any significant differences in mortality between the enclosure replicates may indicate significant environmental variability between enclosures, which could affect natural selection intensity. A chi-square test for independence was executed at each experimental interval throughout the experiment, to test for temporal bias in mortality between the four enclosure replicates.

3.1.6.2 MULTIVARIATE ANALYSIS OF VARIANCE IN SURVIVAL PHENOTYPES.

Significant differences in selection intensity between ecotypes were tested for using a three way MANOVA. This would indicate that the experiment had yielded results regarding phenotype related differential mortality with any significant differences in character traits, between survivors and non-survivors. The program was instructed to

model interactions between the enclosure an individual specimen was maintained in, survival to an identified stage in the experiment, and the source ecotype of the specimen. An interaction was specified between survivorship and ecotype. This interaction was designed to detect any significant differences in the phenotypic characters of experimental specimens between surviving and non-surviving groups when regarding their ecological origins, and a significant interaction would indicate that the selection intensity was dependent on ecotype. The results of which indicate the presence or absence of significant selection intensity acting on character traits.

3.1.6.3 DIFFERENCE IN PHENOTYPE BETWEEN SURVIVORS AND NON-SURVIVORS.

Canonical variates analysis (CVA) was employed to assess multivariate distances, expressed as Mahalonobis distance (D), in phenotype between surviving and non-surviving groups in all translocated experimental populations to provide a measure of selection intensity (Brodie et al 1995). Each of the four replicate populations of each experimental population was tested individually for selection intensity. Analysis was carried out at four stages throughout the translocation experiment, at 28 days, 56 days, 84 days, and 112 days respectively. The CVA analysis was run to step 10 consistently throughout the analysis. As described in chapter two, and characters are added to the analysis, selection intensity represented as Mahalonobis distance (D) asymptotes, but the significance levels reduce. Step ten in the analysis (i.e. run to ten character analyses), provided the best balance of significance indicating the difference between control and montane selection intensities.

3.1.6.4 TESTING ECOLOGICAL DISTANCE AGAINST SELECTION INTENSITY.

Using a principal co-ordinate analysis (PCD), a dissimilarity matrix was generated from both biotic, and physical environmental variables to represent the difference in environment between each of the twelve experimental populations. This is generated from data measuring altitude, average annual temperatures, average relative humididty, and a vegetation ecotype index (Malhotra 1992) for each experimental site. From this matrix, the difference in environment between the translocation environment and the experimental population environments, was extracted. This measure of environmental dissimilarity from the translocation environment was then tested against the Mahalonobis distance between survivors and non-survivors in each of the four replicates, for all twelve experimental populations. This analysis was carried out at all four experimental intervals.

3.1.6.5 TESTING FOR TRAIT SPECIFIC SELECTION COEFFICIENTS.

To observe differential selection at a character trait level between surviving and non-surviving groups, it was possible to perform a partial regression of character states in experimental individuals against an ordinal of survival (Brodie et al 1995). This measure took into account the survival status of the experimental specimen at each stage in the analysis and produced a parametric measure of survival. To carry out such a regression analysis it is necessary to standardise the data set by returning a

normalised value from a distribution characterised by the mean and the standard deviation of the group (Grant and Grant 1993). For a further description of selection coefficient generation, see section 2.2.12, chapter 2.

3.2 RESULTS.

3.2.1 REPLICATION.

A Chi-squared test for independence of survival between experimental replicates at each experimental interval found no independence in the experimental replicates. The results are illustrated in table 3.1. No temporal bias in selection mortality between the four replicates was detected.

3.2.2 MANOVA RESULTS.

MANOVA results illustrated in table 3.2, indicate that the experiment had yielded positive results regarding natural selection having a significant effect on the phenotype of survivors being dependent on the ecotype. Several morphometric variables and four squamous variables proved to have been significantly different between survivors and non-survivors but eye ring magenta colouration ($F=36.03$; $P=<0.0000$) and the body temperature differential ($F=20.51$; $P=<0.0000$) were by far, the most significant.

3.2.3 SELECTION INTENSITY.

Canonical variate analysis (CVA) tested for Mahalonobis distances, which were used as a measure of phenotypic differences between survivors and non-survivors, and

Table 3.1

Table 3.1 illustrates the lack of independence and therefor the non-bias replication of results concerning survival between enclosures.

Chi-Squared Test for Independence of Survival between Experimental Replicates at Four Experimental intervals								
Experiment Interval	Day 28		Day 56		Day 84		Day 112	
Survivor / Nonsurvivor	Surv	Nonsurv	Surv	Nonsurv	Surv	Nonsurv	Surv	Nonsurv
Enclosure Replicate 1.	72	17	64	25	57	32	50	39
Enclosure Replicate 2.	74	15	66	23	59	30	44	45
Enclosure Replicate 3.	78	11	69	20	54	35	52	37
Enclosure Replicate 4.	71	18	64	25	56	33	51	38
Chi-Squared	2.275		0.975		0.63		1.762	
Degrees of Freedom	3		3		3		3	
P-Values	0.517		0.807		0.89		0.623	

Table 3.2

Table 3.2 illustrates that several morphometric variables and four squamous variables proved to have been significantly different between survivors and non-survivors but eye ring magenta colouration (F=36.03; P=<0.0000) and the body temperature differential (F=20.51; P=<0.0000) were by far, the most significant. Stage 3 of the experiment represents day 84 of the 112 day experiment.

MANOVA results of Female Survivorship against Experimental Population Ecotype at Clinal populations Experiment Stage 3.		
Character set	**Frequency (F)**	**P - Value**
Snout to vent length	**2.74**	**0.0030*** **
Femur length	1.20	0.2877
Tibial length	**2.46**	**0.0075****
Toe length	**2.99**	**0.0012*** **
Toe width	0.56	0.8422
Tail depth	1.75	0.0687
Head width	1.56	0.1174
Head length	0.76	0.6683
Around body scale count	**1.98**	**0.0346****
Bet. Supraorbital scale count	**1.94**	**0.0393****
Lamellar scale count	1.34	0.2055
Scale size index	**2.24**	**0.0155****
Ventral scale count	**2.58**	**0.0050*** **
Eye ring yellow	**5.78**	**0.0001*** **
Eye ring magenta	**36.03**	**0.0000*** **
Eye ring cyan	**9.35**	**0.0000*** **
Dorsal yellow	0.79	0.6349
Dorsal magenta	1.05	0.3993
Black marking width	0.80	0.6280
Dorsal cyan	0.08	0.9999
Transect 1	1.85	0.0514
Transect 2	1.19	0.2936
Transect 3	0.31	0.9774
Body Temperature differential	**20.51**	**0.0000*** **

Key – Degrees of Freedom = 10, 335; ** = significant to 0.05; *** = significant to 0.005.

hence a measure of selection intensity (Brodie et al 1995; Malhotra and Thorpe 1992). The significance of difference between these character traits, was provided by the F matrix. The results for all interactions of survivors and non-survivors are tabulated in table 3.3, and graphically represented in figure 3.1 where the difference in Mahalonobis distance between populations is represented.

3.2.4 TESTING SELECTION INTENSITY AGAINST ENVIRONMENT.

Using the matrices of environmental dissimilarity generated in the PCD analysis, the environmental dissimilarity from the translocation enclosure environment at Cabrits, to all twelve experimental populations, was extracted.

This measure of environmental dissimilarity was then tested against the selection intensity observed in each replicate of all twelve experimental populations, expressed as Mahalonobis distance between survivor and non-survivor groups. At 28 days, or stage 1 in the experiment a correlation coefficient of $R^2 = 0.3778$ was recorded, with a probability of $P = <0.001$ (DF = 26). This is illustrated in figure 3.2. At stage 2 in the experiment, at 56 days, an increase in the significant relationship between environmental dissimilarity and selection intensity is seen with a correlation coefficient of $R^2 = 0.5696$ and a probability of $P = <0.001$ (DF = 26), and is illustrated in figure 3.3. Figure 3.4 illustrates the significant relationship between selection intensity and environmental dissimilarity at stage 3 in the experiment (84 days). A correlation coefficient of $R^2 = 0.4082$ is recorded with a probability of $P = <0.001$

Table 3.3

Experiment Mahalonobis (D) Distances Between Survivor and Nonsurvivor Groups representing Selection Intensity.

Table 3.3 (over leaf) illustrates the selection intensity, expressed as Mahalonobis (D) distances, between survivor and non-survivor groups in all twelve experimental populations. Table 3.3 depicts clearly the range of D between populations and the variability in significance of those distances.

Selection Intensity Expressed as Experimental Mahalonobis (D) Distances Between Survivor and Nonsurvivor Groups

Experimental Pop^{n}.	days	D	Replicate 1 D	Replicate 2 D	Replicate 3 D	Replicate 4 D	Survivor/ Nonsurv.	F-Stat.
Cabrits 0-1	28	---	---	---	---	---	---	---
Cabrits 0-2	56	---	---	---	---	---	---	---
Cabrits 0-3	84	2.96	0.33	0.93	1.69	3.64	25 : 5	0.69
Cabrits 0-4	112	3.00	0.75	4.04	1.73	3.16	23 : 7	0.90
Batali 0-1	28	---	---	---	---	---	---	---
Batali 0-2	56	---	---	---	---	---	---	---
Batali 0-3	84	4.83	3.89	1.21	4.3	4.43	25 : 4	1.40
Batali 0-4	112	2.39	7.03	1.87	1.77	3.32	21 : 8	0.58
Eden 0-1	28	---	---	---	---	---	---	---
Eden 0-2	56	5.54	0.95	0.43	5.5	0.55	27 : 3	1.56
Eden 0-3	84	2.53	1.00	2.58	2.72	3.13	23 : 7	0.67
Eden 0-4	112	2.26	2.36	2.95	2.42	1.53	17 :13	0.70
Rosalie 0-1	**28**	**21.74**	**2.62**	**21.04**	**1.72**	**22.79**	**28 : 3**	**25.58****
Rosalie 0-2	**56**	**15.95**	**2.04**	**13.88**	**2.83**	**11.71**	**27 : 4**	**17.68****
Rosalie 0-3	**84**	**12.84**	**2.83**	**13.18**	**2.9**	**11.64**	**24 : 7**	**17.85****
Rosalie 0-4	112	4.96	2.54	6.02	1.56	5.33	20 : 11	2.48
Portsmouth 0-1	**28**	**6.45**	**5.76**	**6.49**	**5.81**	**8.02**	**24 : 6**	**3.75****
Portsmouth 0-2	56	2.63	2.81	2.75	2.39	4.10	18 : 12	0.94
Portsmouth 0-3	84	3.43	3.23	1.75	4.62	4.60	12 : 18	1.59
Portsmouth 0-4	112	3.38	6.38	2.56	4.70	0.92	8 : 22	1.25
Bornes 0-1	**28**	**4.06**	**4.74**	**3.74**	**3.22**	**4.19**	**23 : 10**	**2.63****
Bornes 0-2	56	3.71	4.58	4.37	2.84	3.86	21 : 12	2.32
Bornes 0-3	84	3.53	4.64	3.84	1.81	3.52	17 : 16	2.26
Bornes0-4	112	3.74	4.85	4.02	2.54	3.15	16 : 17	2.04
Hampstead 0-1	**28**	**16.09**	**15.93**	**4.26**	**16.85**	**15.87**	**27 : 8**	**38.20****
Hampstead 0-2	**56**	**12.73**	**12.27**	**4.19**	**12.51**	**11.52**	**23 : 12**	**30.56****
Hampstead 0-3	**84**	**15.42**	**15.67**	**13.20**	**14.98**	**15.07**	**19 : 16**	**49.42****
Hampstead 0-4	**112**	**18.85**	**26.33**	**23.91**	**18.82**	**18.14**	**18 : 17**	**74.31****

Selection Intensity Expressed as Experimental Mahalonobis (D) Distances Between Survivor and Nonsurvivor Groups								
Experimental Pop^{n}.	**days**	**D**	**Replicate 1 D**	**Replicate 2 D**	**Replicate 3 D**	**Replicate 4 D**	**Survivor/ Nonsurv.**	**F-Stat.**
Bense 0-1	**28**	**16.41**	**15.68**	**16.29**	**16.44**	**17.99**	**22 : 10**	**38.93****
Bense 0-2	**56**	**13.41**	**13.75**	**12.28**	**12.78**	**14.61**	**21 : 11**	**27.35****
Bense 0-3	**84**	**35.95**	**35.65**	**34.30**	**35.38**	**36.32**	**20 : 12**	**204.01****
Bense 0-4	**112**	**41.33**	**41.40**	**41.21**	**42.15**	**41.24**	**18 : 14**	**284.56****
Palmist ridge 0-1	**28**	**11.47**	**3.34**	**11.85**	**11.64**	**10.5**	**22 : 8**	**14.49****
Palmist ridge 0-2	**56**	**14.73**	**6.09**	**14.96**	**14.55**	**16.75**	**20 : 10**	**27.16****
Palmist ridge 0-3	**84**	**8.02**	**4.25**	**3.57**	**8.63**	**8.25**	**15 : 15**	**9.08****
Palmist ridge 0-4	**112**	**19.52**	**14.27**	**23.57**	**18.25**	**18.25**	**13 : 17**	**52.76****
Emerald pool 0-1	**28**	**12.7**	**3.19**	**12.55**	**2.97**	**12.87**	**23 : 8**	**19.08****
Emerald pool 0-2	**56**	**9.14**	**8.37**	**8.79**	**8.79**	**8.67**	**15 : 16**	**12.91****
Emerald pool 0-3	**84**	**7.82**	**6.61**	**8.40**	**9.27**	**8.22**	**14 : 17**	**9.36****
Emerald pool 0-4	**112**	**8.52**	**7.98**	**8.24**	**8.80**	**8.67**	**13 : 18**	**10.94****
Syndicate 0-1	**28**	**10.57**	**9.93**	**12.31**	**11.36**	**10.22**	**23 : 12**	**21.08****
Syndicate 0-2	**56**	**8.53**	**9.38**	**10.28**	**6.99**	**8.38**	**14 : 21**	**14.62****
Syndicate 0-3	**84**	**9.12**	**10.31**	**8.38**	**8.53**	**9.25**	**11 : 24**	**15.01****
Syndicate 0-4	**112**	**5.5**	**6.09**	**5.34**	**0.8**	**6.09**	**6 : 29**	**3.6****
F.W.L. 0-1	**28**	**7.93**	**7.81**	**7.61**	**8.34**	**7.43**	**12 : 23**	**11.84****
F.W.L. 0-2	**56**	**10.41**	**10.68**	**8.83**	**11.54**	**1.51**	**4 : 31**	**9.16****
F.W.L. 0-3	**84**	**15.01**	**16.51**	**1.52**	**14.21**	**1.58**	**3 : 32**	**14.77****
F.W.L. 0-4	**112**	**15.01**	**16.51**	**1.52**	**14.21**	**1.58**	**3 : 32**	**14.77****

Key – Hampstead = Hampstead Ridge; F.W.L. = Freash Water Lake. ** = Significant to 0.05.

Figure 3.1

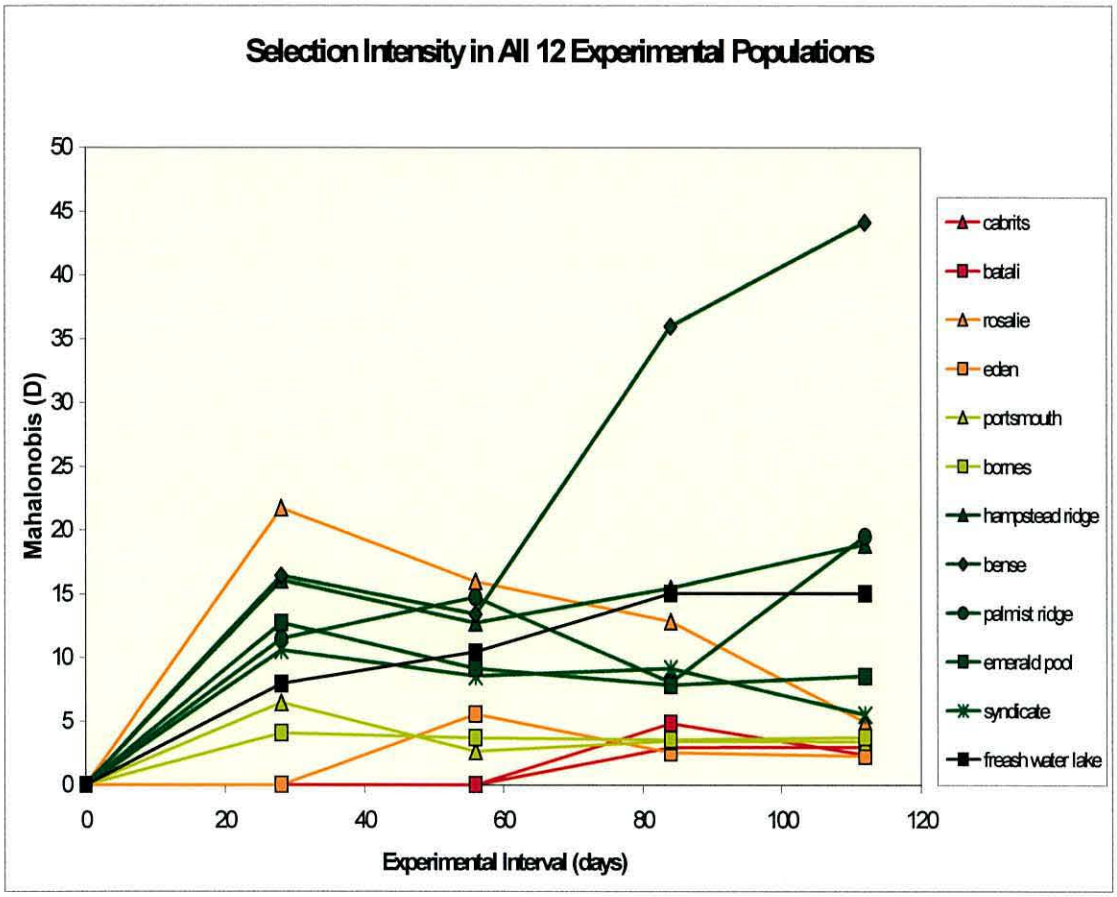


Figure 3.1 illustrates the difference in Mahalonobis distance between the clinal translocation experimental populations. Significance levels are given in table 3.3.

Figure 3.2

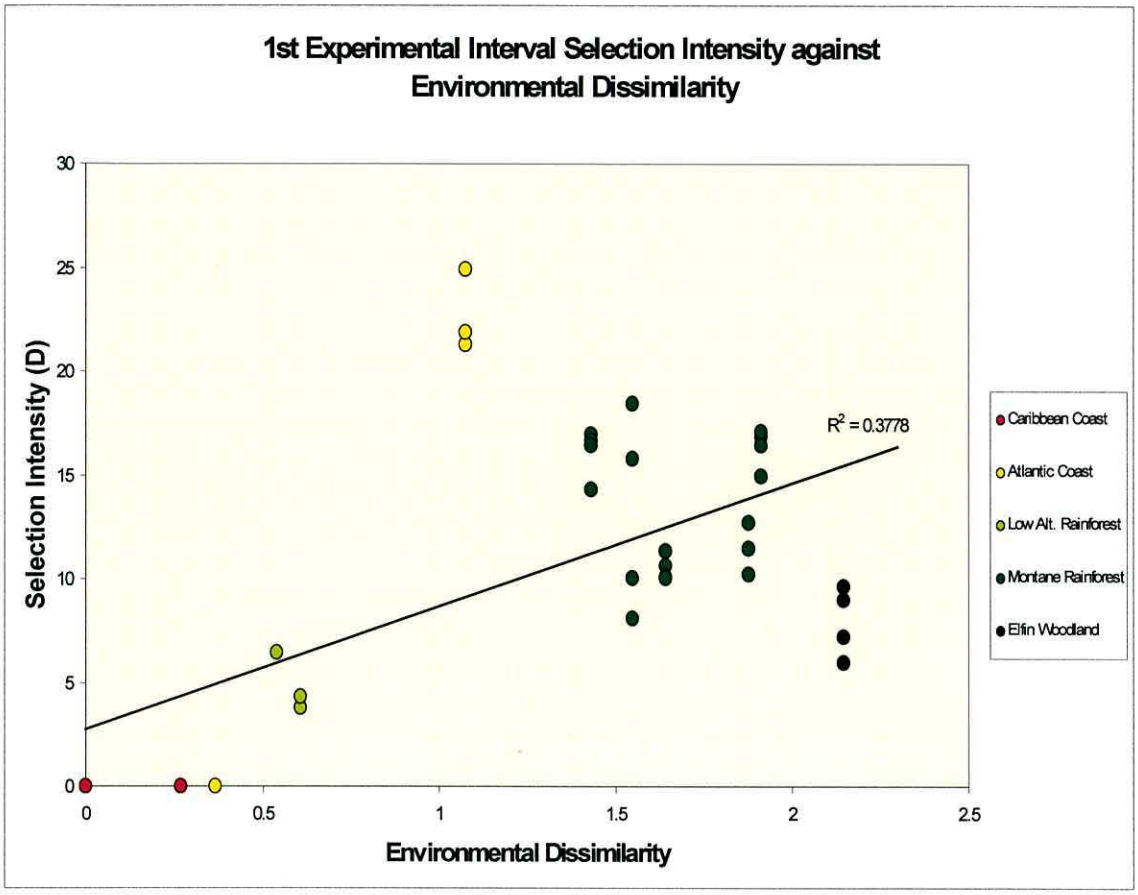


Figure 3.2 illustrates the significant relationship between selection intensity and the environmental dissimilarity from the translocation environment. At 28 days, or stage 1 in the experiment a regression coefficient of $R^2 = 0.3778$ was recorded, with a probability of $P = <0.001$ ($DF = 26$).

Figure 3.3

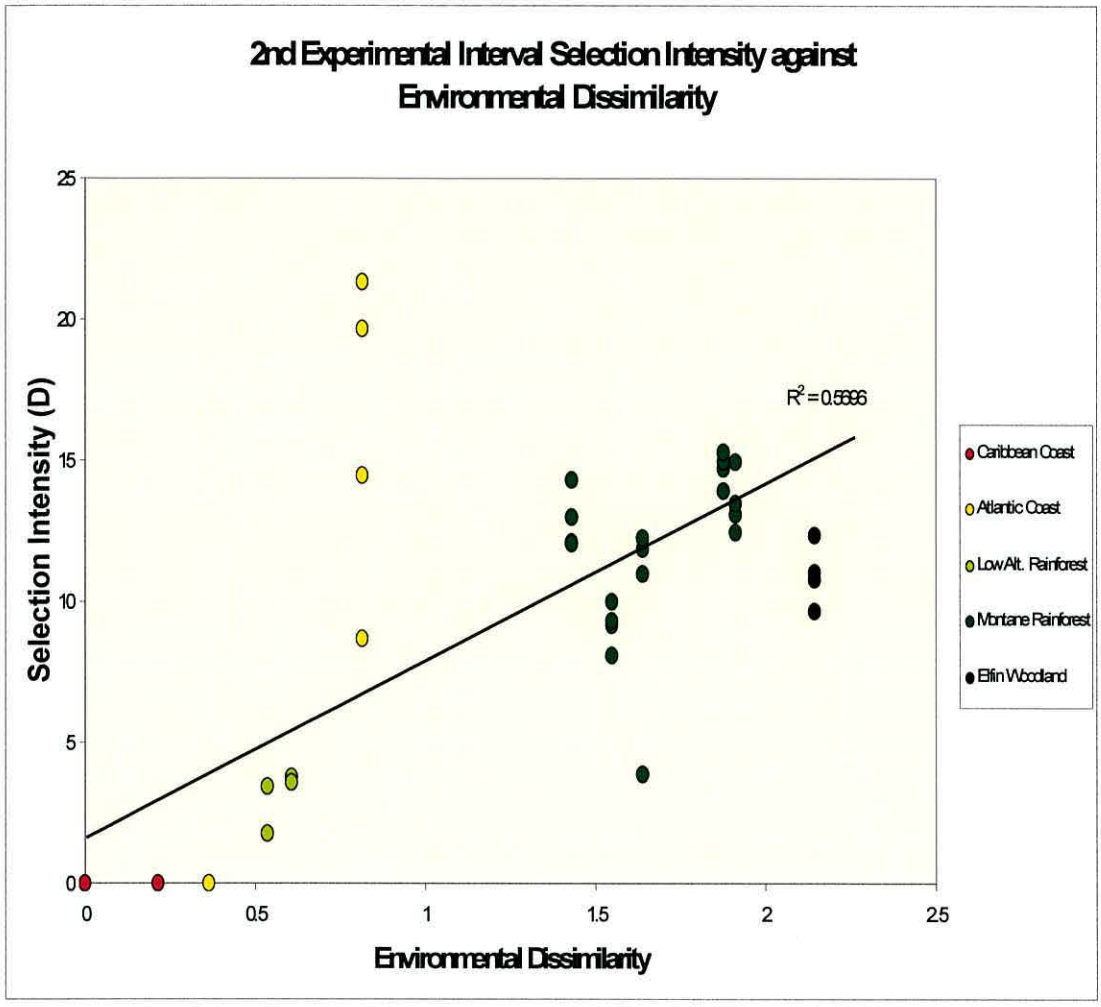


Figure 3.3 illustrates the significant relationship between selection intensity and environmental dissimilarity. A regression coefficient of $R^2 = 0.5696$ and a probability of $P = <0.001$ ($DF = 32$) is shown

Figure 3.4

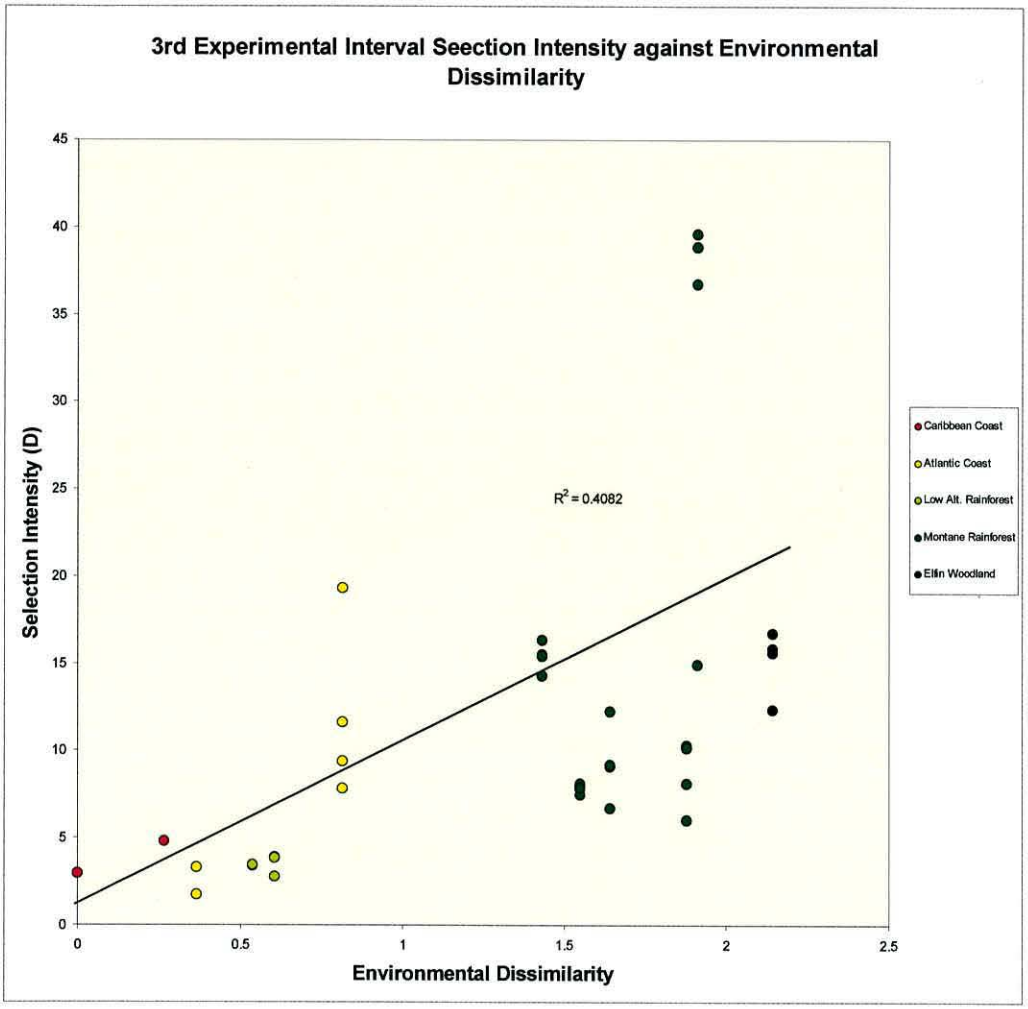


Figure 3.4 illustrates the significant relationship between selection intensity and environmental dissimilarity at stage 3 in the experiment (84 days). A regression coefficient of R2 = 0.4082 is recorded with a probability of P = <0.001 (DF = 32).

Figure 3.5

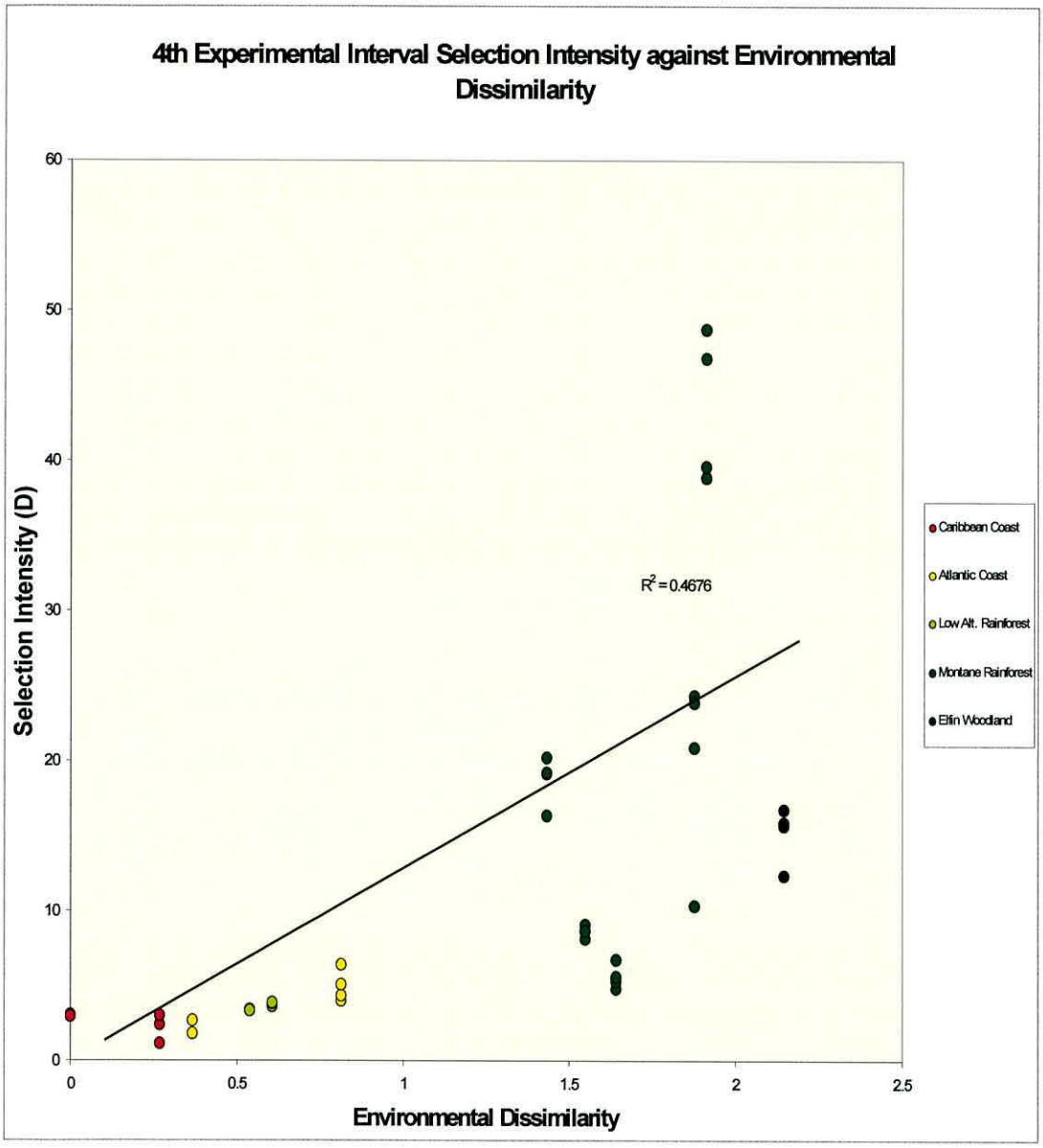


Figure 3.5 illustrates a significant relationship between selection intensity in the 12 experimental populations and the environmental dissimilarity between them of stage 4 at 112 days into the experimental analysis. A regression coefficient of $R^2 = 0.4676$ is recorded with a probability of $P = <0.001$ ($DF = 33$).

(DF = 46). Finally stage 4 of the experiment at 112 days, also provides a significant relationship between selection intensity in the 12 experimental populations and the environmental dissimilarity between them. A correlation coefficient of $R^2 = 0.4676$ is recorded with a probability of $P = <0.001$ (DF = 46). This is illustrated in figure 3.5.

3.2.5 SELECTION COEFFICIENTS.

Character trait selection coefficients were generated from partial regression analyses, details of which are given in section 2.2.12 in chapter 2. Table 3.4 illustrates the selection coefficients indicating their significance and direction. It can be clearly seen that the frequency of significant character trait selection coefficients increases. This increase in significant character trait selection is observed as the experimental sites progress from the translocation enclosure site in xeric woodland towards sites in montane rainforest and elfin woodland. All recorded character traits yield a significant selection coefficient in at least one experimental population with the two character traits providing the most significant selection coefficients across all experimental populations, being the eye ring magenta colour hue and the body temperature differential. The body temperature differential provides a significant selection coefficient over the whole of the rain forest, montane forest and elfin woodland populations. The mean temperature differential between the body temperature of survivors and the ambient environment at each stage in the experiment is given in table 3.5, along with the mean temperatures at midday from each experimental populations' source.

Table 3.4

Key – Cab = Cabrits; Bat = Batali; Born = Bornes; Ports = Portsmouth; Ros = Rosalie; Ham = Hampstead; EP = Emerald Pool; Synd = Syndicate; Palm = Palmist; Ben = Bense; FWL = Fresh Water Lake.
Bold Type = Significance.

Translocation Experiment Character State Selection Coefficients												
Character	Cab	Bat	Eden	Born	Ports	Ros	Ham	EP	Synd	Palm	Ben	FWL
Snout to vent length	-0.29	**-0.54** ****	-0.07	-0.10	0.18	-0.30	-0.21	-0.05	**0.69** ****	**0.48** **	**0.75** ****	-0.10
Femur length	0.27	0.25	0.25	-0.15	**-0.52** ***	0.03	0.02	-0.22	-0.04	**0.64** ****	0.02	**0.57** ****
Tibial length	-0.22	-0.24	0.00	0.27	0.30	0.10	-0.03	0.19	**-0.35** *	**-0.63** ****	0.15	**-0.38** *
Toe length	-0.25	0.21	-0.04	0.11	-0.00	-0.01	-0.04	**0.64** ****	-0.28	**0.59** ****	-0.20	**-0.56** ****
Toe width	-0.01	0.27	0.32	-0.06	0.11	0.24	0.21	-0.07	0.08	-0.04	**0.87** ****	0.20
Tail depth	0.25	**0.43** *	**-0.61** ****	0.28	0.22	-0.20	-0.09	**-0.57** ****	**0.57** ****	-0.11	**-0.61** ****	**-0.39** *
Head width	0.23	**-0.36** *	0.05	0.09	0.06	0.28	**-0.44** **	0.14	**-0.46** ***	**-0.43** *	**-0.77** ****	**-0.44** **
Head length	0.09	**0.63** ****	0.29	-0.22	-0.02	-0.22	0.07	0.19	-0.05	0.15	**-0.61** ****	**0.63** ****
Around body scale count	-0.06	-0.02	**-0.40** *	-0.20	-0.28	**0.42** *	-0.06	**0.53** ***	0.16	**0.35** *	**0.42** *	0.04
Lamellar scale count	**0.451** *	-0.29	-0.28	-0.22	**0.36** *	-0.14	0.03	-0.30	-0.24	-0.07	-0.08	**0.67** ****
Scale size index	0.08	0.16	**0.50** ***	0.01	0.24	0.25	-0.00	**-0.73** ****	**-0.47** ***	0.22	0.00	0.21
Ventral scale count	0.02	-0.13	**0.419** *	-0.06	-0.24	-0.10	0.15	-0.16	0.15	0.29	**-0.61** ****	-0.02
Eye ring yellow	0.09	**-0.55** ***	-0.32	0.00	0.00	-0.13	0.00	**-0.66** ****	0.00	0.00	0.21	0.30
Eye ring magenta	-0.31	**-0.40** *	**-0.53** ****	-0.15	**0.44** *	-0.24	**-0.68** ****	**-0.86** ****	-0.40	0.00	**-0.84** ****	**-0.67** ****
Eye ring cyan	0.03	0.02	-0.05	-0.02	0.00	**-0.40** *	0.00	**-0.84** ****	0.00	**-0.76** ****	**-0.95** ****	**-0.59** ****
Dorsal yellow	0.34	0.31	**0.35** *	0.00	-0.29	0.02	-0.23	0.20	0.00	**-0.36** *	**0.61** ****	-0.30
Dorsal magenta	0.16	-0.02	-0.15	0.02	0.00	0.07	0.00	**-0.69** ****	-0.07	**0.37** *	0.29	-0.26
Dorsal cyan	-0.11	0.08	**0.43** **	0.08	-0.30	0.06	-0.16	**0.37** *	-0.25	**0.37** *	**-0.51** ***	0.01
% anterior white marks	0.11	**-0.44** *	-0.12	0.32	**-0.41** *	0.15	0.28	-0.14	**0.64** ****	**-0.51** ***	**0.38** *	**-0.50** ***
% midbody white marks	0.01	**0.59** ****	**-0.41** *	**0.35** *	0.07	-0.09	-0.11	-0.19	**-0.69** ****	**0.80** ****	**-0.90** ****	0.13
% posterior white marks	0.18	**-0.49** **	-0.21	-0.25	**-0.41** *	-0.11	-0.10	-0.25	0.09	**0.76** ****	**-0.85** ****	0.17
Body Temp. Diff.	-0.12	-0.24	-0.30	0.04	**0.50** ***	0.32	**0.84** ****	**0.72** ****	**0.95** ****	**0.87** ****	**0.44** **	**0.72** ****
Signif. Level	**Critical Selection Coefficient (r) Value of Significance**											
0.05*	**0.355**	**0.361**	**0.334**	**0.339**	**0.355**	**0.349**	**0.329**	**0.349**	**0.334**	**0.355**	**0.344**	**0.334**
0.01**	**0.456**	**0.463**	**0.430**	**0.436**	**0.456**	**0.449**	**0.424**	**0.449**	**0.430**	**0.456**	**0.442**	**0.430**
0.005***	**0.491**	**0.499**	**0.464**	**0.470**	**0.491**	**0.484**	**0.458**	**0.484**	**0.464**	**0.491**	**0.477**	**0.464**
0.001****	**0.562**	**0.570**	**0.532**	**0.539**	**0.562**	**0.554**	**0.525**	**0.554**	**0.532**	**0.562**	**0.546**	**0.532**

Table 3.5

Table 3.5 illustrates the mean temperature differential between the body temperature of survivors and the ambient environmental temperature at each stage in the experiment for each experimental ecotype population, along with the mean temperatures at midday from each experimental populations source environment (given to the nearest degree Celsius).

BODY TEMPERATURE / ENVIRONMENTAL TEMPERATURE DIFFERENTIAL (°C)							
Experimental populations	Ecotype	Source temp °C	Stage 0 Day 0	Stage 1 Day 28	Stage 2 Day 56	Stage 3 Day 84	Stage 4 Day 112
Cabrits (CONTROL)	A	26	-0.321	-0.33	-0.347	-0.351	-0.307
Portsmouth	B	28	0.01	0.0	-0.198	-0.199	-0.201
Batali	A	28	-0.02	0.0	-0.01	-0.02	0.0
Rosalie	C	28	-0.010	-0.089	-0.241	-0.288	-0.295
Eden	C	28	-0.004	-0.121	-0.238	-0.276	-0.41
Bornes	B	26	0.0	-0.241	-0.446	-0.487	-0.635
Hampstead Ridge	D	26	-0.02	-0.224	-0.538	-0.567	-0.582
Bense	D	22	-0.21	-0.401	-0.536	-0.907	-1.102
Palmist Ridge	D	24	-0.04	-0.315	-0.541	-0.763	-0.952
Emerald Pool	D	24	0.01	-0.414	-0.597	-0.862	-1.001
Syndicate	D	22	0.0	-0.565	-0.77	-0.981	-1.294
Fresh Water lake	E	22	-0.38	-0.602	-0.805	-0.934	-0.951

Key: Ecotypes are - A = Caribbean xeric woodland; B = Low altitude rain forest; C = Atlantic coast littoral woodland; D = Montane rain forest; E = Elfin woodland.

3.3 CONCLUSIONS AND DISCUSSION.

3.3.1 REPLICATION.

As table 3.1 illustrates, no independence was observed between the enclosure replicates and so confidence can be placed on the analysis with regard to the support of the enclosure replication.

3.3.2 CORRELATION OF SELECTION INTENSITY WITH ENVIRONMENTAL DISTANCE BETWEEN POPULATIONS.

The correlation of selection intensity with environmental distance between the experimental sites indicates that there is a significant relationship between the two, when tested with both, a correlation of selection intensity against PCD matrix values of environmental dissimilarity between populations, and by testing selection intensity against environmental principal components representing 97.5% of environmental variance.

The pattern of covariance between selection intensity and environmental distance was supported by the testing of Mahalonobis distance selection intensity in all replicated experimental populations against environmental dissimilarity, where a significant correlation was observed at all four stages of the analysis. This is illustrated in figures 3.2 to 3.5.

The resulting gradation of increasing selection intensity is also clearly represented in a graphical form in all the figures. Although elfin woodland is represented as the most extreme environment according to environmental PC1, it does not demonstrate the greatest selection intensity with regard to Mahalonobis distance between survivor and non-survivor groups. This is suggested to be the result of the extreme degree of mal-adaptation to the translocation environment, in that the experimental individuals were so unsuited to the environment, that their was little variance in their relative fitness in the translocation environment. The highest degree of total mortality was observed in the elfin woodland translocated population, and this would also have reduced the 'survivor' group sample size.

Therefor, one may consider the null hypothesis stated in section 3.0.2. From the results of section 3.2.4, it may be concluded that the null hypothesis that 'selection intensity will not increase with the increasing ecological and environmental distance involved in the translocation to the xeric woodland enclosures' cannot be rejected. This result lends great credibility to the statement that variation, both phenotypic and genotypic, observed in *Anolis oculatus*, is maintained by natural selection caused by physical and biotic environmental variables.

It is noticed that in figures 3.2 to 3.5, that the populations sourced from low altitude rain forest exhibit lower selection intensity than some of the Atlantic coastal populations. This is not necessarily unexpected or unexplainable. It is observed that low altitude rainforest populations, such as those at the Portsmouth population site,

experience considerable seasonal desiccation of their environment. Despite the significantly lower altitude, Atlantic coastal environments such as Rosalie, maintain high levels of relative humidity (Lang 1967, pers. obs.). Therefor, translocation to the xeric woodland environment of Cabrits, may be closer to the natural environmental range of physical climatic variables for low altitude rainforest populations than for some Atlantic coastal populations.

3.3.3 CHARACTER TRAIT SELECTION COEFFICIENTS.

All character traits recorded demonstrate significant selection coefficients within at least two, and up to seven of the twelve experimental translocated populations. As previously stated, selection coefficients can only be regarded as representing the general level of selection pressure being exerted on a population, as correlation between biometric traits would make conclusions of trait specific selection un-defendable. However, a general trend in the number of traits under significant selection, and the degree of that selection, illustrate that the general fitness of rainforest populations and elfin woodland populations is lower than coastal, (both Caribbean xeric woodland and Atlantic littoral woodland) and low altitude rainforest populations, when translocated to the xeric woodland experimental enclosures.

However, two character traits have produced highly significant results in both the MANOVA analysis, and the partial regression analysis that generated the selection

coefficients. These are, eye ring colour hues, specifically magenta and cyan, and the body temperature differential.

The results of the body temperature differential were anticipated to show body temperatures higher than ambient at the beginning of the experiment, due to sub-optimal territory occupation, and to become closer to ambient as natural selection took place during the experiment. All forest ecotype experimental populations came from source habitats with lower average ambient temperatures as described in table 3.5. It was anticipated that, due to territory disruption and mal-adapted individuals being unable to locate or maintain an optimal territory, that increased movement and intra-specific conflict may lead to increased activity patterns. This would then lead anole body temperatures to attain levels above the shaded environmental ambient, as indicated in experimental trials conducted with Cabrits individuals translocated into the enclosures prior to the experiment.

However, in this translocation experiment it is observed that mean population temperatures never rise above the ambient. The trend that is observed is that in experimental populations from cooler source environments, as the experiment progresses, mean body temperatures within the populations fall, presumably towards the mean body temperatures that these individuals would exhibit in their source environment. Some data was collected that corroborates this assumption, but it is insufficient in sample size to test.

It may be suggested that, at stage 0 in the experiment (the week in which the enclosures were stocked), body temperature differences in the experimental

population were generally close to 0, indicating that the experimental anoles had little behavioural influence over their body temperature. For an individual experiencing an approximate four degree increase in ambient temperature, this must have been physiologically stressful and therefor placing that individual at a reduced level of fitness. It is suggested that those individuals able to locate and maintain a territory with a lower ambient temperature (characterised by shaded vegetation-with associated increased relative humidity; pers. obs.) would be able to maintain a body temperature that was closer to the general body temperature in their source environment. As those individuals unable to find such optimal territories in the enclosures became less fit, and perished, so the mean body temperatures of experimental populations reduced in those population sourced from cooler habitats. It is worth noting that the population translocated from the elfin woodland ecotype at Fresh Water Lake, were observed burrowing into the leaf litter on the enclosure floor during the experiment. This is highly uncharacteristic anole behaviour and is likely a response to the stress of extreme shift in environment. However, it may also be a behaviour unique to the substantially different environment in elfin woodland when compared to any other ecotype on Dominica.

Such a strong and directional response in body temperature selection may also aid in the suggested reasons for strong selection pressures detected as acting on eye ring colour hue. The literature supports the fact that lizards are capable of limited colour change as a response to both intra specific interactions (Jenssen and Gladson 1984; Macedonia et al 1994), and environmental parameters (Barnett 1997; Christian et al 1996; Forsman and Shine 1995; Tosini and Avery 1993). Much research has elucidated the mechanisms of colour change in the Squamata, from von Geldern

(1920) to Bagnara and Hadly (1973). There are two types of colour in vertebrates. Firstly 'structural colour,' where the colour hue is permanent, and has a basis in various cellular and biophysical attributes of the epidermis. Such colouration generally does not change in response to physiological change within normal functioning of the organism. The second is 'physiological colour,' which broadly implies the following. Pigment cells in the epidermis respond to neuronal and/or endocrine signals, which expose pigments (Bagnara and Hadly 1973; Maddison pers. com.). In anoles this occurs when melanophores in the pigmented cells shift in response to vascular pressure, either darkening or exposing underlying pigments (Sherbrooke et al 1994; Bagnara and Hadly 1973). In the study it is observed that when colour darkening is exhibited by *Anolis oculatus*, in both males and females, the eye ring colour hue remains a lighter hue than the lateral and dorsal colour hues. However, at night, when *Anolis oculatus* becomes extremely pale it can be observed that the eye ring remains the lightest area of the epidermis (pers. obs.).

Therefor, it is suggested that chromatophore function around the eye ring scales may vary from other areas of the dorsal and lateral epidermis. This presumption is unsubstantiated other than by personal field observations, and begs a further histological investigation.

However, if chromatophore function is reduced or absent from the eye ring scales in *Anolis oculatus*, then the colour hues recorded may provide a more standardised measure of dorso-lateral basal colouration, as standardisation of chromatophore activity over other areas of the epidermis cannot be guaranteed.

Taking this speculative reasoning further, if the above suggestions are, in fact, the case, then the eye ring colour hue would be an optimal measure of potential 'paleness' of an individual *Anolis oculatus*. It may then be suggested that the relative 'paleness' of an individual may have beneficial effects for an anole under heat stress, as the experimental anoles seem to be. Even in a eurytherm, functional behaviour such as foraging and territory defence may bring the individual into direct sun light. This will cause T(b) to increase. The effects of ultra violet light penetration through the canopy must also be considered. It is suggested that a darker individual *Anolis oculatus* would experience a more rapid increase in body temperature in such circumstances than would a paler individual (Sherbrooke et al 1994).

Thus a histological analysis of the functional morphology of epidermal chromatophores of the eye ring scales would be required to further this aspect of the study.

3.3.4 HYPOTHESIS TESTING.

Considering the results of section 3.3.2, it may be concluded that the null hypothesis that selection intensity will not increase with the increasing ecological and environmental distance involved in the translocation to the xeric woodland enclosures can be rejected.

The results attempting to assess whether thermoregulatory stress is a contributory factor in the selection intensity are not quite so clear. The significance of the temperature differential between anole body temperature and the environmental temperature indeed indicates a strong trend towards the better survival frequencies of individuals able to manipulate their body temperatures over those with body temperatures that remain close to the environmental ambient. Subsequent speculation on the potential effects of colour hue on thermoregulatory capacity take the question further. It would, however, be presumptuous to consider the null hypothesis that thermoregulatory stress is not a contributory factor in the selection intensity, without more detailed investigation, and control for other extraneous variables.

CHAPTER 4:

SEXUAL SIZE DIMORPHISM

Adult male *Anolis oculatus*, displaying with dewlap, Palmist Ridge.

4.0 INTRODUCTION.

4.1 SEXUAL SIZE DIMORPHISM.

Sexual size dimorphism is a mean difference between the sexes in certain morphological character traits, or whole body structure, and dimension, frequently observed in many animal groups. Sexual size dimorphism will be further abbreviated to SSD in this chapter.

There are two primary explanations for the cause of SSD, both of which were first proposed by Darwin (1871). They are sexual selection, and intraspecific niche divergence (Shine 1989). The sexual selection hypothesis can be further divided into two gender specific hypotheses.

4.1.1 FEMALE FECUNDITY HYPOTHESIS.

Darwin (1871) was the instigator of the 'female fecundity hypothesis'. This theory proposes that larger female bias SSD allows for greater lifetime fecundity. Thus, with larger female body size permitting a higher level of reproductive success than smaller female body size, the genes for larger female body size become more frequent in the population gene pool. Considerable research has been carried out to support Darwin's female fecundity hypothesis (Abell 1998; Forsman 1991; Censky 1995; Luiselli, Capula and Shine 1997). One must however consider Prezioski and Fairbairns (1997) demonstration of lifetime fecundity and the apparent trade off between female size, fecundity and body size related longevity in the waterstrider, *Aquarius remigis*. In

this model greater body size in females did indeed increase reproductive capacity in the short term, but also reduced longevity in the long term. Shine (1989) also suggests that energy limitation on female reproductive capacity may nullify the model in many cases. However, both concede that the 'female fecundity hypothesis' is a selective force influencing SSD in many taxa.

4.1.2 LARGER MALE SIZE ADVANTAGE HYPOTHESIS.

Darwin's second theory on sexually selected SSD is the 'intrasexual selection model' or 'larger male size advantage hypothesis'. This theory proposes that direct male-male competition for access to female mates is the selective factor influencing larger male body size as an advantage for reproductive success. The size advantage hypothesis has also been tested extensively in the modern literature (Perry 1996; Rohwer, Langston and Gori 1996; Abell 1998). Kalsikaros and Shine (1997) demonstrated increased reproductive success in larger male tusked frog, *Adelotus brevis*, over smaller males as a result of direct conflict and acquisition of optimal vocalisation sites. In many species male territory defence relies on agonism between males and thus will often favour greater male body size. This is particularly evident when males maintain a territory within which female home ranges exist (Stamps and Krishnan 1994a; 1994b). Such a system was critically analysed by Stamps (1983) where larger male SSD was shown to reflect directly the degree of polygyny in anole lizards. Larger male size may also convey other adaptive advantages over smaller rival males. Wedell (1997) examined alternative pre-copulatory advantages in larger

male SSD in 20 species of *Tettigoniidae* Orthoptera. Their findings demonstrate how male size co-varied with ejaculate size, and increased fertilisation success. Thus, increased ejaculate volumes promote larger male size as an adaptive response to sperm competition. However, the flexibility of such models should be born in mind. Blomquist et al. (1997) demonstrates such flexibility with reversed SSD in the male dunlin, *Calidris alpina* . Reverse (smaller male) SSD is well documented in waders and Blomquist et al. demonstrate how smaller male dunlin were able to sustain longer aerial displays than larger males and were consequently at a reproductive advantage over such larger males.

All such models, both the 'fecundity advantage model' for greater female size in SSD and the 'male size advantage model' are facultative responses to the reproductive advantage of a bias in body size.

4.1.3 INTRASPECIFIC NICHE DIVERGENCE HYPOTHESIS.

The 'intraspecific niche divergence hypothesis' was also introduced by Darwin (1874). This theory proposes that SSD arises as a result of ecological differences between the sexes. This area of research has received considerable interest from evolutionary biologists in recent years, yet due to the complexity of any ecological model, has yielded relatively few clear and conclusive results. The initial studies giving credence to the theory focused on the ecology and trophic biology of raptors where monogamy, mutual territory defence, and their relation to SSD, are well

observed (Lack 1954). Such adaptation was shown to clearly reduce the competition for dietary resources between the sexes in prey limited environments by adaptation of trophic apparatus not directly involved in reproductive success (Selander 1966). Locomotor morphology has also been shown to vary between different subsets of vegetation where microhabitat specialisation has occurred (Pounds 1988), and may be observed in tandem with trophic apparatus sexual divergence.

However, to encompass in a study, all the relevant interactions of predators, prey and environmental regimes in a SSD species is a considerable challenge (Shine 1989). In more recent years SSD has become a well-observed model for the study and investigation into the role of selective factors influencing evolutionary ecology (Fairbairn and Prezioski 1994; Perezmellado and Delariva 1993; Shine, Harlow, Keogh and Boeadi 1998; Wikelski and Trillmich 1997). In such studies, care must be taken not to take too simple a view of the influencing factors. Early studies (White and Kolb 1974; Madsen 1983) tended towards modelling the cause of SSD in an observed subject by means of correlating an ecological factor to the observed degree of difference in body size between the sexes. Niche divergence associated with SSD within a complex three-dimensional environment may lead to specific divergent adaptations between the sexes. Such an approach is unlikely to yield more than a superficial indication of ecological influences on SSD.

4.1.4 INTERRELATED THEORY.

Shine (1989) was the first worker to point out the complex inter-relation of fecundity selection, sexual selection and ecological divergence, when considering the adaptation of SSD. Shine (1989) also made the prudent point that ecological factors may constrain the degree to which sexual selection can amplify SSD as a result of the limits of energetically feasible body sizes. Thus identified were four potential interactions of ecology with SSD:

i) Ecological inter-sexual divergence as a source of selective forces for SSD.

ii) Ecological inter-sexual divergence as a passive consequence of sexually selected SSD.

iii) Ecological inter-sexual divergence as an adaptation to reduce SSD by minimising intraspecific competition.

iv) Ecological inter-sexual divergence as an expression of constraint on more extreme SSD.

These hypotheses are formulated from the perspective of ecological divergence as the study process, and to understand them they must be interpreted as such. Hypothesis i. is the familiar ecological divergence hypothesis, and hypothesis ii. suggests ecological divergence as passive consequence of sexual selection where no ecological advantage is drawn from the sexually divergent ecology when compared to the non-sexually divergent state. Hypothesis iii. is somewhat more demanding to comprehend, but perfectly logical. Hypothesis iii. suggests that SSD arose as a result of resource competition between the sexes, and by moving towards a divergence in ecology between the sexes, this competition is reduced. Thus SSD may also reduce between the sexes. Hypothesis iv. is more abstract, suggesting that SSD would be greater in

the model if it was possible for further ecological divergence to occur between the sexes, but that in this case such limited ecological resources act as a constraint.

When reviewing such concepts one immediately identifies the difficulty of distinguishing cause and effect. To identify an observed variable or character trait as an adaptation of SSD, or as a selective factor in the evolution of SSD requires a broad experimental outlook. This is the fundamental scientific problem of determining cause and effect.

4.1.5 THE MODEL ORGANISM.

West Indian *Anolis* lizards are regarded as ideal organisms for the study of resource partitioning (Schoener and Gorman 1968) and sexually dimorphic *Anolis* body size is well documented and recognised as associated to intraspecific variance in ecology (Roughgarden 1972, 1974). Analysis into the ecological component of SSD in *Anolis* lizards has been further expanded by individual investigations into specific aspects of *Anolis* ecology such as prey selection (Roughgarden and Fuentes 1977), population density (Stamps et al 1997) and thermal ecology (Stevenson 1985). Ecomorph adaptation and spatial niche divergence between species is well-documented (Roughgarden 1972) and the basic model of spatial niche divergence is well observed in the majority of species. Socio-sexual niche divergence follows a common pattern to varying degrees in the Lesser Antilles, and this is illustrated with specific reference to *Anolis oculatus* in Fig 4.1 (pers. obs.). As many *Anolis* species occur on the islands of the Caribbean, ecological release resulting from deporperate island faunal

Figure 4.1. Sexual/Social Niche Selection in *Anolis oculatus*

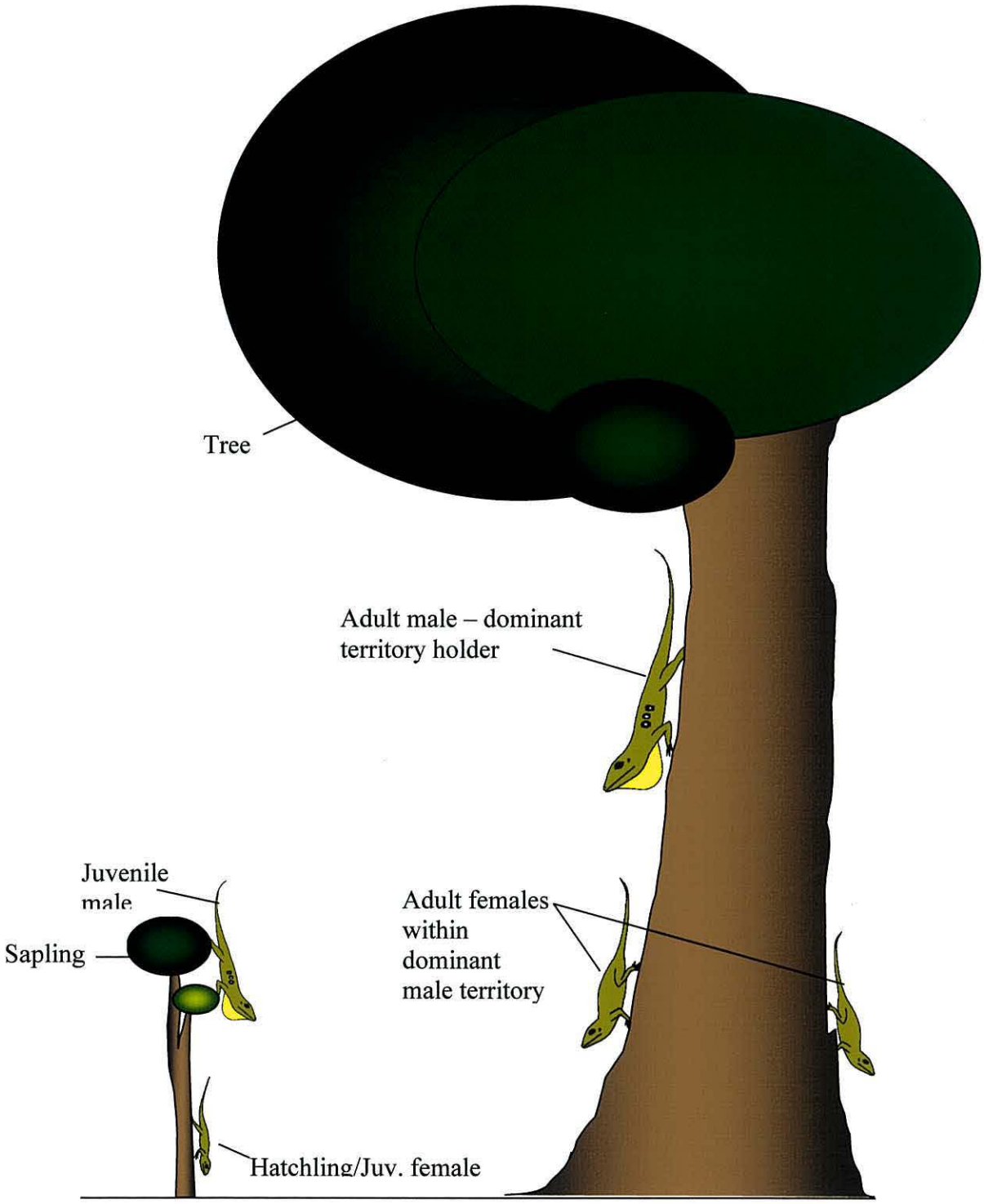


Figure 4.1 represents the social and sexual niche characteristics exhibited by *Anolis oculatus* and the majority of the *Anolis* genus. Within the dominant male territory will be a number of female home ranges (Stamps 1993) . On the periphery and between dominant male territories are the smaller more transient territories of juvenile males and the shifting home ranges of hatchlings and juvenile females.

assemblages, specifically in the case of the Lesser Antilles, (MacArthur and Wilson 1967; Losos and De Queiroz 1997; Grant 1998) may be presumed to enhance the opportunities for intraspecific niche divergence.

Diet selection has become a central aspect of the research conducted into the ecological component of SSD (Preest 1994; Andrews and Stamps 1994; Perry 1996). Perry (1996) gives a convincing account of the sexually selected origin of SSD that has subsequently led to a sexually dimorphic adaptation in diet selection between the sexes in *Anolis polylepis*. The data showed that despite larger male size and trophic apparatus, the male diet consisted of significantly smaller prey items than that of the female *Anolis polylepis* diet. Preest (1994) provides evidence that in *Anolis carolinensis,* females, the smaller gender, prey upon significantly smaller prey items than do males and suggests prey handling time and exposure to predation as an explanation for this. Males consuming larger prey items still maintain shorter prey handling times, and so these results are probably linked to the morphology of trophic apparatus. Such explanations must be met with caution in light of the fact that in a species where the sexes possess different body sizes, feeding rates and diet selection are unlikely to be the same, regardless of the evolutionary cause of SSD. The fact that the literature does not support a genus-wide prediction of the relationship between gender specific diet selection, SSD, and there adaptational inter-relationship in *Anolis* species, means that to suggest the cause of SSD in any one species would be folly without a detailed phylogenetic and ecological profile for the species under investigation. One must also note that intraspecific differentiation in body size is greater in males than it is in females in anole lizards (Losos 1994; Malhotra and Thorpe 1997), a characteristic strongly associated with the male competition

hypothesis. We must therefore consider any *Anolis* model without bias with regard to its trophic ecology.

Such resource partitioning within a species may potentially result in an increase in the density of that species when compared to a similar species in which gender does not influence resource use in situations where available resources are similar. A comparative study of density, and SSD was conducted by Stamps, Losos and Andrews (1997), considering details of diet content in *Anolis aeneus*, and female density in 24 other *Anolis* species. Their analysis detected a statistically significant relationship between female density and SSD. They question however, the validity of the food competition hypothesis (Schoener 1977), although this is discussed with regard to the presence or absence of congeners, which is an issue of phylogenetic history and colonisation sequence (Gianassi 1997) as well as resource use. Conclusions that can be drawn from proving a relationship between density and SSD support the theory of male body size variation as the determining factor in *Anolis* SSD (Schoener 1969). Both of these factors would be influential in establishing male territory defence as a basal instigator for the evolutionary selection of SSD.

One final consideration when examining SSD in *Anolis* lizard populations is their phylogenetic history, and present gene flow between populations. If comparative techniques of analysis are to be employed in testing for selective factors influencing SSD, the phylogenetic status of the populations, or species, must be resolved and accounted for. Closely related species, or populations, may share more characteristics through common descent, that will distantly related populations, or species, and so any comparison of independent population character traits must adjust for relatedness.

A variety of comparative methods exist to test and control for phylogeny depending on assumptions made (Harvey and Pagel 1991). Four methods are prevalent in the literature to account for phylogenetic regency; these are phylogenetic independent contrast (Felsenstein 1985; Purvis 1991; Pagel 1992; Pyron 1996); phylogenetic autocorrelation (Miles and Dunham 1993); ancestor reconstruction (Maddison 1991) and matrix correspondence analysis at an intraspecific level (Thorpe 1996; Daltry et al 1996).

4.1.6 SEXUAL SIZE DIMORPHISM IN *Anolis oculatus.*

This study is intended to take an integrated approach to examining potential ecological and evolutionary causes of SSD in *Anolis oculatus* sampled from 14 widely distributed populations which include a broad range of ecotypes illustrated in figure 4.2 and detailed in chapter 1, section 1.4. The study will take a comparative approach to establish the interrelated nature of many of the factors influencing SSD.

As *Anolis oculatus* is known to exhibit considerable variation in both body proportions and overall size across its range, including SSD (Malhotra and Thorpe 1997), and also has a finely resolved phylogeny (Malhotra 1992), it is an ideal candidate for such a species-specific study. Malhotra and Thorpe (1997) identified geographic variation in the extent of size and shape SSD in *A. oculatus*. This therefore indicates that different selection pressures may exist between the sexes (sexual differentiation in ecology). Such differences may be either cause or effect of SSD. Bullock, Jury and Evans (1993) demonstrated a positive relationship in body

size in *A. oculatus* with the size of prey consumed. One may then presume that the study of any relationship between prey selection and SSD is likely to contribute to a more detailed investigation into the evolutionary ecology of SSD in *Anolis oculatus*. As well as controlling for the phylogenetic history of *Anolis oculatus*, it is necessary to consider the relative geographic proximity of each experimental population with regard to others (Thorpe 1996).

Thus, in this study, aspects of diet, prey availability, population density, sexual selection intensity, spatial niche separation, phylogenetic history, patristic distance, and environment, are considered with regard to SSD.

If diet selection influences the evolution of SSD, then SSD could be predicted to reduce in tandem with a reduction in prey size variability or increase with a reduction in prey density. However, if territory defence (larger male size advantage hypothesis) is the primary factor influencing the evolution of SSD then a stronger relationship of SSD to conspecific density and sexual ethology, in terms of intraspecific display behaviour, could be predicted.

4.1.7 AIMS.

In this chapter the aims are:

i. To examine the relationships of SSD with sexual selection by examining male conspecific display behaviour.

ii. Examine intraspecific niche divergence, both by its spatial segregation of the sexes, and its influence on diet selection, whilst controlling for phylogenetic history, and geographic proximity. Environmental and ecotype habitat parameters are also considered as potential influences on the evolution of SSD in *Anolis oculatus*.

Thus, the general aims of this chapter are to ally the observed patterns of SSD recorded in *Anolis oculatus*, to one of the Shine (1989) hypotheses detailed in chapter 4.1.4, and to give an account of any relationships observed that elucidate the causes of, or limiting influences of SSD.

4.2 METHODS AND MATERIALS.

As this study is essentially comparative, standardising data collection across the experimental populations of *Anolis oculatus* was of paramount importance. All data were collected between July and September 1997, a period of climatic calm over the Commonwealth of Dominica, prior to the onset of the wet season in October.

4.2.1 GRAPHICAL REPRESENTATION OF VARIABLES.

Colour contour mapping of relevant variables was carried out on Unimap 2000 ™ graphical software. Such graphical representation aids in the visualisation of putative relationships between patterns observed and tested for in the data.

4.2.2 QUANTIFYING SEXUAL SIZE DIMORPHISM.

Ten adult males and ten adult females provided SSD data, collected by hand trapping at the fourteen sites illustrated in figure 4.2. A snout to vent measurement was taken from the anterior tip of the snout to the cloaca using RS component™ digital callipers.

The quantification of SSD has been approached using a variety of methods by a variety of researchers (Lovich and Gibbons 1992). Stamps (1993) advises the use of asymptotic size rather than mean size in taxa with asymptotic growth after maturity. Anoles were demonstrated to exhibit a strong correlation between size at maturity and

Figure 4.2. Site Locations of SSD Experimental *Anolis oculatus* Populations.

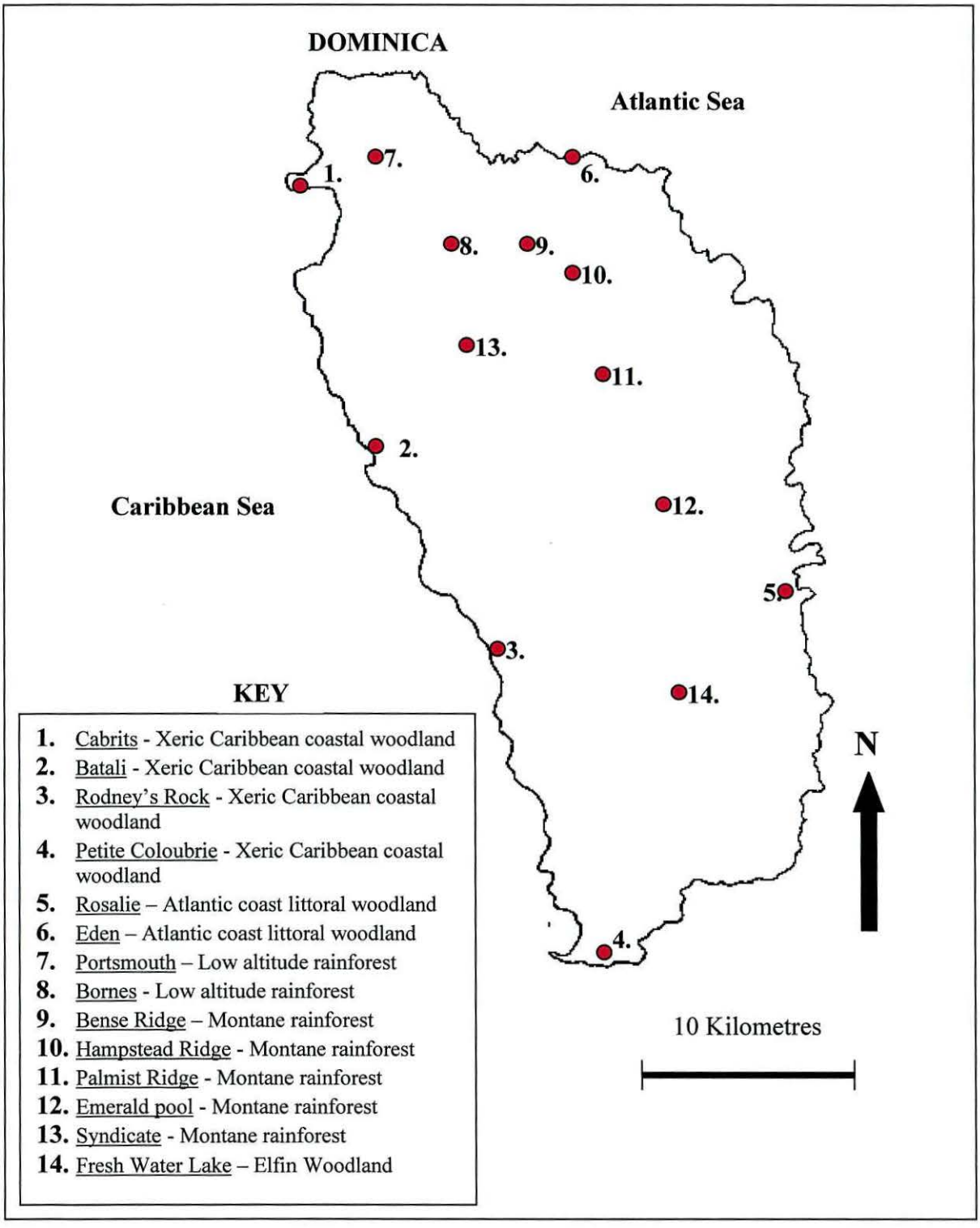


Figure 4.2 depicts the location of SSD experimental site locations on the Commonwealth of Dominica.

The key helps illustrate the range of ecotypes over which the experimental populations range.

asymptotic size by Stamps and Krishnan (1997), but a large sample size of each experimental population is required for this technique. Therefore, considering the population sample sizes under scrutiny, and some scepticism about the value of an asymptotic measure, a mean value of snout to vent length is regarded as the optimal measure of male and female size (Stamps and Andrews 1992). Once such data is established one may consider constructing an indices of SSD from which comparison between experimental populations can be made.

Classical techniques for creating indices of SSD relied largely on permutations of ratio (Anderson 1986) between male and female size, and absolute difference between male and female size (Cheveraud et al 1985). However, variation in body size in the population as a whole may vary between sub-populations, as reported by Malhotra and Thorpe (1997) as occurring in *Anolis oculatus,* and this may confound any relationship between SSD, and supposed cause (Stamps et al 1997). To account for such variation in overall body size between populations, and its influence on the quantification of SSD, a measure of residual distance calculated from a regression of log male against log female mean population snout to vent length, considering the male log means as the independent variable (Ranta et al 1994) is taken as the indices of SSD. At this point a complication arises. The slope of the regression between log mean snout to vent length in male and females from each experimental population may itself be slightly artifactual due to the effects of SSD on male and female body size. The regression slope may not be independent of the measure of SSD across the body size range of the model. Any log linear increase in SSD with body size may well be attenuated or lost in the regression slope. However, by converting the snout to vent length means to logarithmic measures, size variance between population is

supposed to be accounted for. If this is the case, then an alternative slope predicting a 1:1 ratio of logged male to female mean snout to vent length body size may be seen as more arbitrary to record a residual measure of SSD from, rather than the residual measures from the regression slope of logged male against female body size (Ranta et al 1994). If a residual measurement from population plot (mean log male against mean log female snout to vent length where mean logged male snout to vent length in the independent variable,) to the 1:1 slope was used as a measure of SSD in a population then no assumptions have been made regarding SSD but only the log aspect of the data will account for overall variance in population body size between experimental populations. It was decided to analyse variables against both measures of SSD to test for contradictory patterns between the two methods. The measure of SSD taken from the residual measure to the regression slope observed between the mean logged snout to vent lengths of males (independent) to females is further referred to as SSD. The measure of SSD taken as the residual from the population plot to the 1:1 slope of logged male (independent) against logged female snout to vent length will further be referred to as 1:1SSD.

To determine gender bias in the structure of SSD in *Anolis oculatus* the index of SSD will also be tested against both mean log male and female snout to vent length separately.

4.2.3 QUANTIFYING SEXUAL SELECTION DATA.

The degree of male-male competition is taken as the measure of sexual selection pressure (Rand 1967; Trivers 1976; Stamps 1983; Ruby 1984; Andrews 1985; Tokarz 1985) present within a population of *Anolis oculatus*. To quantify the intensity of sexual selection the dewlap extension display of males was recorded (Case 1990; Jenssen 1970; Johnstone 1997) when observed during thrice daily 20 metre transects at each population locality. The extension of the dewlap in *Anolis* lizards is a well documented indication of intra-specific stress, strongly related to both territory defence and pre-copulatory display (Webster and Burns 1973; Williams and Rand 1977). The transects were conducted between 700hrs and 1000hrs in the morning, between 1200hrs and 1500hrs at midday, and between 1700hrs and 2000hrs (from July to September dusk falls from 1740hrs to 1810hrs). This is designed to account for the circadian rhythm of *Anolis oculatus* display behaviour that is at it's peak at dawn and dusk, but which continues, at a high frequency, throughout the day in certain localities (pers. obs.). During transects all individuals are noted, recording sex, age group, perch height and behaviour (including dewlap display). The transect is covered by two minute observations at five metre intervals. Although the conspecific nature of male display can often be deduced through intuitive observation and accumulated field experience, for this study purely the action of dewlap extension in a given male was recorded as a unit measure of sexual selection. Three such days of transect observation were conducted at each site location. Sexual selection pressure at each locality was then indicated as the percentage of dewlap displaying males recorded during all transects.

4.2.4 QUANTIFYING PREY SELECTION AND AVAILABILITY.

When considering diet selection in an organism it is not only essential to record the dietary contents, but also the available dietary resources that the diet is selected from.

In order to establish dietary content, four male and four female *Anolis oculatus* were stomach flushed between 1200hrs and 1400hrs at each site locality. It is worth noting that stomach contents early in the day tend to exhibit advanced digestion of prey making prey quantification difficult (pers. obs.), likely to be the result of prey consumption the previous day and under digestion over night (Vandamme et al 1991). Stomach flushing was achieved by the use of a 5ml syringe of water at ambient temperature with the environment, connected to a 2mm-diameter 50mm latex catheter. The anoles are anaesthetised as described in chapter two, and the catheter carefully inserted into the stomach via the oesophagus lubricated with KY jelly™. The water is then gently injected into the stomach and as the catheter is removed, water and stomach contents are expelled into a petri dish. This procedure is repeated until only water is flushed from the stomach. The stomach contents of each individual were then stored separately for analysis.

Attempts to taxonomically identify prey species proved difficult, as only a proportion of prey items remain sufficiently intact within the gut. Prey items were then classified into size categories (proven to have a linear relationship to mass, see figure 4.3), of less than 4mm, 4mm to 20mm and larger than 20mm using a binocular microscope and RS component™ callipers. Where only part of a prey item was evident, for example a Coleopteran elytra, then an estimation of original whole

Figure 4.3

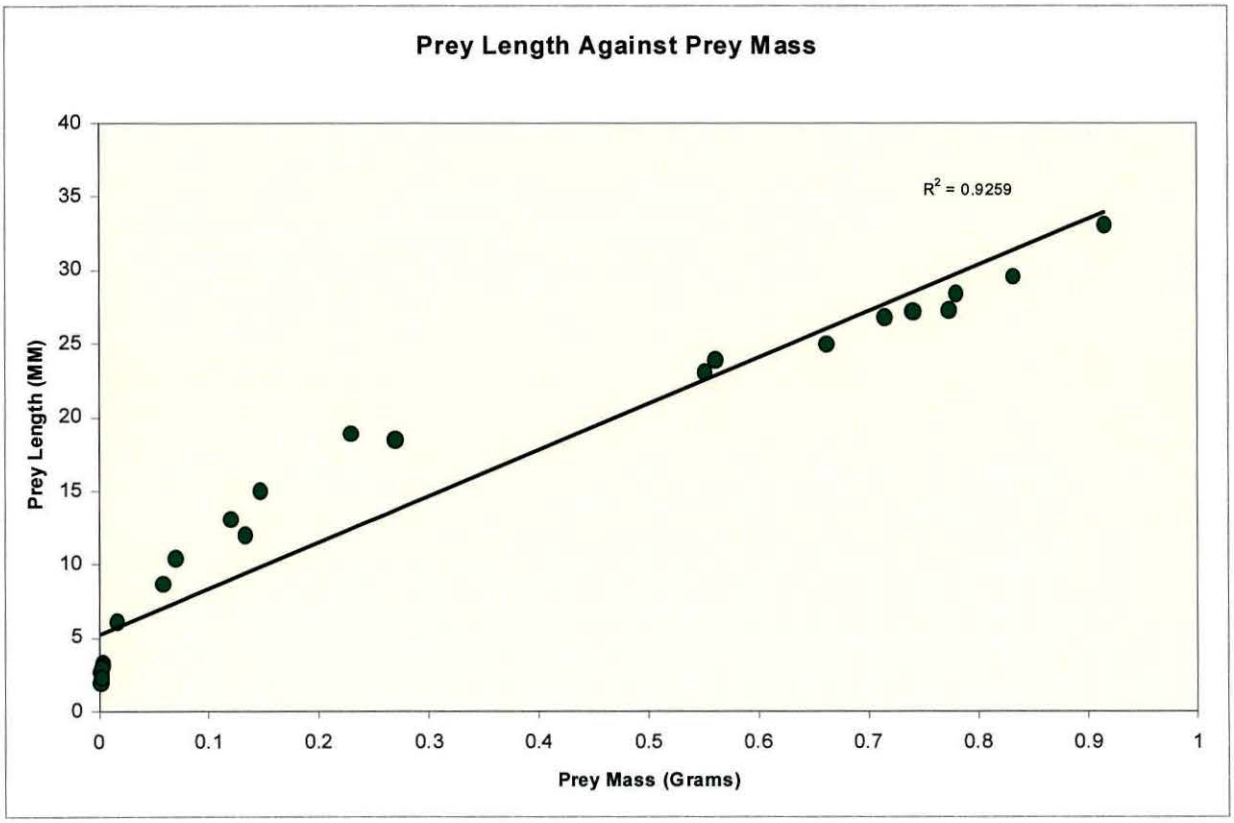


Figure 4.3 represents a scatter plot of invertebrate length against invertebrate mass in grams with a positive linear regression slope of R=0.857 (significant to P=<0.0001), and demonstrates the strong relationship between prey length and prey mass.

organism size was estimated except in the case of Orthopteran hind limbs. The hind limbs of tree crickets are readily autotomised and the whole animal would be too large a food item for even the largest *Anolis oculatus* . Thus, these limbs are regarded as a whole prey item in themselves and constitute a considerable proportion of the dietary content in certain habitats. The following equation was constructed to calculate mean prey size per gender, per experimental site locality:

$[(\Sigma a \times 3.6)+(\Sigma b \times 15.8)+(\Sigma c \times 22.1)] / (\Sigma a+\Sigma b+\Sigma c) =$ mean prey size

where:

Σa = sum of prey items of <4mm

Σb = sum of prey items of 4mm to 20mm

Σc = sum of prey items of >20mm

3.6, 15.8 and 22.1 represent prey size means (mm) per category of prey size.

From these results a factor of sexual difference in prey selection was calculated by subtracting the mean prey size for females from the mean prey size for males at each experimental locality.

In an ecological context, this data would mean little without data pertaining to environmental prey availability. The essential characteristics of which being prey density within the environment and prey size variability. To account for these two variables, both pitfall, and sticky traps were employed. Two meter lengths of Perkin ™ 'fly-paper' were attached by horizontal wrapping to trees at 1.5 metres above the ground within the range of known *Anolis oculatus* territories. Three sticky traps were employed at each experimental site, being deployed at as near to midday as possible as this is the period of least invertebrate activity (pers. obs.). The traps were left for

24hrs, and collected midday the following day. Each invertebrate collected on the sticky traps was measured with RS component ™ callipers to 0.01mm. At each experimental site location three pitfall traps were also employed to record environmental prey availability. The lower 15cms of 2 litre soft drinks bottles, made of clear plastic, were utilised as pitfall traps sunk flush into the ground to above the top of the trap. Each pitfall trap was then filled to approximately 10cms with detergent impregnated water to reduce water surface tension to aid invertebrate capture. Again, three traps were set at each site locality, primed at midday and collected 24hrs later, where upon the contents of the traps were emptied into a container for later analysis. Each invertebrate collected in the pitfall traps was measured with RS component ™ callipers to 0.01mm. Sampling was replicated three times within each experimental site location within the experimental period to control for any temporal fluxes in invertebrate activity that would influence trapping success, such as short-term climatic fluctuations.

To use a numerical basis for estimating prey density would potentially lead to misleading results as an environment containing large numbers of a small prey item such as termites may appear to have a greater prey density than an environment containing a moderate number of large prey items. The comparative mass of the prey items available as a resource to the experimental populations of anoles in question may be equal, or the environment with larger prey items may have a greater prey mass due to individual relative prey mass despite lower prey item numbers. As the relationship between invertebrate length and mass have been shown to be linear (Fig.4.3), the sum of total prey length recorded per experimental site was used as a simple measure of prey biomass.

When considering prey selection in light of SSD, it is necessary to account for the variability in available size range of prey items. Niche divergence theory would predict that if sufficient variance in prey size exists, where prey density is an energetic limiting factor to anole population density, then ecological release by means of niche divergence through SSD will occur to enable the species as a whole, to exploit a wider range of food items. Hence, the knowledge of high and low prey densities in an environment must be accompanied by reference to such prey size variance to consider putative relationships to observed patterns of SSD in *Anolis oculatus.* The variance was calculated from the data of all trapped invertebrate prey lengths per experimental site. This measure of variance was then engaged to represent prey size variability for each experimental locality.

4.2.5 QUANTIFYING NICHE DIVERGENCE AND DENSITY.

To assess the degree of niche divergence between the sexes of *Anolis oculatus,* perch height in metres, gender and age category (adult male, adult female, juvenile when snout to vent length perceived to be less than 30mm) was recorded for all *A. oculatus* individuals recorded during transect analyses. The mean average perch height of all recorded females is subtracted from the mean average perch height of all recorded males, for each experimental location. Juvenile *Anolis oculatus* irrespective of sex are excluded from the analysis due to the transitory nature of their spatial ecology (pers.

obs.). This value is then used to represent spatial niche divergence in the 14 experimental populations.

Anole density is estimated per site by using the mean average number of adults recorded over all transects within each locality. The measure is an entirely comparative one and does not represent a quantified spatial density. Mark-recapture density recordings at each locality was logistically unfeasible in the experimental time frame available.

4.2.6 ENVIRONMENTAL AND PROXIMITY DATA.

To account for variation in climate and ecotype of habitat at each experimental site locality, a range of environmental variables were recorded.

At each site altitude in meters was recorded using a Thomen Classic™ barometric altimeter. At each experimental site locality shaded ambient temperature and relative humidity was recorded between 1200hrs and 1400hrs using an Vaisala™ HMI-31 temperature and relative humidity indicator fitted with a HMP-35 probe. Recordings were made on each visit to site locations throughout the experimental period. The mean average temperature and relative humidity were then calculated for each location.

To test for possible gene flow effect on the observed patterns of SSD in *Anolis oculatus,* the geographical proximity between experimental sites must be quantified. A matrix of direct distances between each site was constructed using a scaled ordinance map of the Commonwealth of Dominica from which a scale measurement of distances between sites was recorded in centimetres for the construction of a half matrix of inter-site distance.

4.2.7 CONTROLLING FOR PHYLOGENETIC HISTORY.

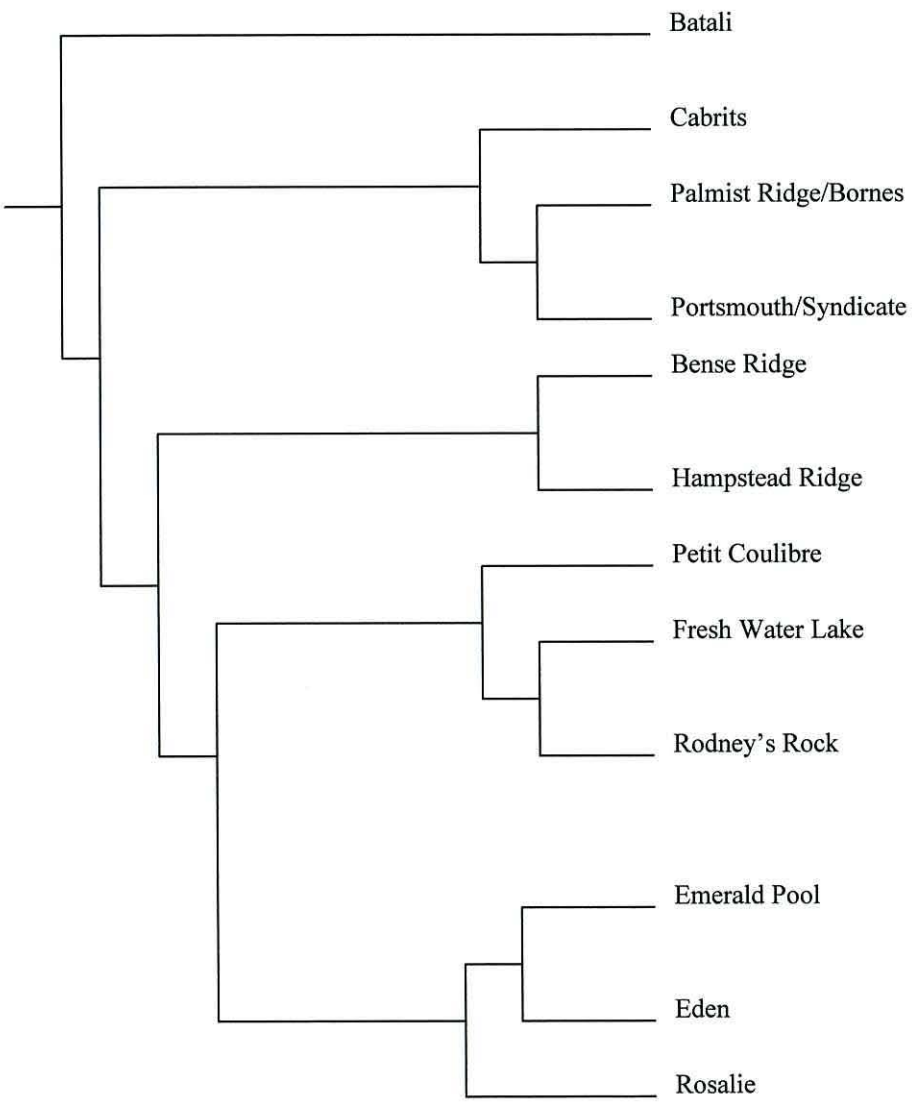
The 14 experimental populations are represented in a 33 population intraspecific phylogeny (mtDNA, Cytochrome b) constructed by Malhotra and Thorpe (in press). Sequence data pertaining to the experimental sites was used to construct a maximum parsimony tree, using the computer program PHYLIP (Felsenstein 1985; Harvey and Pagel 1991), from which COMPARE version 2.0 (Garland et al 1992) was used to calculate contrasts from the phylogeny illustrated in figure 4.4.

4.2.8 STATISTICAL ANALYSIS STRUCTURE.

Three stages of data analysis were conducted. A bivariate correlation, and regression analysis tested SSD, and the 1:1 ratio SSD against each other, without using matrix comparisons or independent contrasts. The second set of analyses employ phylogenetic independent contrasts to allow regressions, and correlations, to be

Figure 4.4. Maximum Parsimony Phylogenetic Tree of 14 *Anolis oculatus* populations.

Figure 4.4 illustrates the maximum parsimony phylogenetic tree generated to represent the 14 experimental populations of *Anolis oculatus* from Malhotra and Thorpe (*in Press*). From the tree phylogenetically independent contrasts of the character traits under analysis were generated.



carried out within a phylogenetic framework. Thirdly, matrix correspondence test permitted partial regressions to be performed between SSD and all variables including geographic proximity and phylogenetic matrices.

4.2.9 BIVARIATE NON-PHYLOGENETIC ANALYSIS.

Minitab ™ version 12.0 statistical software was used to correlate (Pearson's correlation) (Langley 1970) the non-phylogenetically adjusted index of SSD and 1:1 ratio SSD against log male snout to vent length, log female snout to vent length, spatial niche divergence, *Anolis oculatus* comparative density, sexual diet selection divergence, available prey size variance, environmental prey density, male dewlap display rate, altitude (M), temperature (°C) and relative humidity.

4.2.10 PHYLOGENETIC INDEPENDENT CONTRAST ANALYSIS.

Independent contrast was employed to control for the effects of phylogenetic relatedness as described in section 4.2.7. Contrasts were calculated without the use of phylogenetic branch lengths from the maximum parsimony tree. The relationships between the contrasts generated were then tested for strength and statistical significance using correlations and regressions (Garland et al 1992).

4.2.11 MATRIX CORRESPONDENCE TESTS.

Matrix correspondence tests permitted the inclusion of phylogenetic relatedness in the form of a patristic distance matrix (Thorpe 1996; Thorpe et al 1996) and geographic proximity in the form of Euclidean distance matrices in the test against SSD. Such matrices were also generated for log male snout to vent length, log female snout to vent length, spatial niche divergence, *Anolis oculatus* comparative density, sexual diet selection divergence, available prey size variance, environmental prey density, male dewlap display rate, altitude (M), temperature (°C) and relative humidity.

Both pair-wise and partial matrix correspondence analysis (Manly 1991) were used to assess association between SSD, 1:1 ratio SSD, and all variable matrices. Significance of variables tested in the pair-wise analysis was used as sanction to include variables in the partial analysis. The probability of correlation is deduced by 10,000 matrices randomisations. The resulting probabilities generated from the partial matrix correspondence analyses are subject to table Bonferroni correction (Korn and Graubard 1990), accounting for the accumulated nature of probability in such a test.

4.3 RESULTS.

4.3.1 SEXUAL SIZE DIMORPHISM INDICES.

The indices of SSD were established for *Anolis oculatus* using log mean snout to vent length for both males, and females as the measurement. The overall heterogeneity of the log mean snout to vent lengths between the sexes across the 14 experimental populations is illustrated in figure 4.5.

The two measures of SSD were calculated, firstly the residual measure from population plot to the regression slope of log mean male snout to vent length against log mean female snout to vent length and secondly the 1:1 slope between male and female log mean snout to vent lengths where the residual of population deviation from the slope represented the indices of SSD(1:1SSD). The two measures yielded near identical results when tested against the experimental variables and when tested against each other a near perfect linear relationship was determined. The bivariate analysis tested SSD against 1:1SSD using Pearson's correlation with the result of $r = 0.983$ with a p-value of less than 0.0001 (figure 4.6; table 4.1). When tested with phylogenetically adjusted contrast data, again a strong correlation of $r = 0.9967$ was observed ($p = <0.0001$; figure 4.7; table 4.2). Finally SSD was tested against 1:1SSD in a pair-wise matrix Mantel correspondence test, and again a strong relationship was proven with a correlation of $r = 0.9655$ ($p = 0.0001$) as is illustrated in table 4.3.

Due to the consistently similar results from the two measures of SSD, only the results of testing variables against the residual measure taken from the regression slope taken

Figure 4.5

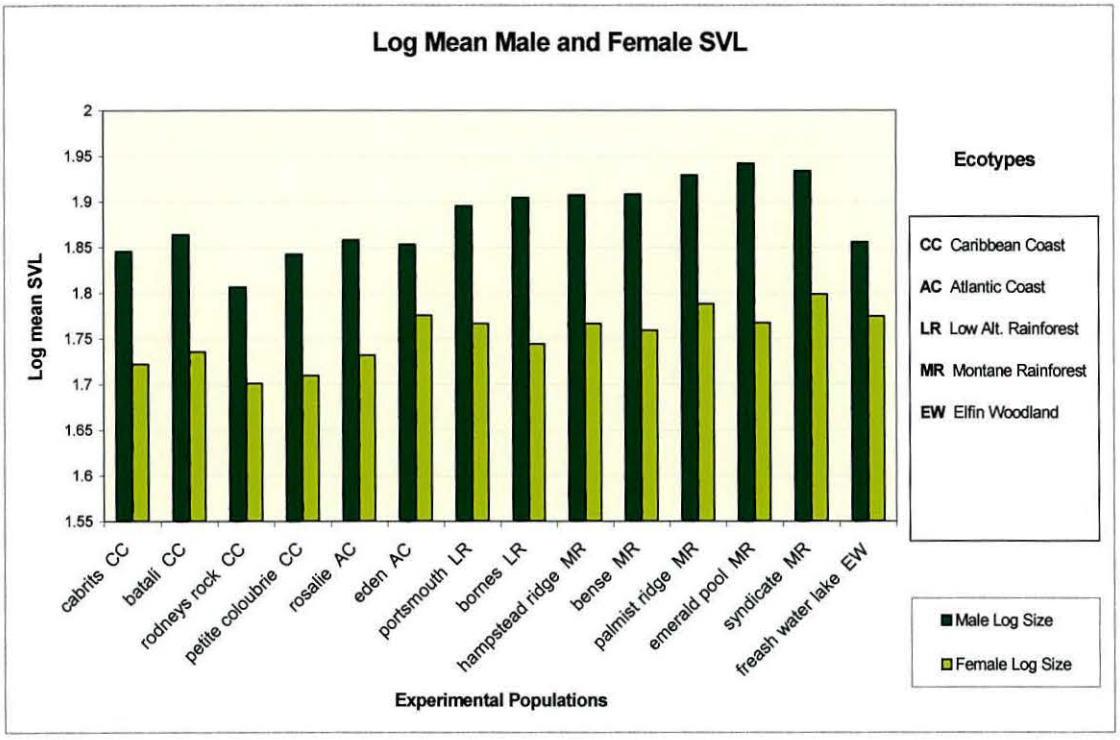


Figure 4.5 illustrates the relationship between male and female log mean snout to vent lengths across the 14 experimental populations of *Anolis oculatus* on Dominica. It is evident that overall size and degree of fluctuation is greater in males than females when considering the 14 populations as a whole.

Figure 4.6

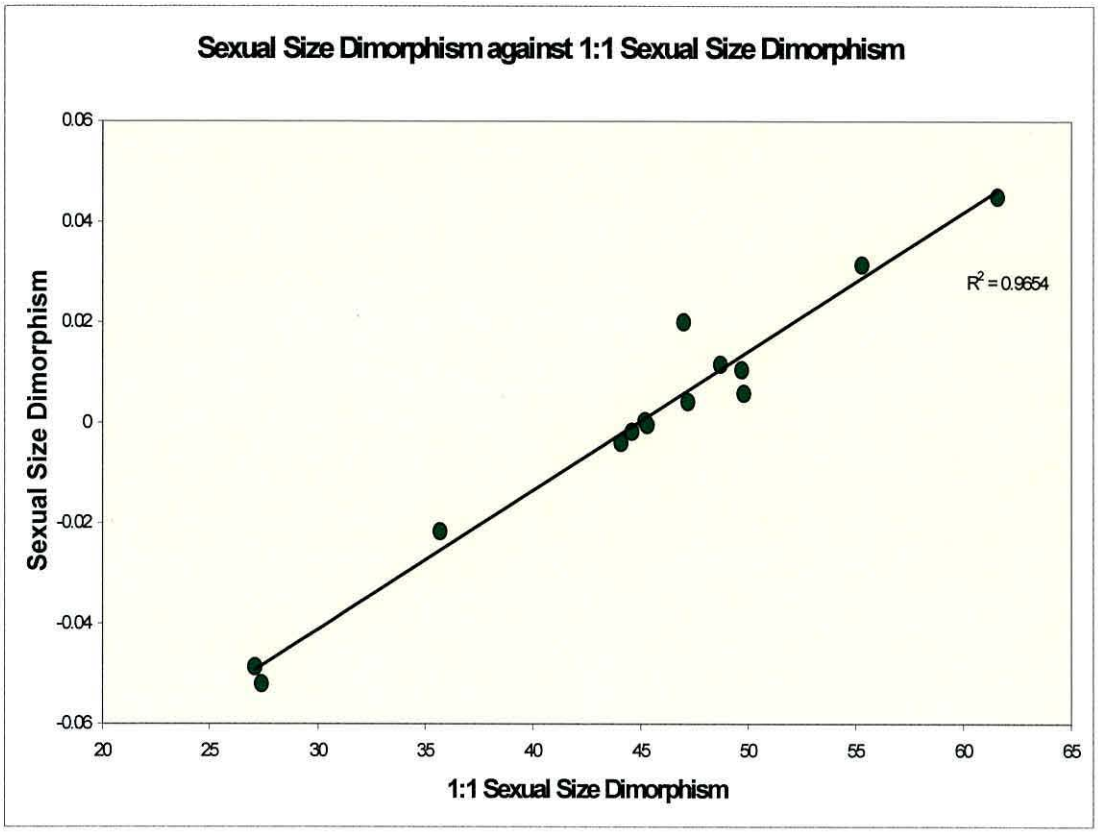


Figure 4.6 illustrates the near linear relationship between the two measures of sexual size dimorphism ($p = <0.0001$).

Figure 4.7

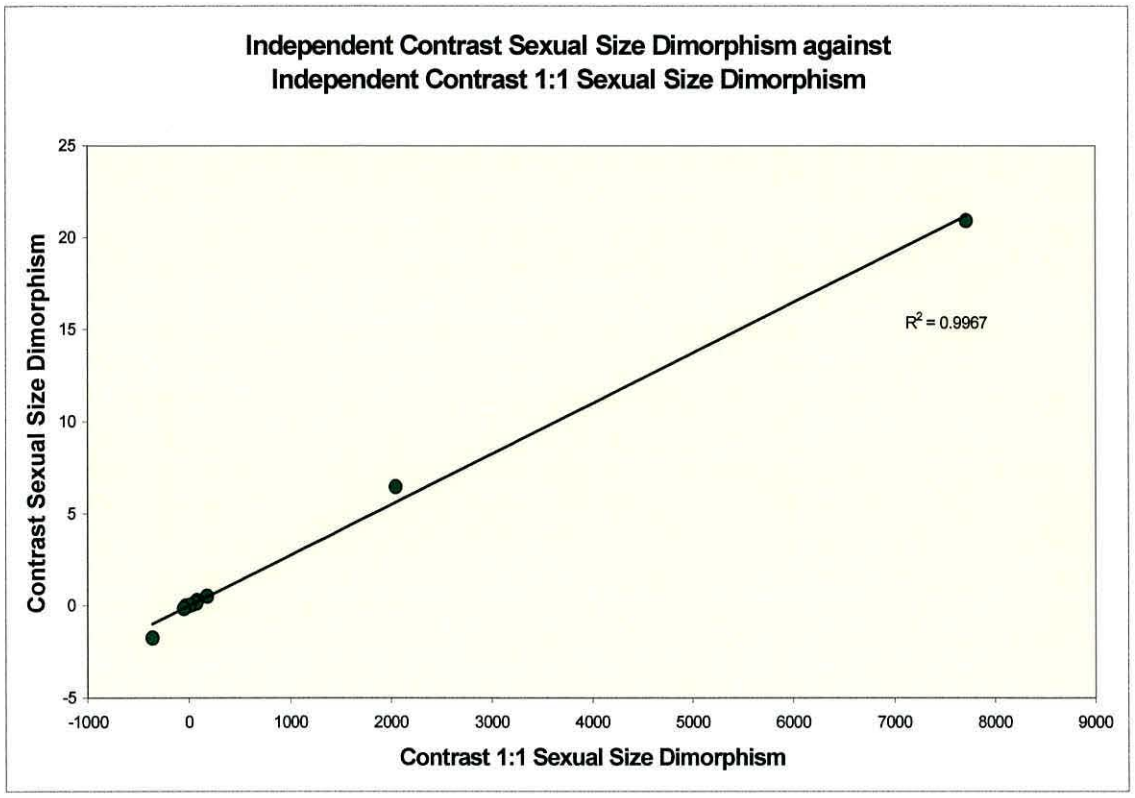


Figure 4.7 illustrates the near linear relationship of contrast SSD when plotted and correlated against contrast 1:1SSD ($p = <0.0001$).

Figure 4.8

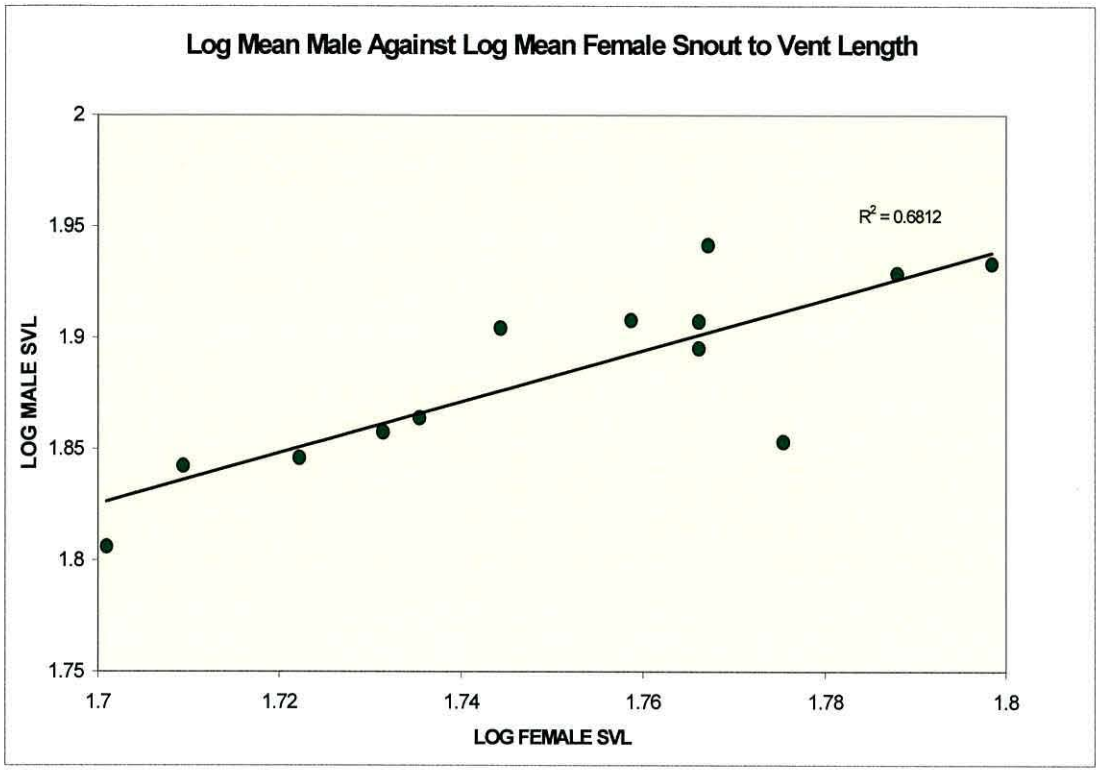


Figure 4.8 illustrates the strong relationship between male and female snout to vent lengths across the 14 experimental populations of Anolis oculatus under study (r2 = 0.6812; p = <0.001) although in several populations a significant deviation from the trend is observed. It is the residual distance to the regression slope that constitutes the measure of SSD for each experimental population.

Figure 4.9

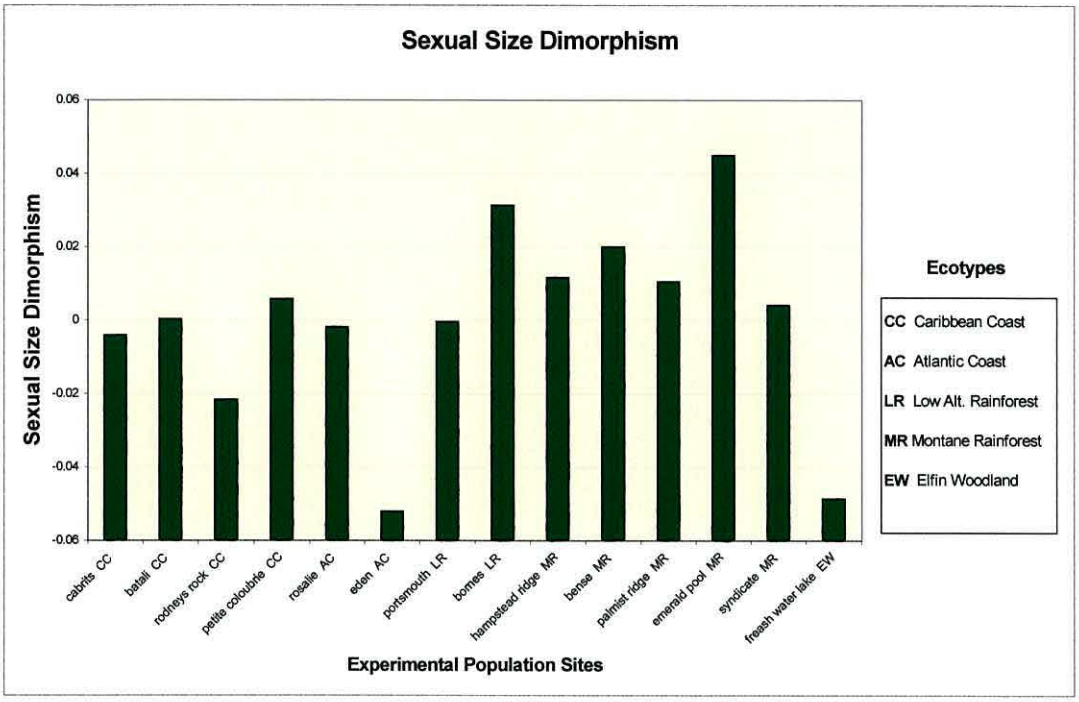


Figure 4.9 illustrates the degrees of SSD exhibited across the 14 experimental populations of *Anolis oculatus*. As the ecotype key depicts, the populations are identified with reference to their source habitat ecotype.

Table 4.1

Pearson's Correlation of Sexual Size Dimorphism against Biometric, Biotic and Environmental Variables		
Variables	Correlation Coefficient (R)	P-Value
Log male snout to vent length	**0.658**	**0.01****
Log female snout to vent length	0.000	1.000
1:1 Sexual size dimorphism	**0.983**	**0.000*****
Sexual difference in niche height	**0.717**	**0.004****
Anole density	-0.164	0.576
Sexual difference in dietary prey size	**0.907**	**0.000*****
Environmental prey size variability	**0.843**	**0.000*****
Environmental prey density	-0.168	0.565
% male conspecific display	**0.939**	**0.000*****
Altitude	0.080	0.786
Temperature	-0.041	0.888
Humidity	0.129	0.661

Key - ** = significance to 0.05; *** = significance to 0.001.

Table 4.2

Sexual Size Dimorphism Contrast Correlation against Phylogenetically Adjusted Variables		
Variables	Correlation Coefficient (R)	P-Value
Log male snout to vent length	**0.7549**	**0.0001*****
Log female snout to vent length	0.0707	0.403
1:1 Sexual size dimorphism	**0.9967**	**0.0000*****
Sexual difference in niche height	**0.8823**	**0.0002*****
Anole density	0.0369	0.550
Sexual difference in dietary prey size	**0.9201**	**0.0001*****
% male conspecific display	**0.982**	**0.0000*****

Key - *** = significance to 0.001.

Table 4.3

Pair-Wise Mantel Test of Sexual Size Dimorphism against Biometric, Biotic and Environmental Variables		
Variables	Regression Coefficients	P-Value
Log male snout to vent length	**0.24841**	**0.0500****
Log female snout to vent length	-0.132	0.3956
1:1 Sexual size dimorphism	**0.9655**	**0.0001****
Sexual difference in niche height	0.3145	0.0566
Anole density	-0.1908	0.3560
Sexual difference in dietary prey size	**0.78292**	**0.0001****
Prey availability size variance	**0.65606**	**0.0007****
Prey density	-0.089014	0.5913
% male conspecific display	**0.8535**	**0.0001****
Altitude	0.29917	0.0645
Temperature	0.18421	0.2245
Relative humidity	0.10325	0.6418
Geographic distance	-0.063463	0.6545
Patristic distance	-0.042105	0.6889

Key - ** = significance to 0.05; *** = significance to 0.01; **** = significance to 0.001.

Table 4.4

Partial Mantel Test of Sexual Size Dimorphism against Biometric and Biotic Variables			
Variable	Regression Coefficient	P-Value	Bonferoni adjusted significance (0.05)
% male conspecific display	**0.87217**	**0.0001****	**0.0125**
Sexual difference in dietary prey size	0.10478	0.7682	0.0166
Prey availability size variance	0.01445	0.9675	0.025
Log male snout to vent length	-0.18037	0.4902	0.05

Key - **** = significance to 0.001.

from the male, and female log mean snout to vent lengths (figure 4.8) are illustrated or discussed. This indices of SSD is illustrated in figure 4.9.

4.3.2 BIVARIATE NON-PHYLOGENETIC RESULTS.

As discussed in 4.3.1, log mean male snout to vent length was strongly correlated to log mean female snout to vent length ($r = 0.464$; $p = <0.001$, fig. 4.8). No statistically significant relationship was elucidated between SSD and log female snout to vent length ($r = 0.000$; $p = 1.000$, fig. 4.10) but when tested against log mean male snout to vent length, a correlation of $r = 0.658$ was recorded ($p = 0.01$, fig. 4.11). Spatial niche separation, tested by the sexual difference in niche height provided a significant correlation to SSD ($r = 0.717$; $p = <0.005$, fig. 4.12). Sexual prey difference also showed a significant relationship with SSD ($r = 0.907$; $p = <0.001$, fig. 4.13) across the 14 experimental populations of *Anolis oculatus*, as did environmental prey size variability ($r = 0.843$; $p = <0.001$, fig. 4.14).

However, of all variables being tested, % male conspecific display rate provided the strongest correlation in the non-phylogenetic bivariate analysis with a regression coefficient of 0.939 ($p = <0.001$). This relationship is depicted in figure 4.15.

Neither *Anolis oculatus* or environmental prey density gave a significant correlation to SSD ($r = -0.164$ and $r = -0.168$ respectively). Similarly, none of the environmental parameters of altitude, temperature or relative humidity provided significant

Figure 4.10

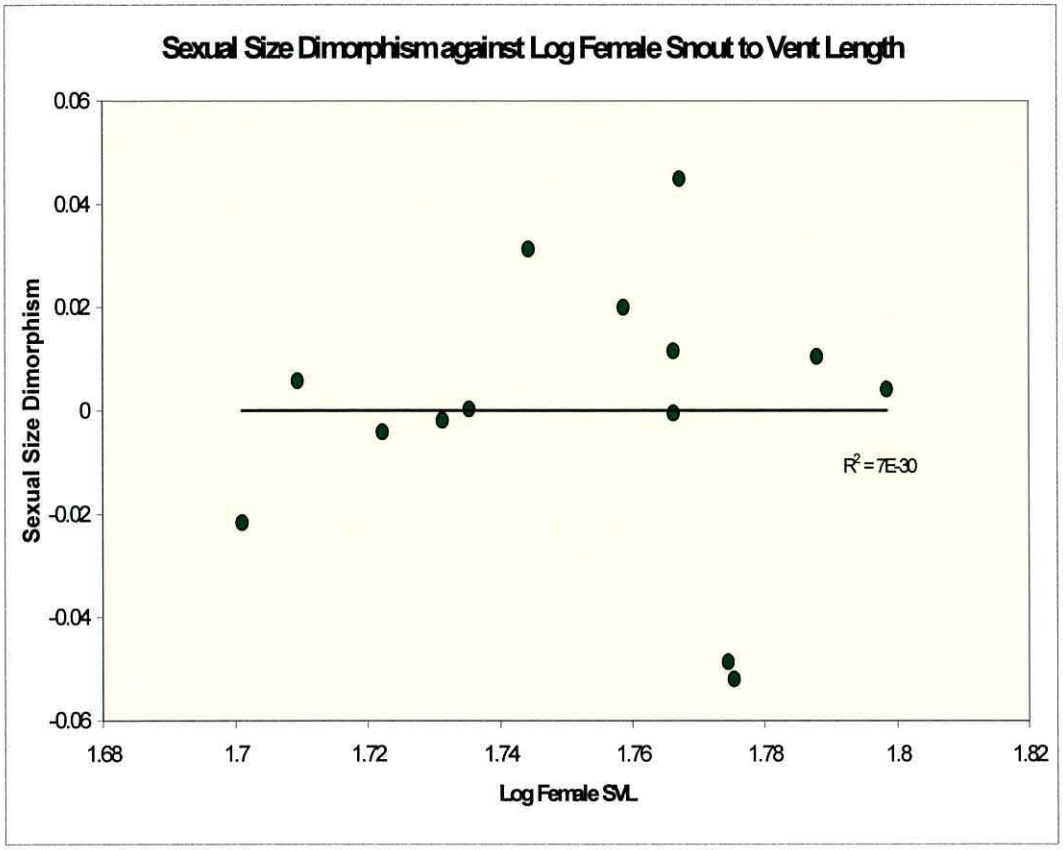


Figure 4.10 illustrates the fact that no significant relationship exists between female snout to vent length and the measure of SSD across the 14 experimental populations of *Anolis oculatus*.

Figure 4.11

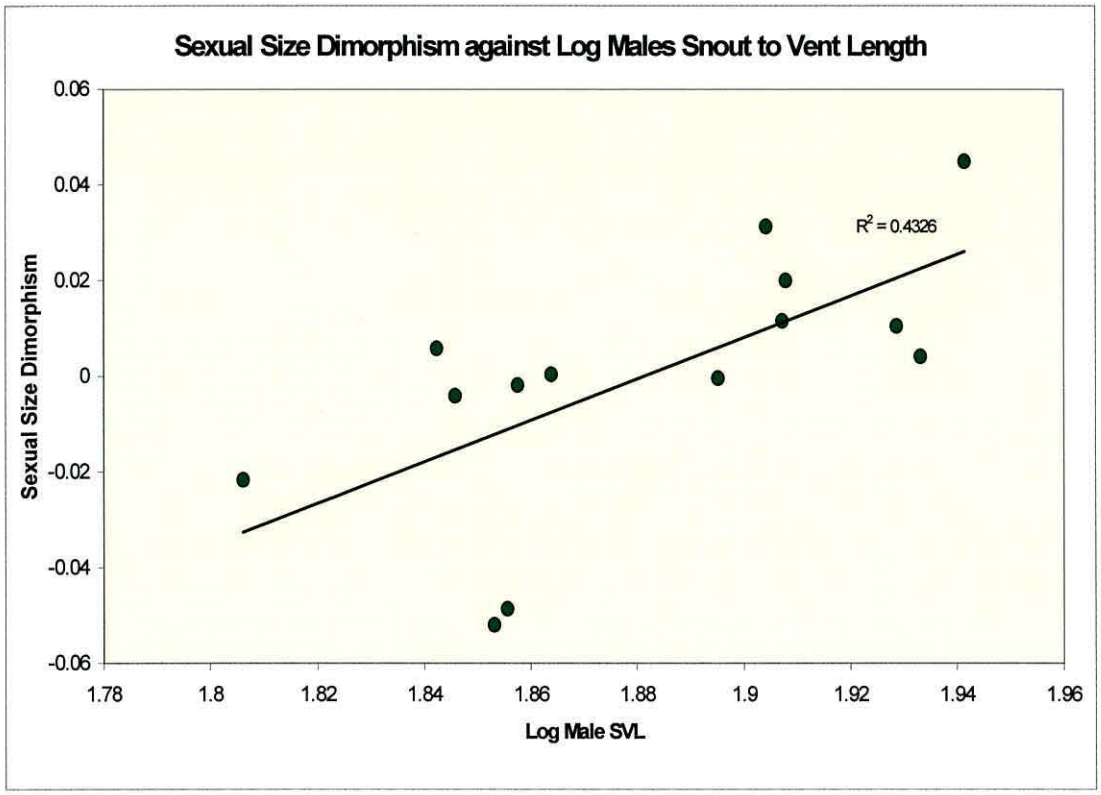


Figure 4.11 is an illustration of the significant correlation between SSD and log mean male snout to vent length in *Anolis oculatus* ($r = 0.658$; $p = 0.01$).

Figure 4.12

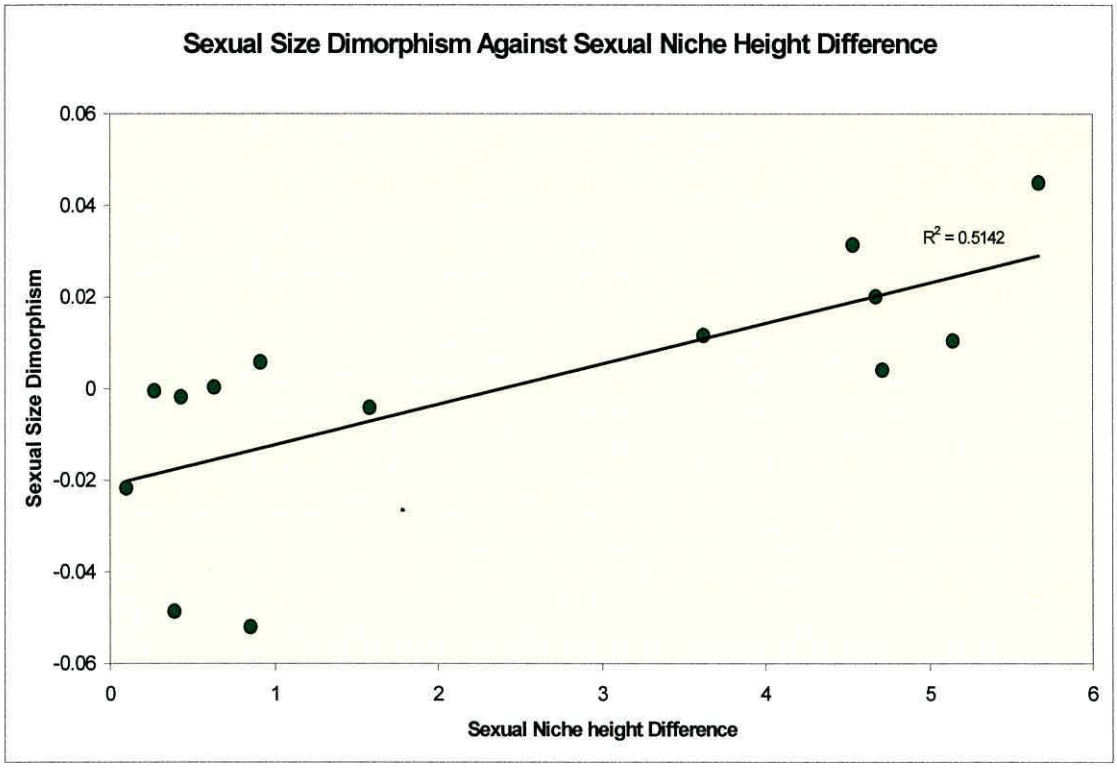


Figure 4.12 illustrates the significant relationship between SSD and sexual niche height differentiation between the sexes thus proving spatial niche divergence ($r = 0.717$; $p = <0.005$).

Figure 4.13

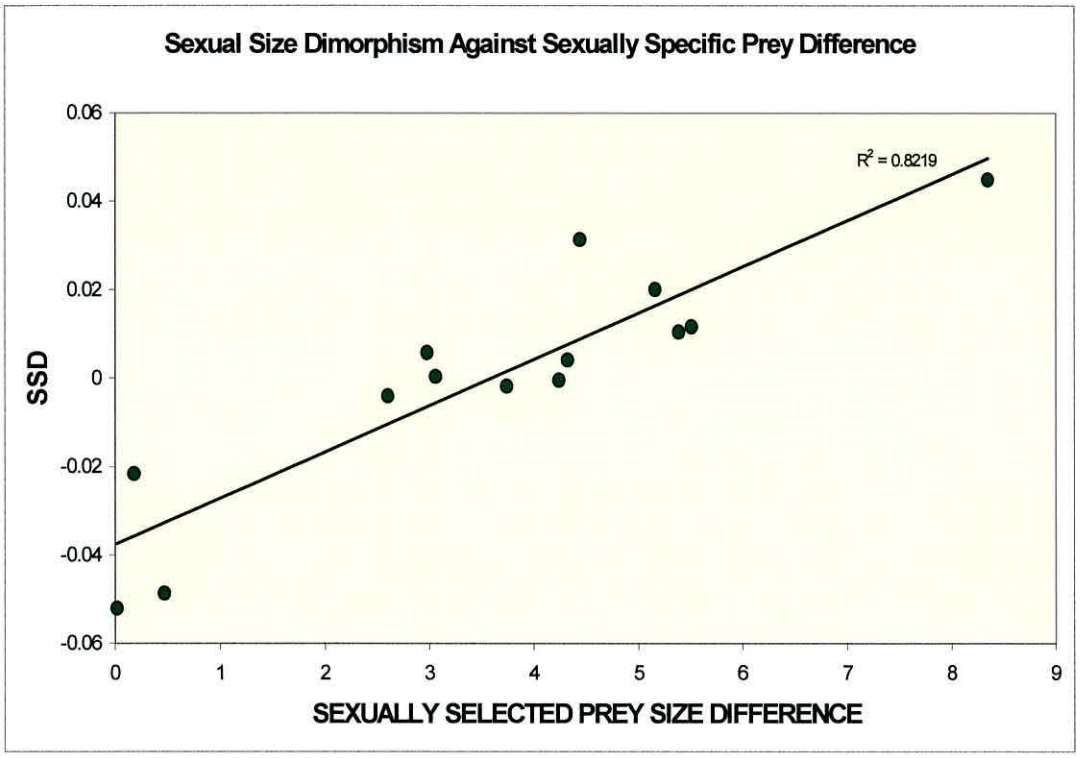


Figure 4.13 illustrates the significant relationship between SSD and the sexual divergence in prey size selection ($r = 0.907$; $p = <0.001$).

Figure 4.14

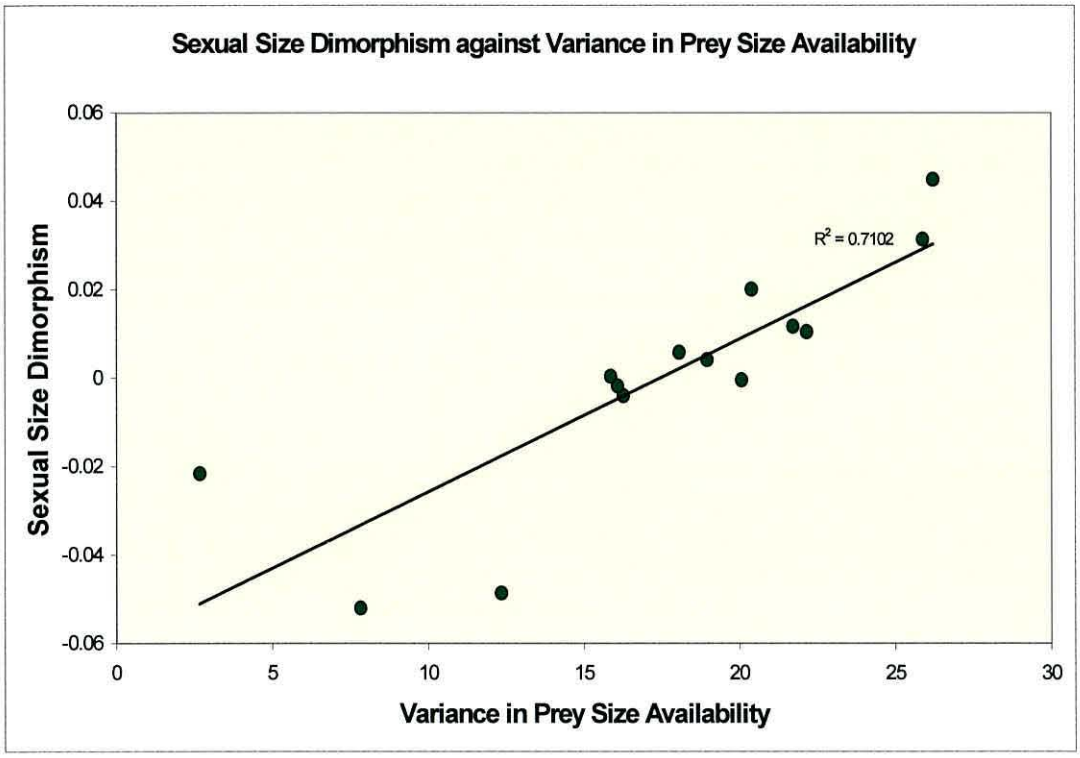


Figure 4.14 illustrates the significant interaction of SSD with the environmental variance in prey size availability ($r = 0.843$; $p = <0.001$) across the 14 experimental populations of *Anolis oculatus*.

Figure 4.15

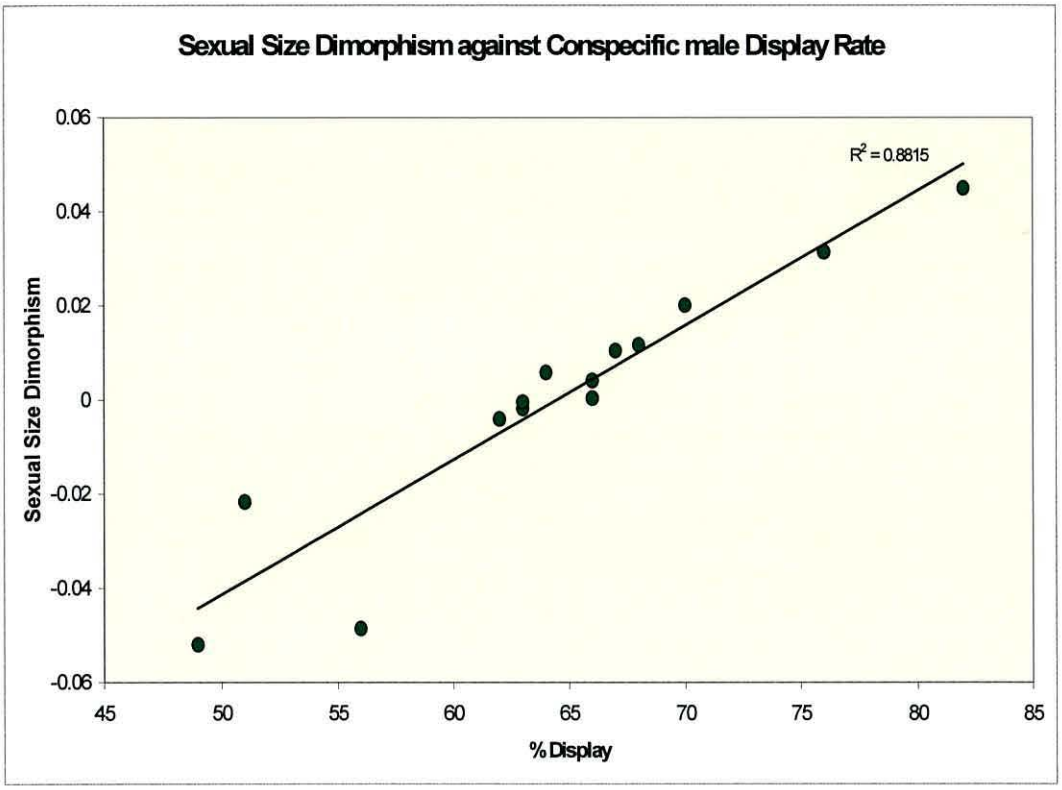


Figure 4.15 illustrates the strongest relationship detected in the non-phylogenetic bivariate analysis with the interaction of SSD with the % observed conspecific display rate of male *Anolis oculatus*(r = 0.939; p = <0.001).

relationships to SSD. All the results of the Pearson's bivariate correlations, and the probability of the respective correlation coefficients are listed in table 4.1.

4.3.3 PHYLOGENETIC INDEPENDENT CONTRAST RESULTS.

The phylogenetic independent contrast analysis generated 12 independent contrasts between the 14 populations of *Anolis oculatus* represented in the phylogeny. Of the eleven variables tested against the measure of SSD in the non-phylogenetic bivariate analysis only six are appropriate for consideration within a phylogenetic framework.

Contrast log male snout to vent length provided a significant correlation against contrast SSD with a regression coefficient of 0.7549 ($p = 0.0001$, fig. 4.16) where as contrast log female snout to vent length generated an insignificant correlation ($r = 0.0707$; $p = 0.403$). Contrast *Anolis oculatus* density also showed an insignificant relationship to contrast SSD ($r = 0.0369$; $p = 0.550$).

Contrast sexual difference in niche height provided a significant correlation with contrast SSD with $r = 0.8823$ ($p = 0.0002$, fig. 4.17). Sexually specific diet difference also demonstrated a significant correlation to SSD between contrasts ($r = 0.9201$; $p = -0.0001$, fig. 4.18), but the highest correlation was drawn between contrast SSD and contrast male conspecific display rate, with a regression coefficient of 0.982 ($p = <0.0001$) as illustrated in figure 4.19.

Figure 4.16

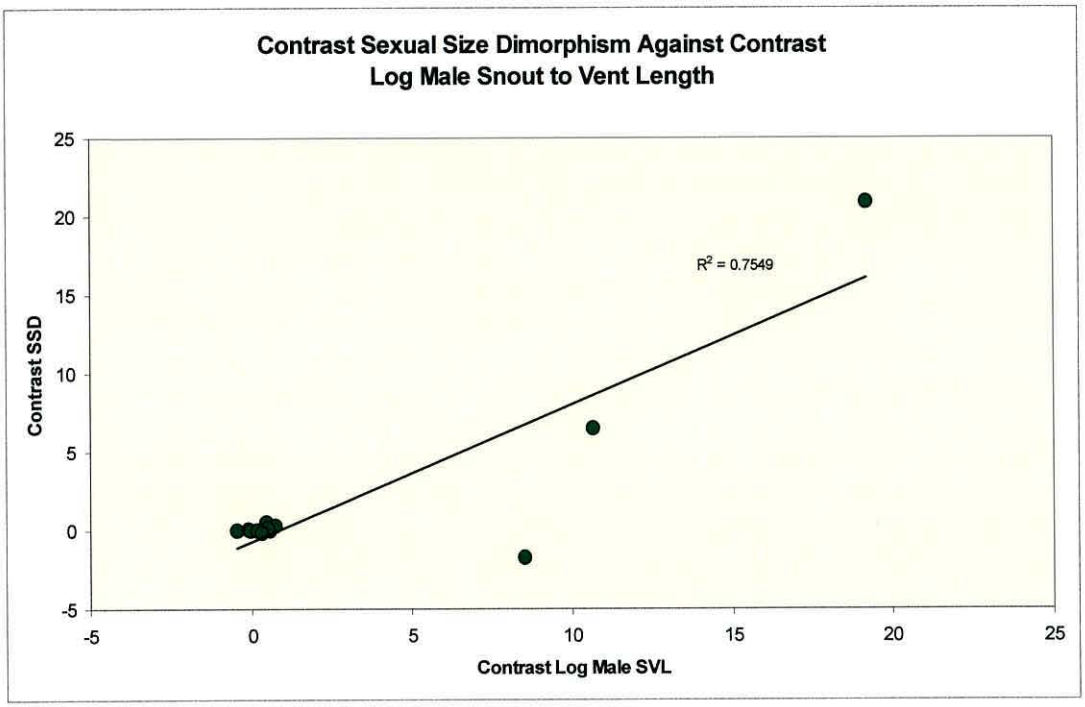


Figure 4.16 illustrates the significant correlation between contrast SSD and contrast Log mean male snout to vent length in *Anolis oculatus* ($r = 0.7549$; $p = 0.0001$).

Figure 4.17

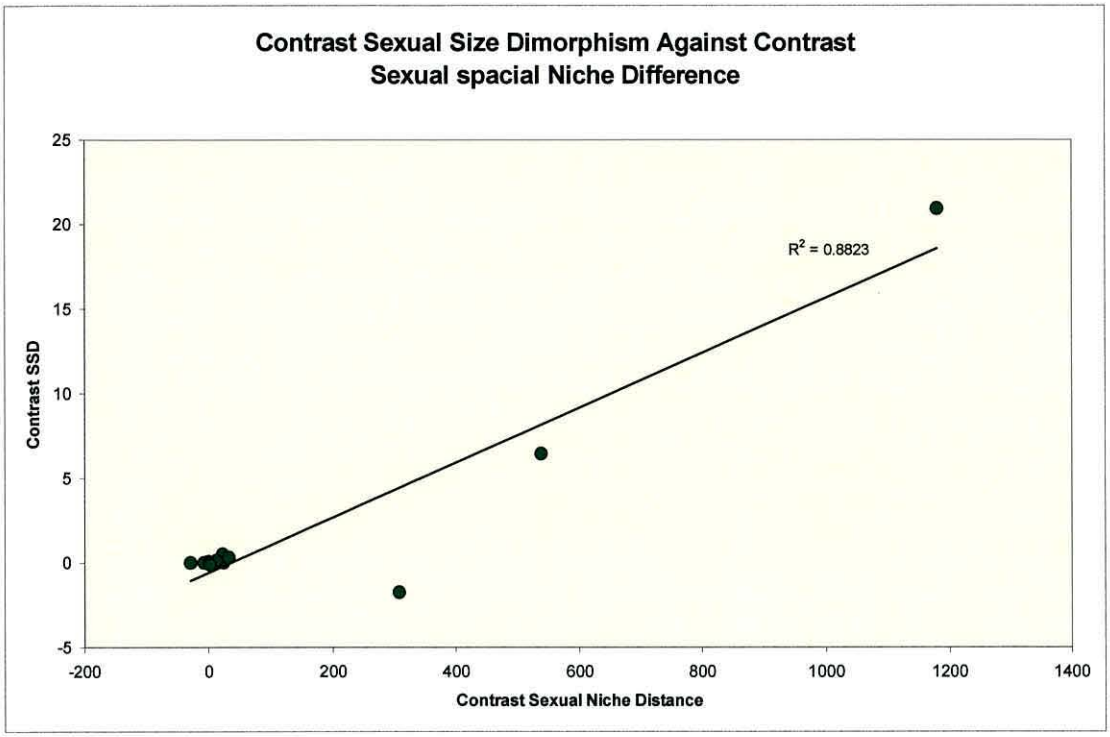


Figure 4.17 illustrates the significant correlation between the contrast values of SSD and sexual spatial niche divergence ($r = 0.8823$; $p = 0.0002$).

Figure 4.18

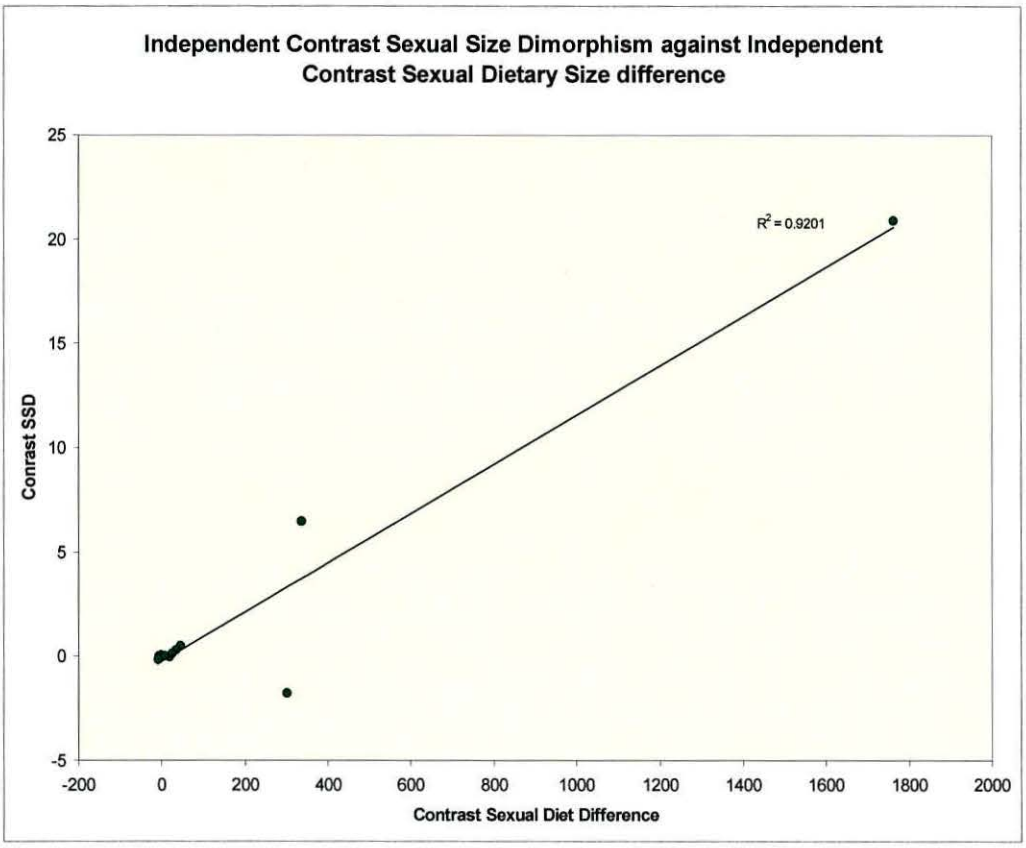


Figure 4.18 illustrates the relationship between contrast SSD and contrast sexual dietary prey size difference between populations of *Anolis oculatus* with the significant regression coefficient of $r = 0.9201$ ($p = 0.0001$).

Figure 4.19

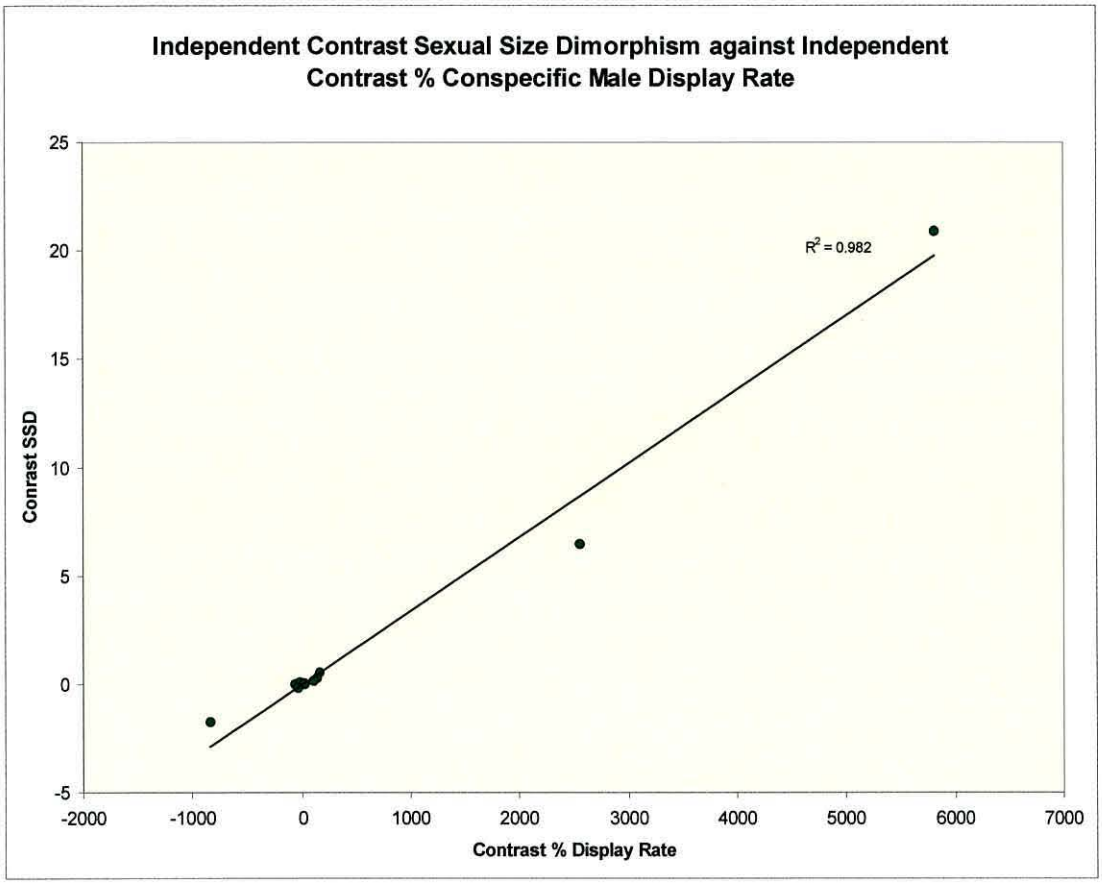


Figure 4.19 illustrates the strong correlation between the measures of contrast SSD and contrast conspecific male display rate in *Anolis oculatus* ($r = 0.982$; $p = <0.0001$).

The results of Pearson's correlations between contrast values are given in table 4.2.

4.3.4 MATRIX CORRESPONDENCE RESULTS.

4.3.4.1 PAIR-WISE MATRIX CORRESPONDENCE RESULTS.

At this stage of the analysis of data, geographic proximity and phylogenetic patristic distance were also able to be entered into the analysis as variables.

Log male mean snout to vent length shows a significant correlation of its matrix with the matrix of SSD ($r = 0.24841$; $p = 0.05$). An insignificant regression coefficient was again generated in the matrix comparison of log mean female snout to vent length with SSD ($r = -0.132$; $p = 0.3956$). Neither *Anolis oculatus* density, prey density nor in this analysis sexual difference in niche height provided significant regression coefficients when considered individually against SSD.

Sexual difference in dietary prey size selection, and environmental prey size variance both showed a significant regression against SSD between matrices with $r = 0.782$, $p = 0.0001$ and $r = 0.656$, $p = 0.0007$ respectively. Once again the strongest correlation with SSD was observed in the male conspecific display rate with a regression coefficient of 0.8535 at $p = 0.0001$. None of the environmental variables or the additional variables of geographic proximity and phylogenetic patristic distance gave

a significant correlation to SSD between matrices. The results of the pair-wise Mantel matrix correspondence test are illustrated in table 4.3.

4.3.4.2 PARTIAL MATRIX CORRESPONDENCE RESULTS.

Using a partial Mantel matrix correspondence test allows the inclusion of both geographic proximity, and phylogenetic patristic distance between populations to be included in the analysis. A partial matrix correspondence analysis also permits the all the putative causes of SSD, in the form of matrices, to be partially regressed against the matrix of SSD, across the 14 experimental populations of *Anolis oculatus*. To prevent the degeneration of significance only variables providing significant correlations in the pair-wise Mantel matrix correspondence tests are included as variables in the partial matrix correspondence tests.

Thus, of the 13 variables representing putative causation in SSD that were tested in the pair-wise matrix correspondence analysis, the four providing a significant correlation to SSD were included in the partial matrix correspondence analysis. These were log mean male snout to vent length, sexual difference in dietary prey size, environmental prey availability size variance and conspecific male display rate. Of these four variables tested against SSD, only male conspecific display rate yielded a significant correlation to SSD with a regression coefficient of 0.87217 with standard probability of 0.0001 which remains robust under a table Bonferroni adjusted probability of significance at 0.0125 (0.05). The results of this partial Mantel matrix correspondence analysis are illustrated in table 4.4

4.3.5 GRAPHICAL REPRESENTATION OF VARIABLES.

In order to aid the interpretation and discussion of the results of this investigation into SSD, and the variables that may potentially influence its patterns, a visual description of the variables was generated in the form of colour coded contour maps. Variables providing a significant correlation at any stage during the analysis are illustrated in figures 4.20 to 4.25.

Figure 4.20

Figure 4.20 illustrates the range of sexual size dimorphism across the range of *Anolis oculatus.*

Sexual Size Dimorphism

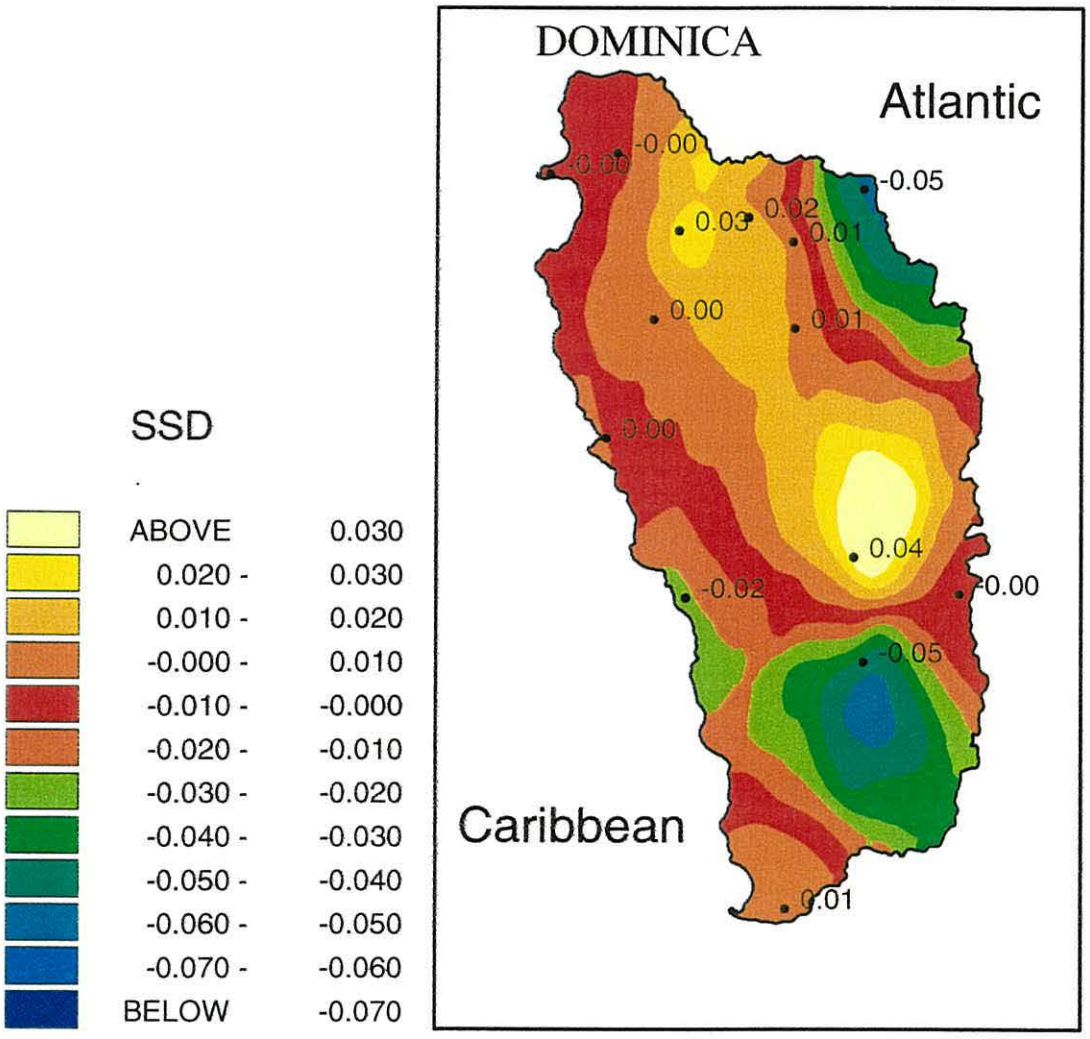
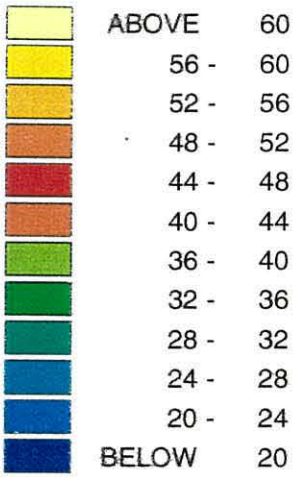


Figure 4.21

Figure 4.21 illustrates the range of sexual size dimorphism taken from the 1:1 slope of male to female snout to vent lengths, across the range of *Anolis oculatus.*

1:1 Sexual Size Dimorphism



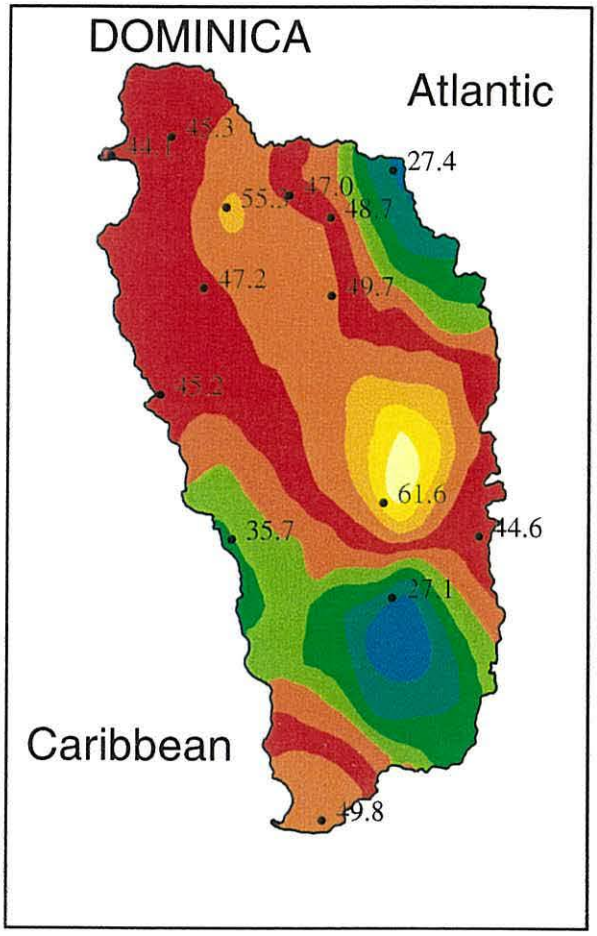
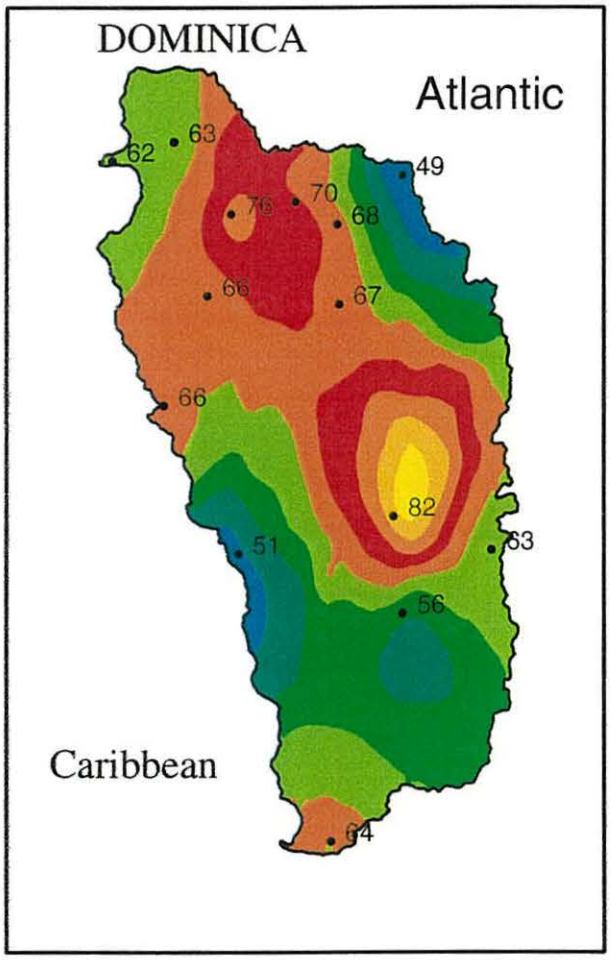


Figure 4.22

Figure 4.22 illustrates the range of male dewlap display rates for the experimental populations across the range of *Anolis oculatus*.

Male % Conspecific Display



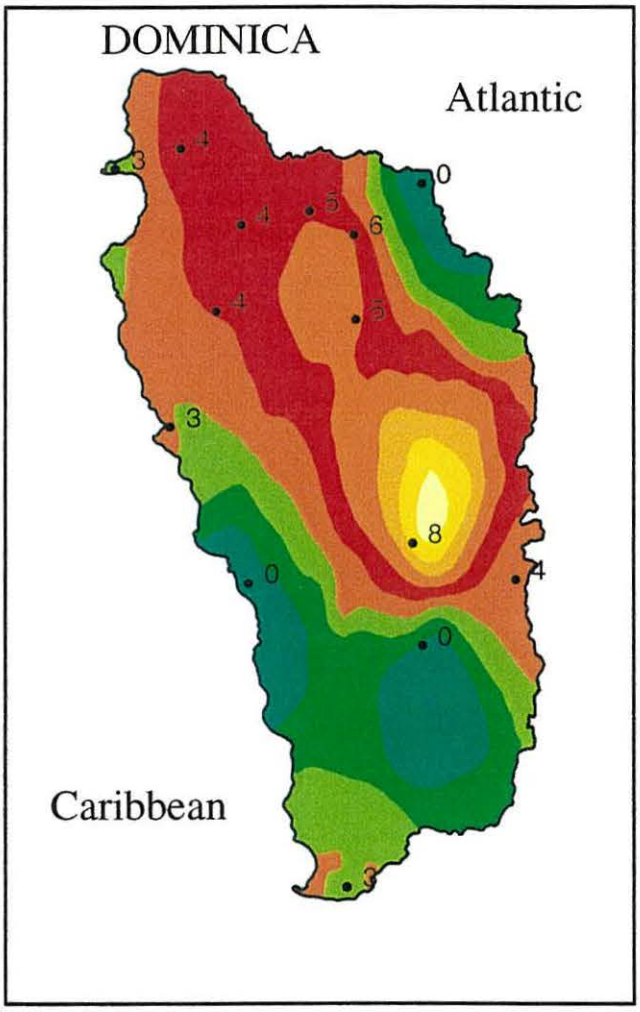
Display %

	ABOVE	84
	80 -	84
	76 -	80
	72 -	76
	68 -	72
	64 -	68
	60 -	64
	56 -	60
	52 -	56
	48 -	52
	44 -	48
	BELOW	44

Figure 4.23

Figure 4.23 illustrates the difference in prey size between male and female diets for the experimental populations across the range of *Anolis oculatus*.

Difference in Prey Size Dietary Content



Prey Size Difference (mm)

ABOVE	8
7 -	8
6 -	7
5 -	6
4 -	5
3 -	4
2 -	3
1 -	2
0 -	1
-1 -	0
-2 -	-1
BELOW	-2

Figure 4.24

Figure 4.24 illustrates the variability in prey size availability in the environment, across the range of *Anolis oculatus.*

Environmental Pray Size Variability

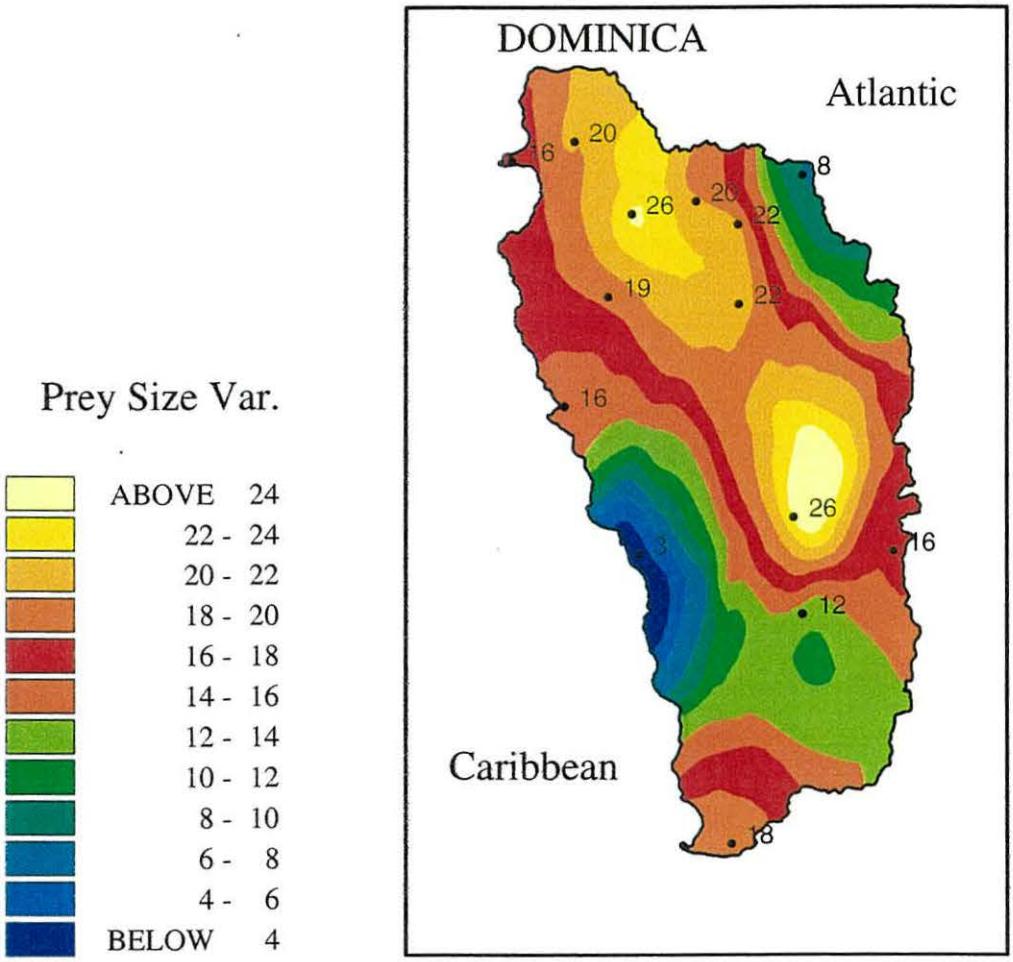
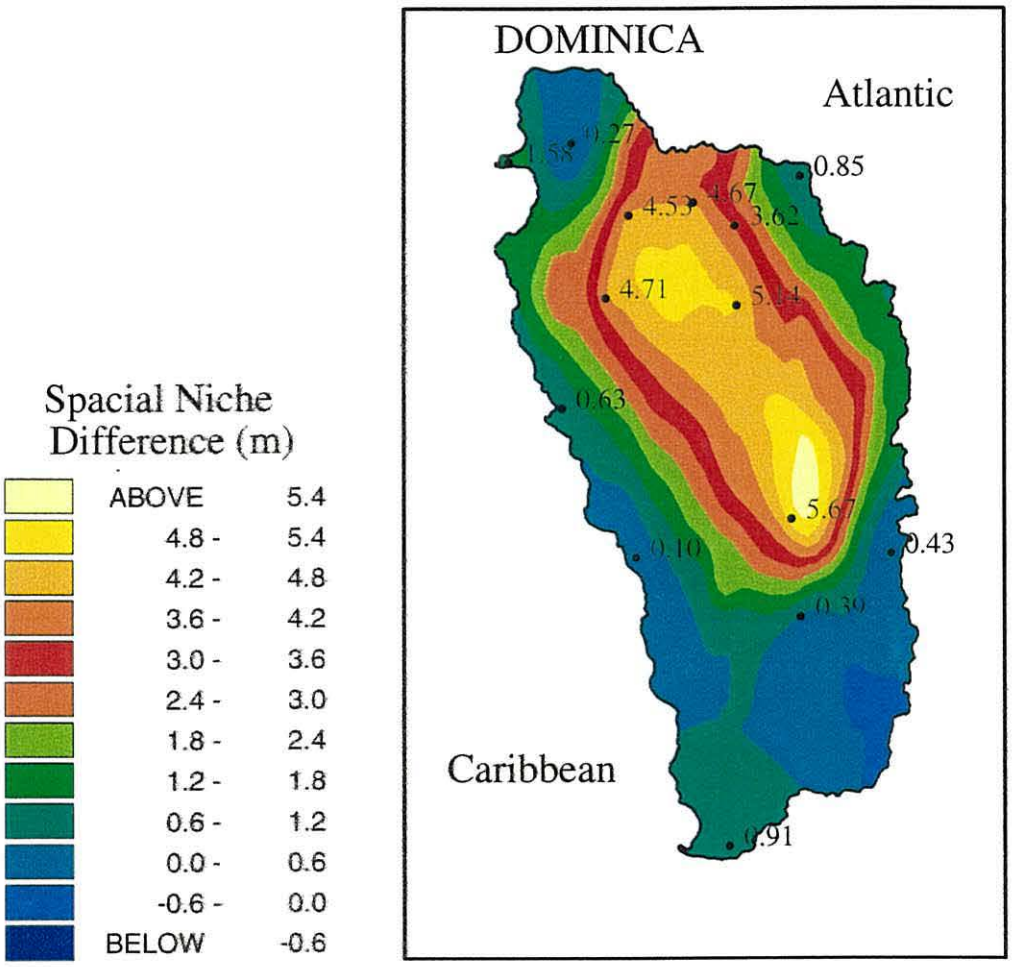


Figure 4.25

Figure 4.25 illustrates the sexual difference in spatial niche occupation between male and female *Anolis oculatus*, across their range.

Sexual Difference in Spacial Niche



4.4 CONCLUSIONS AND DISCUSSION.

4.4.1 QUANTIFYING SEXUAL SIZE DIMORPHISM.

Due to the consistently similar pattern of results yielded by testing both measures of SSD (as described in 4.3.1) against the variables in this study, one may conclude that the two techniques of quantifying SSD are of equal function (figure 4.6). As both techniques were seen to possess different weaknesses in their modelling of SSD, the fact that the two measures when regressed against each other provide an almost linear relationship indicates that the potential problems of either model are not realised. Therefor, in discussion, no further reference is made to the 1:1SSD indices.

4.4.2 THE MALE COMPETITION HYPOTHESIS.

In simple terms, the results of this study are a clear indication that sexual selection in the form of the 'male competition hypothesis' has a significant interaction with SSD within the 14 experimental populations of *Anolis oculatus* (figure 4.11). The 'female fecundity hypothesis' may be dismissed out of hand on three accounts. Firstly, as our data describes, SSD is the result of larger male size in *Anolis oculatus* to which the trends in SSD provide a significant correlation. Stamps et al (1997) discovered this relationship to exist in 20 of 25 *Anolis* species studied, with no cases of larger female SSD known from the genus. Secondly, female snout to vent lengths demonstrate no significant pattern when tested against SSD in *Anolis oculatus*. These results concur with those of Andersson (1994) and his predictions for the modelling of SSD under

sexual selection from the male competition hypothesis. Thirdly, in *Anolis* lizards it has been shown (Andrews and Rand 1974) that female snout to vent length and mass presents no significant relationship to individual egg or clutch size as anoles lay but a single egg at a time. This is supported as the case in *Anolis oculatus* through extensive personal observation. In over 400 females discovered to be gravid by palping, only a single egg (clutch size = 1) was ever detected (Reardon, unpublished data). The evidence that larger males have greater reproductive success when compared to smaller males (Trivers 1972) coupled with the evidence that male *Anolis* compete for territories in which exist the smaller home ranges of female *Anolis* (Stamps 1993) from whom the copulatory prerogative falls to the territory holding male, all emphasise the likely-hood that the relationship between SSD and male conspecific display rate, a measure of sexual selection is of causational significance to observed SSD. Indeed, a positive association has been identified between SSD and success in inter-male agonistic encounters, copulatory success and relative female density within male territories (Rand 1967; Trivers 1976; Stamps 1983; Andrews 1985 and Tokarz 1985).

From these results we may conclude that our chapter aim, 'to examine the relationships of SSD with sexual selection by examining male conspecific display behaviour,' has been explored, and has shown a positively significant relationship between SSD and sexual selection from a relationship to male conspecific display behaviour.

4.4.3 TRENDS IN DIET AND PREY SELECTION.

Dietary selection, and sexually specific ecological divergence in *Anolis* lizards is an area of some conflict between the results of various researchers (Bullock et al 1993; Preest 1994; Perry 1996). From the results of these researchers work we may conclude that if such a genus wide trend in larger male SSD exists it is unlikely to be the result of present selection pressures exerted by prey resource limitation, and any such trends observed in prey selection may be historical, or a facultative consequence of resource availability.

However, this study has demonstrated that the sexual difference in dietary prey size in *Anolis oculatus* offers the second highest level of significance to SSD across the analysis, closely followed by environmental prey availability size variance and sexual difference in niche height respectively. Such results indicate a strong ecological component to SSD with particular reference to sexually dimorphic prey selection. This brings into question Shines (1988) models of ecological divergence.

By looking at the relationship between sexual difference in dietary prey size with environmental prey size variability (figure 4.26) we see that with regard to the size of prey items available in the environment, *Anolis oculatus* utilises the full range of available resources. We may then take the investigation a step further by testing the interaction of environmental prey size variability against sexual difference in niche height (figure 4.27). These results with the correlation of 0.733 ($p = 0.003$) suggest that the spatial niche separation may be the result of an evolutionary attempt by natural selection to remove any competition between the sexes for food resources

Figure 4.26

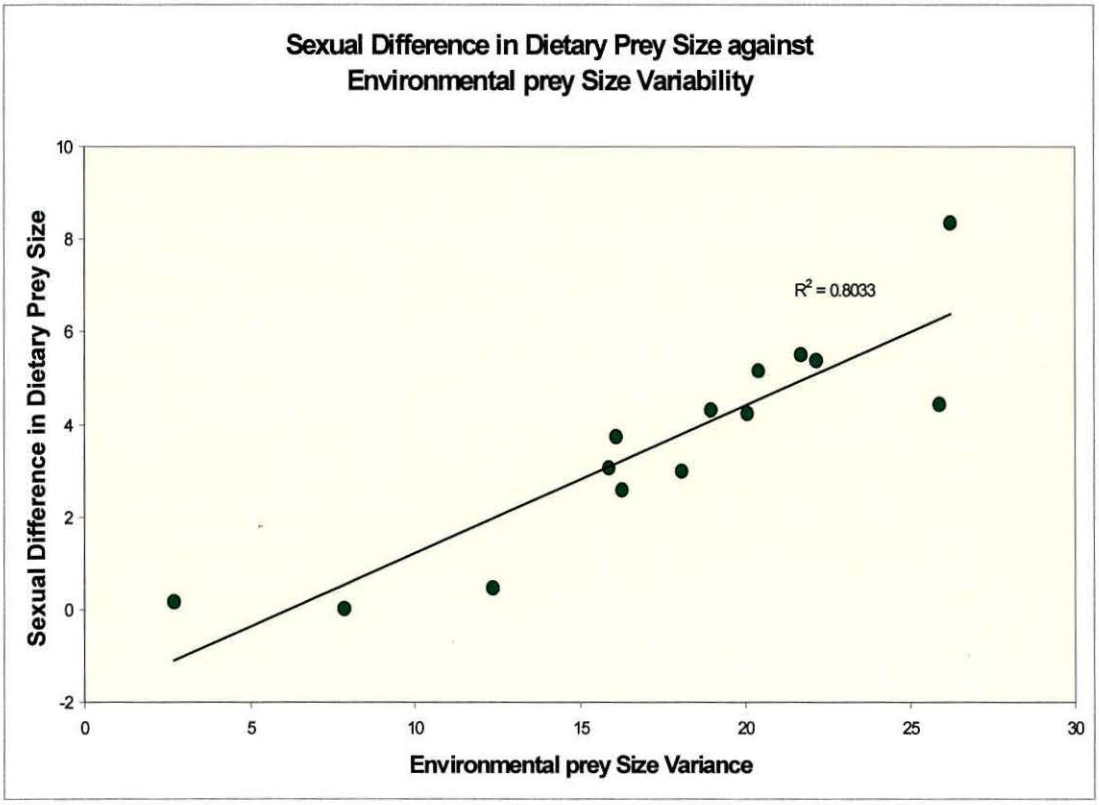


Figure 4.26 Illustrates the significant relationship between sexual difference in dietary prey size and environmental prey size variance ($r = 0.645$, $p = <0.05$) in *Anolis oculatus*.

Figure 4.27

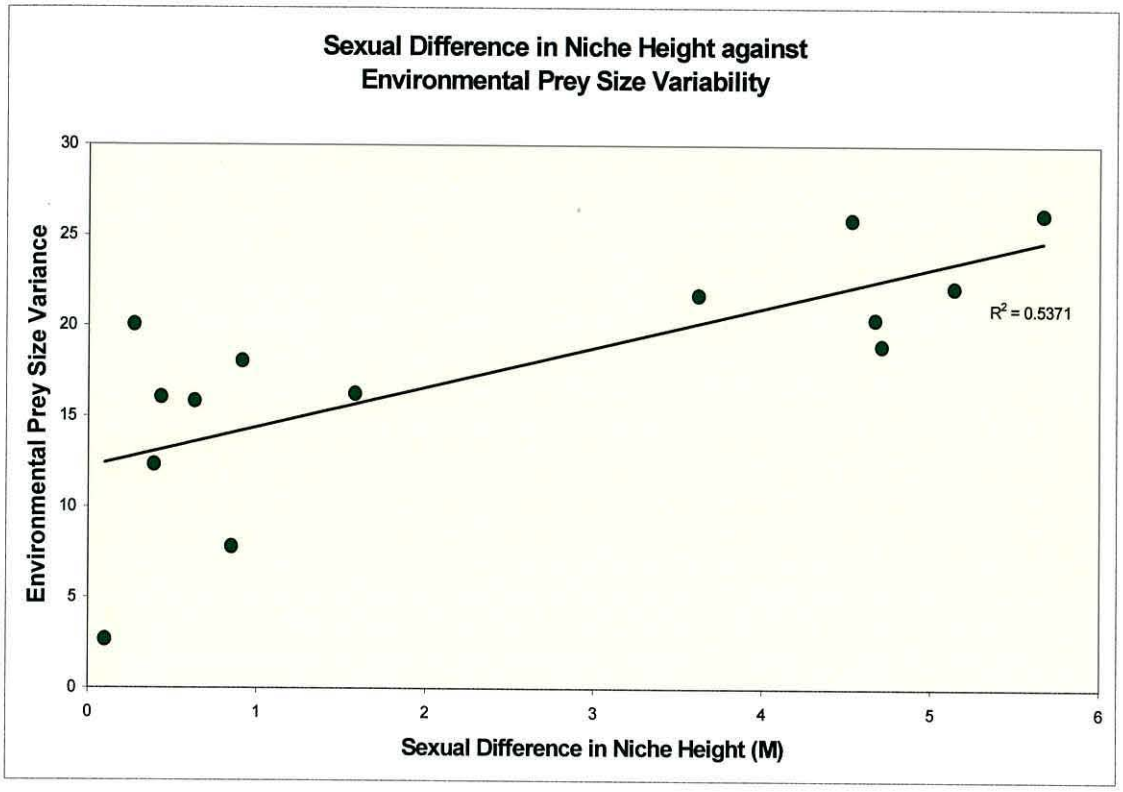


Figure 4.27 illustrates the significant correlation between environmental prey size variance with sexual difference in niche height ($r = 0.733$; $p = 0.003$).

Figure 4.28

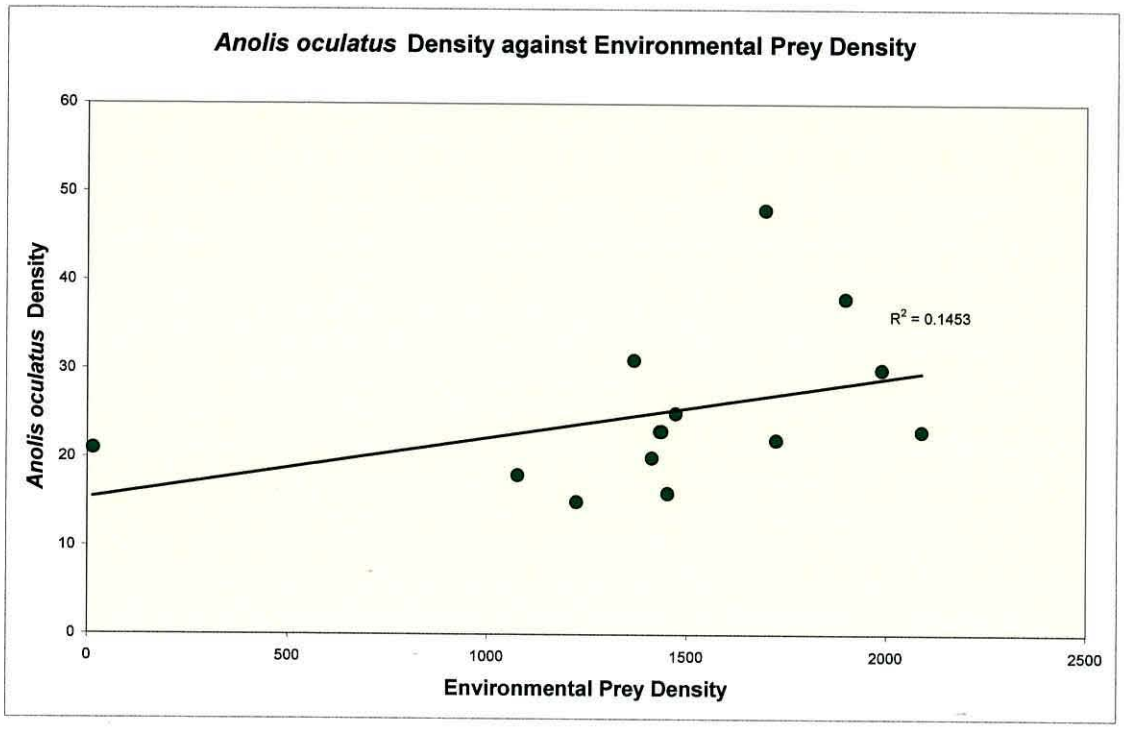


Figure 4.28 depicts the lack of a significant correlation between comparative Anolis oculatus density and Environmental prey density (r = 0.0211; p = 0.388), providing evidence that Anolis oculatus appears not to be prey resource limited in it's density.

cause by prey selection overlap. However, if this was the case one would expect to observe a negative regression slope between environmental prey size availability and sexual niche height separation as one would anticipate that as the breadth of available size of prey items increased the factors of selection causing niche segregation between the sexes would become weaker. In this study the opposite has been demonstrated. Therefore one can only conclude that the observed trend in niche height separation between the sexes is driven by the ethological nature of territory defence, and that the observed sexual difference in diet selection has further ecological consequences.

Thus, the second aim of this chapter, 'to examine intraspecific niche divergence both by its spatial segregation of the sexes and its influence on diet selection' has shown that significant sexual divergence in spatial ecology and diet selection is present in *Anolis oculatus.*

4.4.4 REVIEWING THE INTERRELATED MODEL.

When observing the interaction of SSD with environmental prey size variance (figure 4.14), and sexual difference in dietary prey size (figure 4.13), we observe some strong interactions. Certain populations, notably populations from Rodney's Rock, Eden and Fresh Water Lake exhibit the lowest measures of SSD with the indices of –0.021, -0.052 and –0.048 respectively. These three populations of *Anolis oculatus* also provided the lowest measures of sexual dietary size difference (0.18, 0.02, 0.47 respectively) and the lowest measures of environmental prey size variance among the

14 populations. Obviously these factors bear some inter-related significance to each other. Essentially, where environmental prey size variability is low sexual difference in dietary prey size also reduces, as does SSD. We may therefore look at Shines (1988) second prediction that ecological inter-sexual divergence as a passive consequence of sexually selected SSD as being a likely model for *Anolis oculatus*. One may alter this theory slightly to state that inter-sexual ecological divergence is the beneficial expression of ecological release permitted by sexually selected SSD.

An interesting point raised by this study is that in *Anolis oculatus*, it would appear that the ecomorph adaptation observed between species, as defined by Williams (1972), seems to exist, to some degree between gender, and age groups within the species over the range of *Anolis oculatus*. Adult male *Anolis oculatus*, with regard to micro-habitat occupation, appear to inhabit the trunk anole niche, adult females appear to inhabit the trunk-ground anole niche, and hatchlings, juveniles, and sub-adults appear to inhabit the twig anole niche. A morphological comparison to the niche parameters described by Williams (1972) has not been conducted in *Anolis oculatus*, and the above associations are the result of field observations of anole microhabitat niche occupancy.

4.4.5 FURTHER RESEARCH.

It would be most revealing to translocate populations of *Anolis oculatus* from environments of low environmental prey variability into similar ecotype habitat, but where environmental prey size variability is greater. The observations of this study,

despite being phylogenetically controlled, give no indication of the interaction between phenotype and genotype with regard to SSD. It may be the case that *Anolis oculatus* SSD is a genetically controlled trait, specific to each population. In which case, only gradual natural selection favouring individuals of larger size in the case of males and/or smaller females, in a translocation experiment, would elucidate the fact of genotype control over SSD.

However, it is also possible that *Anolis oculatus* share a similar genetic disposition to asymptotic body size across its range, and that observed variation in body size is the result of ecological constraint (for example in resource availability) on a morphometrically plastic trait. If body size in *Anolis oculatus* is such a plastic trait, then translocation of an experimental population into a similar ecotype habitat but of greater environmental prey size variability, would be predicted to result in ecological release, and a subsequent population wide shift in SSD.

CHAPTER 5:

PHENOTYPIC PLASTICITY

Day old hatchling male *Anolis oculatus* from Batali, Caribbean coast.

5.0 INTRODUCTION.

Research into the geographic variation in phenotype of organisms, is both a broad and well-established science. Indeed, the majority of Wallace's (1865) and Darwin's (1871), seminal work into the mechanisms of evolution rested on the patterns, and congruence of geographic variation in biometric aspects of phenotype. Geographic variation is present in nearly all species. The study of geographic variation, and its cause, has, lead to the development of a substantial portion of modern evolutionary theory (Cracraft 1990; Endler 1977; Futuyma 1986). The processes of both phylogenesis (Thorpe 1984), and ecogenesis (Johnston and Sealander 1971; Malhotra and Thorpe 1992) shape the genotype of any species, or population.

In any study of evolutionary ecology, before substantiated suggestions can be made about the evolutionary mechanisms at play, it is important to understand the relationship between observed phenotype, and genotype of the organisms in question, especially when only phenotypic character traits are under consideration. Generally, phenotype may be interpreted as a reflection of genotype, except where phenotypic plasticity is at play. Where phenotypic plasticity exerts a significant effect on a trait, care must be taken in determining the cause of variation, and extrapolating genetic and plastic trait expression. This is an especially important point when testing for the effects of natural selection acting on populations (Malhotra and Thorpe 1992; Losos et al 1997).

5.1 PHENOTYPIC PLASTICITY.

Phenotypic plasticity is regarded as the expression of alternative phenotypes, produced from a single genotype, resulting from different exogenous influences (Spitze and Sadler 1996). Exogenous influences dictating the expression of phenotypic plasticity are largely cited as environmental (McNamara 1998; Thompson 1999; VanBuskirk and Relyea 1998; Soares et al 1998).

Central to the concept of phenotypic plasticity is the reaction norm (Bradshaw 1965). This is the variety of different phenotypes that are produced by a single genotype, across the spectrum of environmental conditions that are usually encountered by the population. A vital aspect of the reaction norm is that the variation observed in the environments involved, are repeatable and predicable aspects of the organisms habitat.

A second concept of phenotypic plasticity must also be addressed. This is the plastic response to unpredictable variability within environments. In such situations, the generation of variable progeny via genetic means, or through responsiveness to environmental fluctuations during embryonic development (Bull 1987), can provide a selective advantage by ensuring that some progeny are suited to the current environmental conditions. Both these concepts are included in, rather than define, the modern interpretation of phenotypic plasticity.

Scheiner (1993) conducted research into both the genetics, and evolution of phenotypic plasticity, and produced results suggesting that the environment was largely responsible for the change in expressed phenotype of a genotype in several

grass species. Scheiner (1993) states that genetic variation can be partitioned into portions that are dependent and independent on the environment. From this partition, two heritability measures were derived and compared to make predictions about the response to selection. Genetically, plasticity is likely due both to differences in allelic expression across environments and to changes in interactions among loci. Most significantly, phenotypic plasticity is not a function of heterozygosity.

Environmental cues during early developmental stages are more likely to result in phenotypic plastic effect in a trait than are similar cues in an adult organism (Rhen and Lang 1995). This was demonstrated by Rhen and Lang (1995) in their study of snapping turtle *Macroclemys temmincki,* incubation temperatures. They concluded that incubation temperature is likely to have a differential fitness effect on the sexes, mediated via differences in growth regimes. Similar influences of incubation temperatures are exemplified by VanDamme et al (1992), where neonate *Podarcis muralis* incubated at low temperatures had larger snout to vent lengths and body masses, grew faster, and had higher sprint speeds than hatchlings incubated at higher temperatures. However, Qualls and Shine (1998) have conducted the most comprehensive study of temperature dependent phenotypic plasticity to date. Qualls and Shine (1998) examined phenotypic responses of hatchling skink, *Lampropholis guichenoti*, incubated in the laboratory, from two study populations with significantly different natural incubation temperatures. Eggs from both sites were incubated under both environmental temperatures. The results showed that certain characteristics such as hatchling mass, and snout to vent length showed little or no phenotypic plasticity in response to the different incubation temperatures. Tail length, inter-limb length and body shape were all strongly influenced by incubation temperature, suggesting that a

significant proportion of the observed geographic variation in phenotype in *Lampropholis guichenoti* may be attributed to plasticity rather than genetic divergence.

Queral Regil and King (1998), demonstrate how diet composition can also have an influence on phenotypic plasticity in *Nerodia sipedon*. Experiments in which small and large prey items were fed to experimental populations lead to a significant univariate effect on jaw length in the snakes.

Two further examples of investigation into phenotypic plasticity in non-herpetological subjects include the work of Lecompte et al (1998), and Cordell (1998).
Environmental temperature variation has also been shown to elicit phenotypic plasticity in traits other than gender, and growth rates. Lecompte et al (1998), demonstrate that in *Helix aspersa,* the continuous colour gradient from red to black in the shell is temperature dependent. A darker pigmentation was characterised by low temperatures, while red bands were related to higher environmental temperatures.

Undetermined environmental characteristics also exhibit themselves as the cause of phenotypic plasticity when observed along environmental gradients. Cordell et al (1998) examined the foliage of *Metrosideros ploymorpha* trees in a wide range of Hawaiian habitats. The study showed that the morphological characteristics such as leaf size, petiole length, and internode length decreased with increasing elevation in the field.

5.1.2 PHENOTYPIC PLASTICITY AND EVOLUTION.

It is hypothesised that phenotypic plasticity is an adaptation to environmental heterogeneity. Such a theory relies upon two assumptions. They are that phenotypic plasticity improves the performance of individuals, and that it evolved in response to selection imposed in heterogeneous environments (VanBuskirk and Relya 1998). In this context, phenotypic plasticity is a response to the forces of natural selection.

Thompson's (1991) paper argues that phenotypic plasticity represents a fundamental component of evolutionary change rather than acting as a buffer to the genetic effects of natural selection. Thompson concludes by stating that a response to environmental variation is only adaptive if it represents a mechanism by which relative fitness is maintained in the presence of environmental variation. This paper raises some contentious issues, and is contradictory to the findings of Behera and Nanjundiah (1995). They suggest that in a theoretical model (following Hilton and Nowlan 1987), phenotypic plasticity invariably leads to accelerated evolution, but in the non-theoretical fitness schemes observed in nature, plasticity, to an optimal level, will slow the rate of evolutionary change, and ultimately improve the level of adaptation finally achieved.

It must be remembered that assessing the relative adaptation of wild populations to their respective environments is a largely theoretical process. Whitlocks (1996) work on the phenotypic plasticity exhibited by *Drosophila melanogaster* clarifies the concept of plasticity slowing the process of evolutionary change. The work discusses its limitations, with species with broader niche breadths having a slower rate of

evolutionary response, whereas species with a narrower niche having higher probabilities of fixing beneficial alleles, and taking less time to do so. Further more, Whitlock states that niche breadth is likely to evolve to be more narrow, because of the association between location and alleles favoured in local habitats for individuals with reduced migration, assortative mating, or habitat selection.

5.1.3 TESTING FOR PHENOTYPIC PLASTICITY.

Common garden experiments are ideal for testing for phenotypic plasticity as a response to environmental variables. Common garden experiments involve the movement of individuals from different environments into a control environment. This then allows for a comparison to be made between populations under common garden translocation and against their respective source populations.

Sorci et al (1996) translocated hatchling *Lacerta vivipara* from two French populations located at 150 metres above sea level, and 1400 metres above sea level respectively, into the laboratory. The hatchlings grew at a uniform rate under identical laboratory conditions, suggesting that the differences in growth rates observed in the experimental populations in their natural habitat, are driven by environmental factors, more precisely the thermal environment. Cordell et al (1998), translocated sapling *Metrosideros polymorpha,* also from an altitudinal gradient in Hawaii, to a common garden site. The experiment proved that the observed variation in *M. polymorpha* was due to a combination of environmentally induced variability in physiological, and anatomical characteristics, and genetically determined variation.

However, as stated above, plasticity may be at its most sensitive to environmental variation during the developmental, or embryonic stage. Therefor, one must consider imposing the shift in environment as early as possible during an organism's development. Jockusch (1997) did just this in the experimental raising of *Batrachoseps* salamanders from 10 source populations (representing four species). The specimens were collected as eggs and raised under standardised environmental conditions. The results demonstrate that the number of trunk vertebrae can be altered by the developmental temperature. A prudent point made, however, is that the degree of phenotypic plasticity observed is insufficient to account for the geographic variation recorded between the salamander populations in their natural habitats.

5.1.4 PHENOTYPIC PLASTICITY IN *Anolis oculatus.*

As detailed in section 1.5, chapter 1, *Anolis oculatus* exhibits an exceptional degree of geographic phenotypic variation across its range. Chapters 2 and 3 tested for the environmental cause of natural selection that may have contributed to the observed variation. However, a response to differential selection regimes may be expressed through phenotypic plasticity rather than by genetic differentiation in the phenotypic traits under selection (Appleton and Palmer 1988; Palmer 1990; Gibbs 1993). Some consideration of phenotypic plasticity in *Anolis oculatus* would therefor be beneficial to any understanding of the forces of natural selection resulting in the observed degree of variation.

5.1.5 AIMS.

The aim of this chapter is simple to test for the presence of environmentally induced phenotypic plasticity in the recorded character traits of experimental *Anolis oculatus* raised in a common garden enclosure.

Thus, the null hypothesis states that:

'Environmentally induced phenotypic plasticity is not primarily responsible for the character traits recorded in the experimental *Anolis oculatus* individuals.'

5.2 METHODS AND MATERIALS.

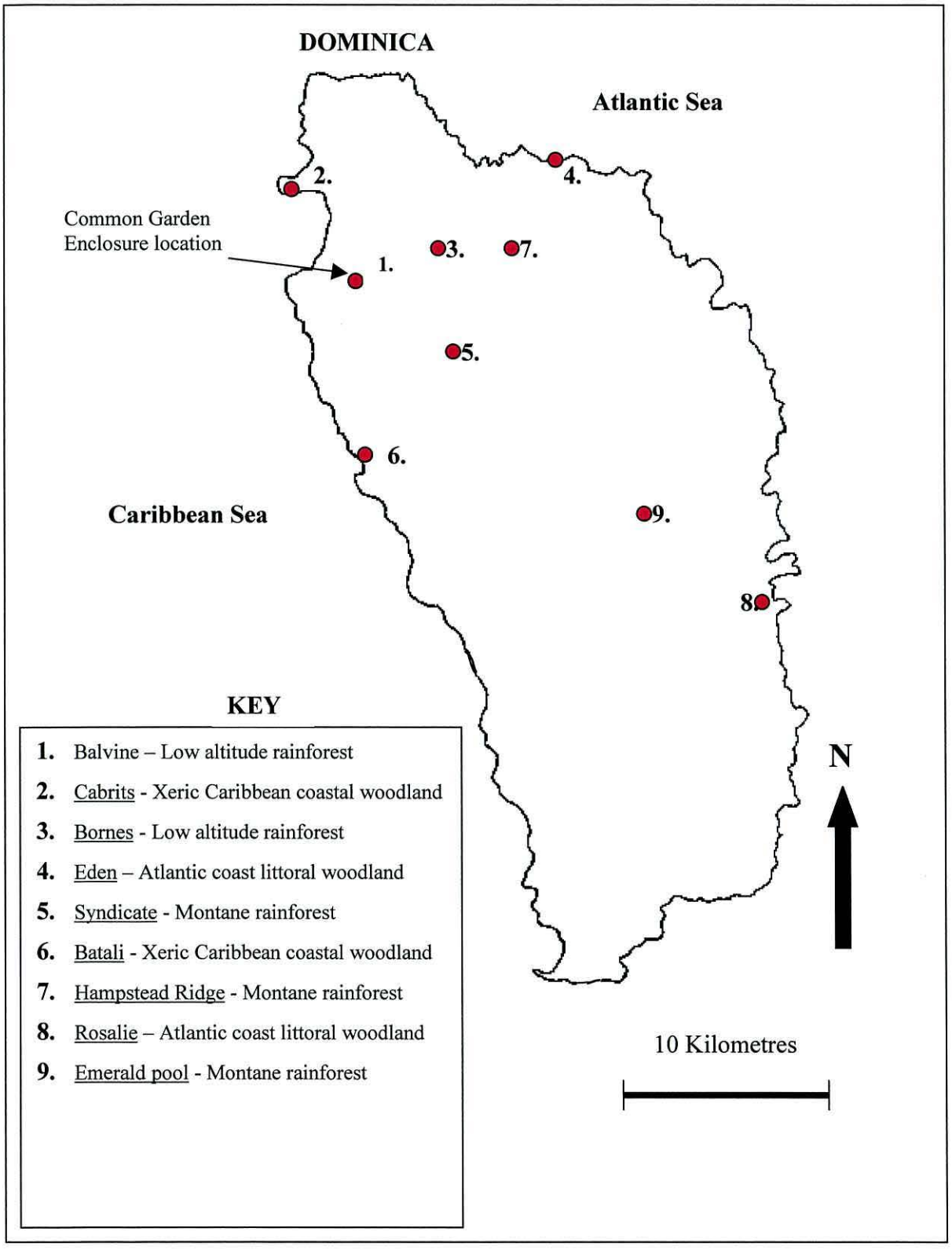
To test for phenotypic plasticity in *Anolis oculatus*, gravid females were collected from 14 experimental locations and all relocated to common garden enclosures. The eggs of these individuals were then allowed to hatch and the juveniles maintained in the common garden enclosures.

5.2.1 EXPERIMENTAL POPULATIONS.

Throughout the experiments within this study, an attempt has been made to sample as widely as possible from all ecotypes and regions of the range of *Anolis oculatus* on Dominica. To make use of both the biometric data and environmental data previously recorded, the fourteen experimental locations illustrated in figure 4.2, which includes those analysed during the translocation experiments and the investigation into sexual size dimorphism, were used to collect gravid female anoles. Gravid female *Anolis oculatus* were collected over a three-week period of June 1997. Although at least ten heavily gravid females were collected from each of the fourteen experimental locations, several locations failed to produce any viable juveniles for the common garden enclosures. Therefor only nine experimental populations were considered for the analysis. These nine populations are illustrated in figure 5.1. These populations include the vital control population, sourced from Balvine, the site of the common garden enclosures. To provide a biometric comparison to the common garden juveniles, 30 individual biometric profiles were taken from each experimental

Figure 5.1. Site Locations of Common Garden Experiment *Anolis oculatus* Populations.

Figure 3.1 illustrates the site locations of all 9 experimental populations of *Anolis oculatus* included in the common garden experiment. Their habitat ecotypes are given in the key below.



population that had been recorded for analysis for the chapter 3 translocation experiment.

5.2.2 COMMON GARDEN ENCLOSURES.

On collection and translocation to the common garden environment, the gravid female anoles were maintained in individual enclosures, constructed from plastic soft drinks bottles, separated by a tube of wire mesh. In the base of the bottle, humus and leaf litter provided suitable conditions for oviposition. Invertebrate prey items were offered daily and the cages were misted with water twice a day. The cages were maintained outdoors at Balvine adjacent to the large common garden enclosures. Females were repatriated to their native environment after oviposition. The oviposition cages are illustrated in figure 5.2.

Once laid, the eggs were maintained in the cages. Upon hatching, the juveniles were toe clipped to provide a permanent identification number. This was done under anaesthesia, according to the techniques outline in section 2.2.5, chapter 2. The hatchling juveniles were then introduced into the common garden enclosures. This enclosure was constructed on a wooden box frame of 200cms x 70cms x 70cms, and lined with 3mm plastic 'greenhouse' shading mesh. This is illustrated in Plate 5.1. To provide adequate habitat, the enclosure was built prior to the collection of the gravid female and vegetation was allowed to grow throughout the enclosures. To ensure an adequate supply of invertebrate prey, broken fruits such as mango, and grape fruit, were placed in the enclosures every few days to attract insects. These fruit

Figure 5.2. Common Garden Experiment Oviposition Enclosure.

Figure 5.2 illustrates the cage enclosure in which gravid female *Anolis oculatus* were maintained until oviposition. The eggs remained in the cages until hatched, whereupon the hatchlings were given individual identification numbers by 'toe clipping' and moved into the common garden enclosure.

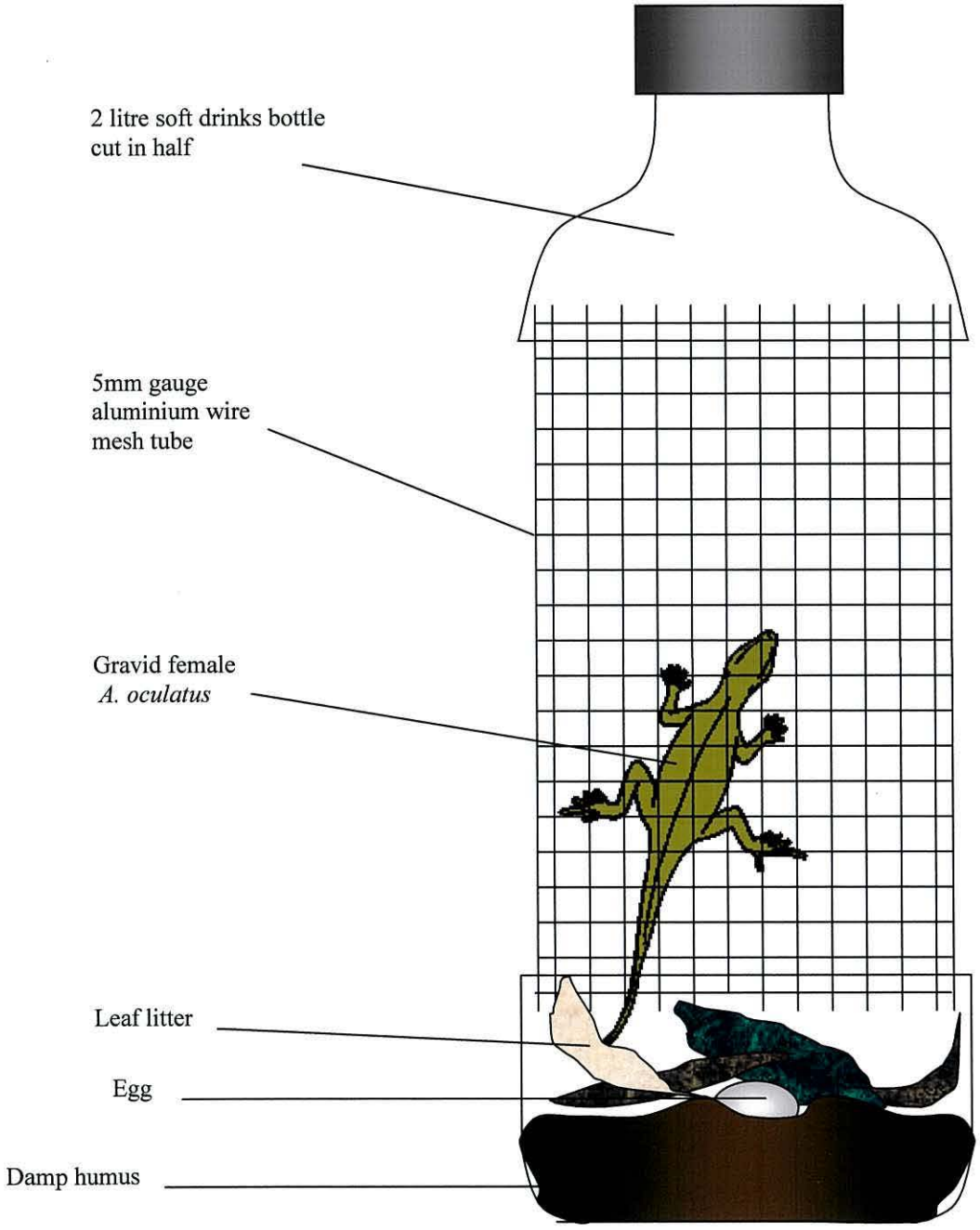


Plate 5.1

Plate 5.1 illustrates the common garden enclosure that was used to raise common garden juvenile anoles to a appropriate age for biometric analysis. The enclosures were located at the authors house, at Balvine, North-west Dominica, in low altitude rainforest.

were removed after several days to prevent fouling of the enclosure. The enclosures did not receive additional watering as the vegetation captured sufficient moisture during precipitation.

The enclosures were maintained for a six month period, when the common garden juveniles had reached an adequate sub-adult level of growth that permitted them to be biometrically analysed.

5.2.3 DATA COLLECTION.

As stated above, source population data was taken from previous experimental population biometric analyses that were conducted for the investigation into the ecology of sexual size dimorphism in *Anolis oculatus*. The biometric recording was carried out according to the protocols described in section 2.2.5, of chapter 2. The common garden juveniles were analysed using the same experimental protocols as outlined in section 2.2.5, chapter 2. Similarly, physical and biotic aspects of the environments of the experimental populations were also taken from the previous sexual size dimorphism study.

5.2.4 STATISTICAL ANALYSIS.

An ANOVA was run on squamous character sets, and an ANCOVA on morphometrics, using snout to vent length as the covariate, to test for significance

between populations, and between common garden juveniles and source population adults for each population. The two way analysis tested between the common garden juveniles and the source population adults, and modelled the interaction between common garden juveniles and source population adults with the source ecotype of the population.

A canonical variates analysis (CVA) was then run on both the morphometric character sets and the squamous character sets, for both the common garden juveniles, and the source population adults. This allowed the first canonical variate scores from each analysis to be tested against each other to assess the similarity in patterns of canonical variates, between common garden juveniles and the source population adults.

The first and second canonical variate scores for all character traits under analysis were plotted against each other for both the common garden juveniles and the source population adults. This was done to compare the congruence between the constellations of common garden juvenile and source population adult populations. To test the significance of this relationship, the first and second CV scores for both common garden juveniles and source population adults were transformed using a principal co-ordinates analysis (PCD), and tested against each other using a Mantel matrix correspondence analysis.

Finally, the Mahalonobis distance between common garden juveniles and source population adults were generated using a CVA. These distances are intended to illustrate any trends in plasticity of character traits within a population. The Mahalonobis distance (D) between common garden juveniles and source population

can be tested against the source environmental dissimilarity from the common garden enclosure environment. Environmental dissimilarity matrices are constructed from the environmental data recorded for chapter 3 and 4, entered into a PCD analysis to provide a matrix measure of environmental dissimilarity between sites. The environmental variables are listed in Appendix 5.0. This matrix is then edited to illustrate only the environmental distance between experimental population environments and the common garden environment at Balvine. A comparison would then test for trends in Mahalonobis distance of dissimilarity in biometrics, between source population and common garden population, against environmental dissimilarity from the common garden enclosure site.

5.3 RESULTS.

When the common garden juveniles were collected for the biometric analysis, it was noted that very few male juveniles were still alive. Therefor, only female individuals are considered in the analysis. The colour hue and pattern characters were also dropped from the analysis as many common garden juveniles still possessed the characteristic juvenile markings and colouration. These would not be comparable to the adult source population females used in the comparative analyses.

5.3.1 ANCOVA AND ANOVA RESULTS.

As illustrated in table 5.0, the ANCOVA and ANOVA results yield significant and supporting results. The ANCOVA depicts that a significant difference exists in morphometric body proportions, between population ecotypes when both common garden juveniles and source population adults are considered in the same data set. However, when common garden juveniles are tested against the source population adults, with ecotype specified, no significant difference in morphometrics are observed in any of the seven character traits except for tail depth (even this character trait is not significant if Bonferoni corrected, when $P = 0.0032$).

The ANOVA analysis of squamous character sets provides further significance of difference between ecotype origins, when considering common garden juveniles and source population adults in the same data set. When common garden juveniles are

Table 5.0

Table 5.0 illustrates the morphometric body proportion ANCOVA (snout to vent length co-variate) and squamation ANOVA results, clearly showing the significant difference in the biometrics between each population, and the insignificant difference between the common garden juveniles (C.G. juv.), and the source population adults regarding both morphometrics and squamous character traits, within each ecotype population.

Common Garden Experiment ANCOVA of Morphometrics				
Character	ANCOVA test	F-statistic	DF	P value
Upper leg length	Population ecotype	9.52	8, 254	0.0000
Lower leg length	Population ecotype	17.87	8, 254	0.0000
Toe length	Population ecotype	7.42	8, 254	0.0000
Toe width	Population ecotype	6.43	8, 254	0.0000
Tail depth	Population ecotype	14.47	8, 254	0.0000
Head width	Population ecotype	4.77	8, 254	0.0000
Head length	Population ecotype	4.65	8, 254	0.0000
Upper leg length	C.G. juv. / source pop.	0.90	1, 254	0.3445
Lower leg length	C.G. juv. / source pop.	0.60	1, 254	0.4379
Toe length	C.G. juv. / source pop.	2.32	1, 254	0.1287
Toe width	C.G. juv. / source pop.	0.64	1, 254	0.4234
Tail depth	C.G. juv. / source pop.	8.36	1, 254	0.0042
Head width	C.G. juv. / source pop.	0.48	1, 254	0.4902
Head length	C.G. juv. / source pop.	0.33	1, 254	0.5678
Common Garden Experiment ANOVA of Squamation				
Character	ANOVA test	F-statistic	DF	P value
Around body scale count	Population ecotype	2.56	8, 254	0.0106
Lamella scales	Population ecotype	2.52	8, 254	0.0118
Scale size index	Population ecotype	6.02	8, 254	0.0000
Ventral scale count	Population ecotype	22.24	8, 254	0.0000
Around body scale count	C.G. juv. / source pop.	0.15	1, 254	0.6956
Lamella scales	C.G. juv. / source pop.	0.08	1, 254	0.7788
Scale size index	C.G. juv. / source pop.	0.66	1, 254	0.4184
Ventral scale count	C.G. juv. / source pop.	0.44	1, 254	0.5065

compared against the source population adults in their squamous character sets, no significant differences are detected.

5.3.2 CANONICAL VARIATES ANALYSES.

The CVA analyses were carried out separately for both the morphometrics and the squamous character sets of the experimental populations.

The first two CV scores for all biometric characters, except tail depth, were tested for the similarity of the CV constellations. This provided a significant similarity through a Mantel matrix test with a correlation coefficient of 0.58, and a probability of P = 0.005. The constellations of CV1 and CV2 for both common garden juveniles and source population adults are illustrated in figure 5.3.

5.3.3 ENVIRONMENTAL DISSIMILARITY.

Finally, using the Mahalonobis distance (D) between common garden juveniles and source population adults, the populations are tested against the source environmental dissimilarity matrices, and yields the insignificant regression coefficient r = 0.0044, p = 0.877. This is illustrated in figure 5.4.

Figure 5.3

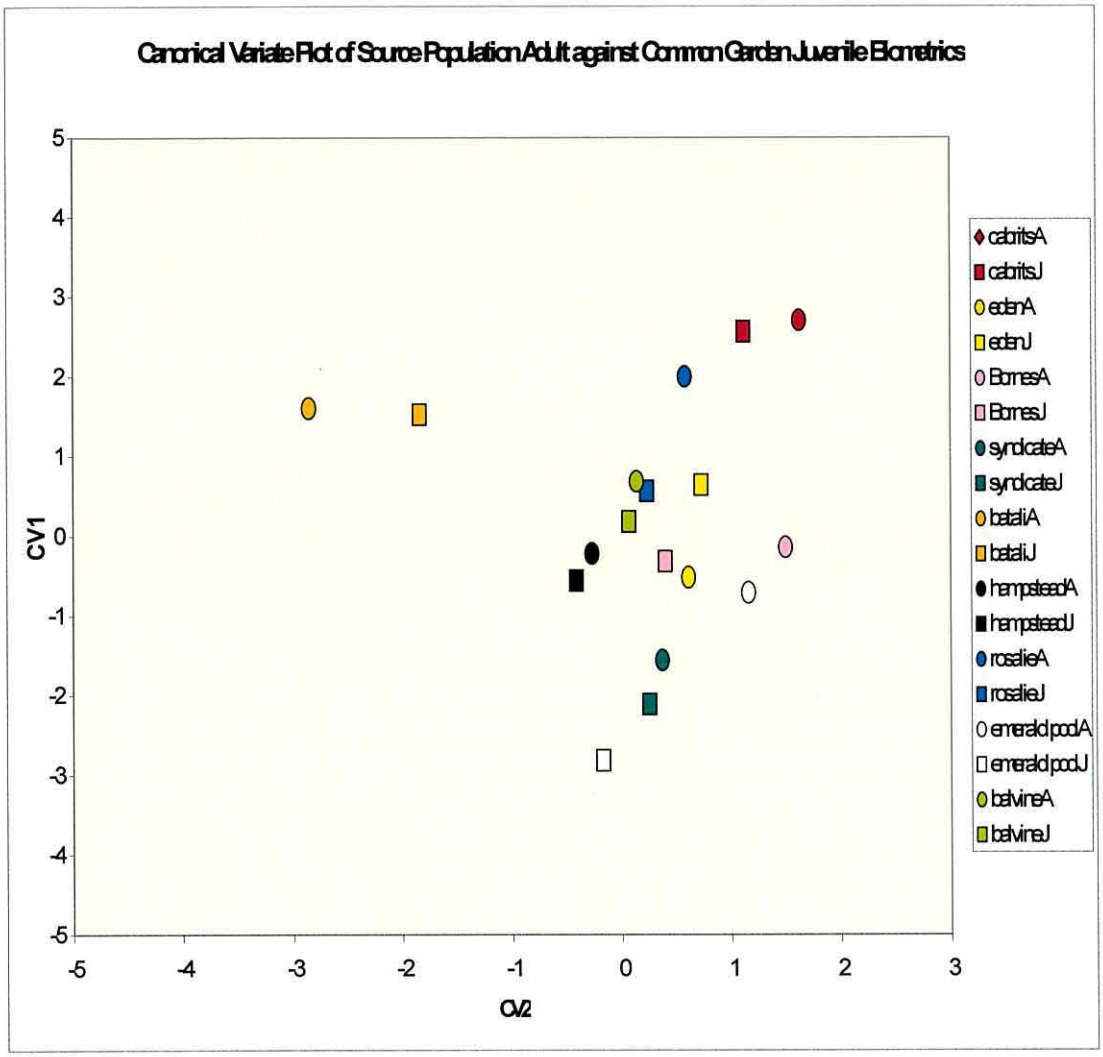


Figure 5.3 illustrates the close relationship of the first two canonical variate scores of biometrics between the common garden juvenile populations and the source population adults. This is supported by a mantel matrix correspondence analysis which produced the significant correlation coefficient of 0.58, (P = 0.0055), for the common garden juvenile CV1 and CV2, against the source population CV1 and CV2, for biometric characters.

Figure 5.4

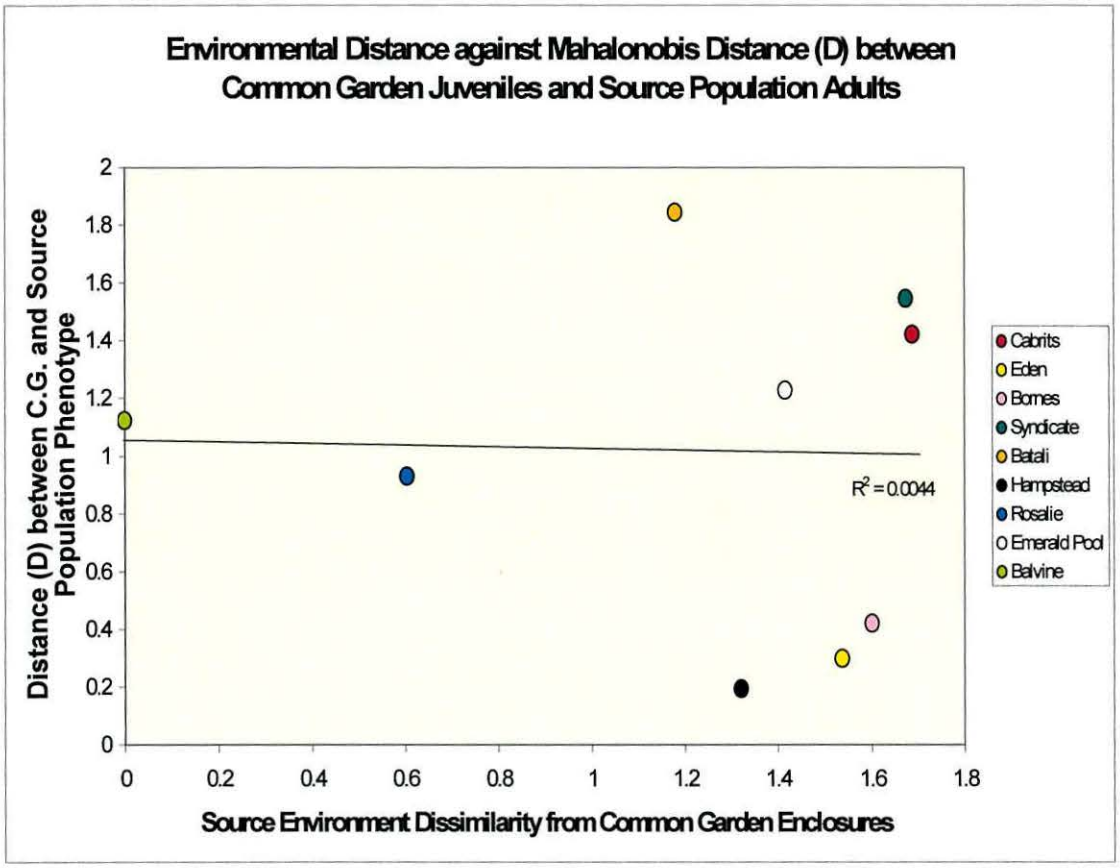


Figure 5.4 illustrates the dissimilarity in phenotype between common garden juveniles and source population adults against the environmental dissimilarity of the experimental populations from the common garden enclosure site ecotype (Balvine). This yielded the insignificant regression coefficient of $R^2 = 0.0044$, $P = 0.877$.

5.4 CONCLUSIONS AND DISCUSSION.

5.4.1 ANCOVA AND ANOVA.

The ANOVA and ANCOVA results (table 5.0), suggests that the biometrics of the common garden juveniles, with the exception of the tail depth character trait, are not significantly effected in phenotype, by the shift in environment, to the point that they remain statistically indistinguishable from the source adult population. It is likely that the reason for significant difference in tail depth is that this character trait is subject to long term ontogenetic development. The tail is a fat storage area in Squamata (Pough et al 1998). In the sub-adult common garden individuals, this character trait would not be as developed as in the adult source population.

However, the populations remain distinct from one another when the common garden juveniles and source adults are pooled into the same data set. This provides further indication that the common garden juvenile biometrics have not been significantly influenced by environmentally induced, developmental phenotypic plasticity.

5.4.2 CANONICAL VARIATE ANALYSIS.

To test all biometric characters, both squamous and body proportions, the first and second CV scores generated from the combined data set, were tested for similarity between both common garden juveniles and source population adults. The Mantel matrix correspondence analysis generated a correlation coefficient of 0.58 ($P = 0.0055$, figure 5.3), which clearly illustrates that even with a data set comparing both

squamous and body proportion characters, the common garden juvenile biometrics have not deviated significantly from the source population biometric profile. As already stated, if the common garden juveniles had been allowed to grow for a further few months, then it could be anticipated that their body proportions would have developed to further resemble those of their source population.

5.4.3 ENVIRONMENTAL DISSIMILARITY.

Despite the suggestion that the body proportions of the common garden juveniles are under developed and thus do not compare well to the source population adults, it is feasible that the incongruence is the result of phenotypic plasticity. However, if this was the case, one would anticipate that the deviance in phenotypes between common garden juveniles and source population adults, would increase with increasing environmental dissimilarity of source habitat with that of the common garden experiment. To test this possibility, the difference in biometrics of common garden juveniles from the source population adults, the Mahalonobis distance (D) was tested against environmental dissimilarity from Balvine. Considering both squamous and morphometric body proportions in the same data set, a lack of any significant trend in the difference between common garden juvenile, and source population phenotype is recorded (R^2 = 0.0044, P = 0.877, figure 5.4). This indicates that there is no detectable influence of the shift in environment on the common garden juvenile phenotypes, and supports the previous suggestion that the reason for a lack of congruence between common garden juvenile and adult body proportions is a lack of ontogenetic development.

HYPOTHESIS TESTING.

In section 5.1.5 the null hypothesis stated, 'Environmentally induced phenotypic plasticity is not primarily responsible for the character traits recorded in the experimental *Anolis oculatus* individuals.' The results, and conclusions of this study mean that the null hypothesis cannot be disproved.

5.4.5 DISCUSSION.

The results of this study offer some evidence that phenotypic plasticity is not a significant factor in effecting the state of the phenotypic character traits in *Anolis oculatus*, when translocated to a different environment. However, although several key biometric traits have been tested in this experiment, one must remember the vast array of potential traits on which phenotypic plasticity may be acting (Qualls and Shine 1998).

As vanTienderen (1997) points out, the concepts and study of phenotypic plasticity is subject to several interpretations, of both the mechanisms and function of phenotypic plasticity. However, this study has taken a purely comparative approach to test for a divergence in the phenotype of the common garden juveniles, away from that of the source population adults (Sorci et al 1996; Jockusch 1997). By testing for an environmental trend in the difference between common garden and source populations, any environmentally induced plasticity would likely have been detected if any of the characters under analysis had been plastic.

The results may have been more conclusive had the experiment been run for a further four to six months, as this would have permitted the common garden juvenile anoles to have achieved an adult morphology, which would have allowed for a better comparison of body proportions between experimental groups. Once adult, colour pattern, and hue would also have been incorporated into the character set, broadening the range of testable character traits. Another limiting factor in the interpretation of the results of the experiment is that only female specimens have been analysed. This is the result of a high mortality in common garden juvenile males in the enclosure. It is suggested that this may be the result of increasing male-male aggression developing as the specimens matured and began to establish and defend territories within the enclosure. Therefor it is suggested that several smaller enclosures, where less inter-male contact is possible, would improve survival.

It is also plausible that the constraining effects of un-naturally high density in the common garden juveniles may influence plasticity.

A final suggested improvement to the experimental testing for phenotypic plasticity is to biometrically analyse the maternal individuals and maintain a record of common garden juvenile parent-offspring relationships so that a direct test of related individuals could be achieved. This was a possible option in the original experimental design of this study, but achieving a sufficient sample size proved problematic in the time frame allowed.

This study has shown that phenotypic plasticity has not been proven to exist in the development of *Anolis oculatus* in a translocated environment, significantly different, in many of the experimental populations, from their source habitats.

CHAPTER 6:

GENERAL DISCUSSION.

Sunrise over the rainforest canopy of Bense Ridge.

6.0 GENERAL DISCUSSION.

The immediate conclusions and discussion of each chapter's findings have all ready been discussed in the text. This chapter, however, will attempt to draw together the results and consider their interrelationships and wider implications to the study of natural selection and evolutionary ecology.

6.1 EVOLUTIONARY ECOLOGY.

This thesis encompasses a broad range of topics relating to the testing of natural selection and evolutionary ecology. Biometric geographic variation, ethology, autecology, phylogenetic history, phenotypic plasticity, biotic and environmental parameters, and thermoregulation have all been considered in relation to the biology of *Anolis oculatus*. This has been a deliberate attempt to deal with the ecological investigation in a more holistic manner. Modern biological science is now capable if the most detailed and intricate study of chemical physiology (Wainwright et al 1996), the phylogenetic history of populations (Felsenstein 1982), and the quantification of ecological process (Daltry et al 1996). Whilst such studies are essential to furthering our knowledge of the complexity of nature, their fashionable status within science means that, in general, scientific studies are becoming progressively more specific. The more fundamental studies of natural history are now less well represented in the literature.

However, a fundamental understanding of a species ecological mandate, together with ethology, is essential if attempting to bring relevance to investigations of biometric

geographic variation or phylogeny (Greene 1983). This study has been fortunate to rest on a base of extensive research into the geographic variation in phenotype and genotype (Malhotra and Thorpe 1991, 1991b, 1997, 1999) of *Anolis oculatus,* across the island of Dominica. Without such a foundation of knowledge the specific nature of the experiments in this study would have been difficult to theoretically conceive and logistically conduct. Broad ecological studies deal with a near infinite array of possible variables to record and test. Therefor a research foundation of productive character traits and experimental parameters, already tested and proven to influence the model being tested, provides an excellent basis for further field research into evolutionary ecology.

6.2 INTEGRATING AN UNDERSTANDING OF NATURAL SELECTION.

Natural selection can be tested for using a wide range of analytical techniques (Endler 1985), from basic field observation to complex translocation experiments. As stated in the general introduction, correlating observed patterns of biometric and environmental variation has been the most common and classical of the techniques used to elucidate the processes of natural selection. However, in many earlier studies, sample sizes have been particularly large per site, but the number of sites sampled inadequate to detect more subtle aspects of morphometric adaptation to the environment. Such low numbers of sample locations often resulted in false positive results due to random chance of sampling over a species' range (Endler 1985). Thus, in more recent years, researchers have increased sampling frequencies over the

studied range of a species. The results have shown geographically complex and environmentally coherent variation in the traits under analysis (Endler 1985; Thorpe et al 1994). Such intensive sampling techniques have yielded a variety of successful studies engaging the complex ecology of a species with observed patterns of geographic variation. Endler (1980), in his study of guppy, *Poecilia reticulata*, illustrated responses in colouration and behaviour to stream substrates, predation regimes and geographic isolation. Intricate studies of geographic variation in Squamata, were later carried out by Thorpe and Brown (1991), and in *Anolis oculatus* by Malhotra and Thorpe (1997; 1997b). The latter two studies formed the firm basis for the formulation of the experiments in this study. However, Endler (1985), states that evidence of natural selection remains only speculative, even in studies over well sampled large geographic areas, which show strong correlation between biometrics, and ecological-environmental factors.

Analysing the geographic variation in more than one species, occurring sympatrically over a given range, may also aid the clarification of natural selection processes occurring over large areas. Such studies have shown strong parallels in patterns of geographic variation. Such a situation is tested in the Squamata of Tenerife. *Gallotia gallotia*, (Thorpe and Brown 1989), in *Tarentola delallandii* (Thorpe 1991), and in *Chalcides viridanus* (Brown et al 1993). All exhibit similar patterns of latitudinal micro-geographic variation in a variety of biometric character traits. However, due to the common history of volcanic activity on such island models as Tenerife, it is difficult to distinguish between the effects of phylogenetic history and the processes of ecogenesis shaping the extant geographic variation in character traits (Thorpe and Malhotra 1991).

In replicating such studies of geographic variation with the use of parallel species in different, but similarly quantifiable environments, assumptions of natural selection are given greater strength. This technique is especially strong when considering island archipelagos (Grant 1998). Where such archipelagos have independent geological histories and have never been connected, but are similar in their ecological zonation and colonisation events, they represent a valuable method of observing parallel patterns of ecogenesis (Endler 1985). Where this is observed it represents a strong argument for natural selection (Thorpe and Malhotra 1996).

This is the case with the *Anolis* species of the Lesser Antilles. Both Dominica and Basse Terre of Guadeloupe possess a single endemic anole. They occur in all habitat types, which are also similarly represented on both the islands. Malhotra, Thorpe (1991), Malhotra (1992) illustrated how *Anolis oculatus*, and *Anolis marmoratus* demonstrate congruent patterns of variation in several character traits in similar environments on the two islands. This result gives considerable credence to the assumption that such observed biometric variation in the anoles is due, to some extent, to environmental natural selection.

Even with the use of phylogenetically independent contrasts (Felsenstein 1985), to remove the effects of phylogenetic history, observed patterns of geographic variation remain only a suggestive indication of natural selection. A manipulative approach is required to begin to truly quantify the suggested processes of natural selection. The natural selection experiments in this study are designed to observe both natural (in control populations), and artificially induced, (in translocated populations), selection

events. Thus, the natural selection being tested for is short term in the translocated populations, but considerable in its effects on character trait means. Where as the natural selection observed in the control populations is considerably less than that observed in the montane populations, and is likely a reflection of seasonal shifts in selection regimes. The observed rapid response in translocate phenotype to a shift in environment and ecology, as illustrated and explained in chapters two and three, is proposed as natural selection, resulting in mortality, and largely environmentally induced, and not an effect of environmentally induced phenotypic plasticity (as discussed in chapter five). The results give further support to the findings of Malhotra and Thorpe (1991), who also translocated *Anolis oculatus* populations into xeric woodland enclosures. Their studies and the results of the first three experiments of this study illustrate the startling speed at which selection intensity is able to shift phenotypic means within a population exposed to a selection event.

However, it must be remembered that the results of specific studies of natural selection, are given significant support by the study of geographic variation within the subject species (Endler 1985). Selection event studies without consideration of the geographic variation exhibited by a species will be limited in their use, when interpreting shifts in character trait means. This is not to say that the results of a selection event need to fit within the framework of existing patterns of phenotypic variation within a species (Wright 1935). The direction of selection in a trait may move towards a local ecological optima other than any previously occupied by the species. Continuing selection pressures may also take a population through a variety of phenotypic optima before stabilising. This may be suggested to have occurred in the translocated montane anoles in the first two experiments of this study. Selection

coefficients indicate that larger individuals were selected for by the translocation event. However, the native populations at the translocation enclosure are significantly smaller in snout to vent length than the translocates. One may speculate that immediate thermal selection pressures selected for larger males due to their more robust thermal capacity (Tosini and Avery 1993). It may also be that larger individuals were able to compete better for prime territories, enhancing their chances of survival. In the longer term the population may move towards a smaller body size in response to more subtle ecological influences, such as diet, and predation.

Such short term studies of natural selection sit well with studies such as Losos et al, (1997), where introduced anoles were phenotypically monitored before and during an introduction event over a ten to fourteen year period. Such studies emphasis the long-term changes in phenotype, which drive towards the development of the optimum and stable phenotype within the given environment. This lends support to the fact that short term selection as observed in this study is likely to ultimately lead to an altered phenotype in the population exposed to the selection event. From such studies rates of evolutionary change are calculated. However these rates of change are calculated from long term data It is suggested that short term experiments such as in this study, depict natural selection as occurring very rapidly indeed, (in some instances quantifiable within two weeks of a selection event).

An observed shift in phenotype from a selection event occurs according to a variety of influences. Genetic bottlenecking and drift may result if the population is small or mis-representative of the source population gene pool. However, specific and directional selection will also result from the shift in environment, (both physical and

biotic), and ecology. It is suggested that it is this type of evolutionary change, which is likely to follow the influences of drift and bottlenecking in colonisation events, such as those experienced by anoles in the Lesser Antilles (Losos 1996; Roughgarden 1995). Following such events ecological and environmental parameters are likely to be responsible for specific adaptations that accumulate and which ultimately may lead to the evolution of a new species. Thus, following the patterns of biology, including the ethology and ecology of a species, such as sexual size dimorphism (as tested and discussed in chapter four), over a selection event, would likely prove most instructive as an explanation of the more intricate aspects evolutionary ecology.

The study of sexual size dimorphism in this thesis, emphasises the need to consider each model species individually and to refrain from making genus wide assumptions about ecological interactions. Andrews and Stamps (1994), and Perry (1996), all carried out research that suggests that diet selection is an insignificant influence on sexual size dimorphism in the genus *Anolis*, although experimental techniques are unclear. However, the results of the study in this thesis illustrate that although the primary factor linked to patterns of sexual size dimorphism is male display behaviour, indicating sexual selection, the next most significantly linked factor is diet selection. This is an example of how the ecology of each species must be considered on its own merits.

With some understanding of the role of phenotypic plasticity investigations into the processes of natural selection gain substantiation . The experiment conducted in this study to test for environmentally induced developmental phenotypic plasticity, detected no clear signs of plasticity in any of the traits analysed. However, as stated

in the discussion of chapter five, some caution is required in interpreting the results due to the juvenile nature of the common garden population. In addition conclusive detection of phenotypic plasticity is not an easy process. Qualls and Shine (1998) conducted extensive analysis of reciprocal incubation temperature regimes on incubation period, physical performance, and biometrics in *Lampropholis* skinks. Their results attempt to differentiate between the variance observed in the source populations and the variance attributed to the experimental incubation treatment. This is the issue of testing for environmentally induced phenotypic plasticity: to differentiate between genetically controlled variation which is observed naturally in the population and that which is plastic. Qualls and Shine also state that 'ignoring the effects induced by the local environment (i.e. nest conditions) on the embryo could lead to significant error in the interpretation of experimental results.' The experiment in this study has combated this factor by beginning the experimental treatment prior to oviposition, by translocating the gravid females to the common garden enclosure site. Thus, no greater control can be taken to prevent pre-hatching 'trait fixing' without unduly effecting the environment of the parental stock. In the study of Qualls and Shine (1998), even traits shown to exhibit developmental plasticity also exhibited considerable trait variation attributable to their source population.

In conclusion, the experimental studies of this thesis reinforce the evidence that environment plays a significant role in the processes of natural selection. In addition, close analysis of species ecology reveals intimate patterns of interrelationships between environment, ecology and adaptation in the species. Finally, a provisional assessment of the role of phenotypic plasticity within the character traits used in these

experiments, suggests that observed micro-geographic variation in *Anolis oculatus* is not significantly influenced by environmentally induced phenotypic plasticity.

BIBLIOGRAPHY.

A view of barrel sponges, surrounded by shoals of blue and brown *Chromis* fish, on one of the coral walls that occur within the coastal waters of Dominica.

BIBLIOGRAPHY.

Abell, A.J. 1998. Phenotypic correlates of male survivorship and reproductive success in the striped plateau lizard, *Sceloporus virgatus*. *Herp. J. Vol.8, No.4*: 173-180.

Ambrose, S.H. 1998. Late Pleistocene human population bottlenecks, volcanic winter, and differentiation of modern humans. – *J. Human Evol. 34:* 623-651.

Anderson, C.A. 1986. Predation and primate evolution. – *Primates 27*: 15-39.

Andrews, R.M. 1976 Growth rates in island and mainland anoline lizards. – *Copeia 1976:* 477-482.

Andrews, R.M. 1979 Evolution of life histories: a comparison of *Anolis* lizards from matched island and mainland habitats. – *Brevoria 454:* 1-51.

Appleton, R.D. and Palmer, A.R. 1988. Water borne stimuli released by predatory crabs and damaged prey induce more predatory resistant shells in a marine gastropod. – *Proc. Nat. Acad. Sci. USA, 85:* 4387-4391.

Arnold, S.J. and Wade, M.J. 1984 On the measurement of natural and sexual selection: theory. – *Evolution, 38:* 709-719

Ayre, D.J. 1985. Localised adaptation of clones of the sea anemone *Actinia tenebrosa* – *Evolution 39:* 1250-1260.

Avery, R.A. 1982. Field studies of body temperatures and thermoregulation. In *Biology of the Reptilia. Vol.12* (eds. Gans and Pough) pp93-146. Academic Press, London.

Bagnara, J.T. and Hadley, M.E. 1973. *Chromatophores and colour change*. Prentice –Hall

Barnett, A. 1997. Hot lizard shows its true colours. – *New Scientist, 153:* 19

Bauwens, D., Garland, T. jr., Castilla, A.M. and VanDamme, R. 1995 Evolution of sprint speed in a lacertid lizard: morphological, physiological, and behavioural covariation. – *Evolution 49:* 848-863.

Beard, J.S. 1948 *The natural vegetation of the Windward and Leeward islands.* Clarendon Press Ox.

Begon 1979 from: *Ecology-Techniques and Analysis*. Camb. Press. Masse.

Behera, H., and Nanjundiah, V. 1995 An investigation into the role of phenotypic plasticity in evolution. – *J. Theoretical Biol. 172:* 225-234.

Bell, G. 1991 The ecology and genetics of fitness in *Chlamydomonas*. III. Genotype by environment interaction within strains. – *Evolution 45*: 668-679

Bennett, A.F. 1987. Inter-individual variability: an underutilized resource. In *New Directions in Ecological Physiology* (Editors: Feder, Bennett, Burggren and Huey), p147-169. Cambridge Uni. Press

Blomqvist, D., Johansson, O.C., Unger, U., Larsson,M. and Flodin, L.A. 1997. Male aerial display and reversed sexual size dimorphism in the dunlin. – *Anim. Behav. 54*: 1291-1299.

Bloxam, Q.M.C. 1982. The feasibility of reintroduction of captive bred Round Island skink *Leiolopisma telfairii* to Gunner's Quion. – *Dodo, J. Jersey Wildl. Preserv. Trust. 19:* 37-41.

Bradshaw, A.D. 1965 Evolutionary significance of phenotypic plasticity in plants. – *Advances in Genetics, 13:* 115-155.

Brodie, E.D.III, Moore, A.J. and Janzen, F.J. 1995 Visualising and quantifying natural selection. – *Trends in Ecology and Evolution. 10:* 313-318.

Brooks,G.R. 1968. Body temperatures of three lizards from Dominica, West Indies. – *Herpetologica 24:* 209-214.

Brown, R.P., and Thorpe, R.S. 1991. Within island microgeographic variation in body dimensions and scalation of the skink, *Chalcides sexlineatus*; pattern and cause. – *J. Evol. Biol. 4:* 557-574.

Brown, R.P., Thorpe, R.S. and Baez, M. 1991 Lizards on neighbouring islands show parallel within island micro-evolution. – *Nature, 352:* 60-62.

Bull, J.J. 1987 Evolution of phenotypic variance. – *Evolution, 41*: 303-315.

Bullock, D.J., Jury, H.M. and Evans 1993. Foraging ecology in the lizard, *Anolis oculatus* (Iguandidae) from Dominica, West Indies – *J. Zoo. 230*: 19-30.

Bulmer, M.G. 1980 *The mathematical theory of quantitative genetics*. – Oxford Uni. Press.

Burke, R. L. 1991. Relocations, repatriations and translocations of amphibians and reptiles: taking a broader view. – *Herpetologica 47:* 350-363.

Campbell, A. 1983. *The designer's handbook*. –QED Publishing, London.

Carlier, P. and Lefebvre, L. 1996. Differences in individual learning between group foraging and territorial Zenaida doves. – *Behaviour 133:* 1197-1207.

Carr, M.J. and Stoiber, R.E. 1990 Volcanism. - *The Geology of North America. Vol. H. Geol. Soc. Amer.*

Case, S.M. 1990. Dewlap and other variation in the lizards *Anolis distichus* and *Anolis breviorstris* (Reptilia: Iguanidae) – *Biol. J. Linn. Soc. 40:* 373-393.

Censky E.J. 1995. Mating stratergy and reproductive success in the Teiid lizard, *Ameiva plei.- Behaviour 132:* 529-557.

Cheveraud, J.M.,Dow, M.L. and Leutenegger, W. 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight amongst primates. – *Evolution 39*: 1335-1351.

Christian, K.A., Bedfors, G.S. and Shannahan, S.T. 1996 Solar absorbency of some Australian lizards and its relationship to temperature. – *Australian J. Zoo. 44:* 59-67.

Cordell, S., Goldstein, G., MullerDombios, D., Webb, D., and Vitousek, P.M. 1998 Pysiological and morphological variation in *Metrosideros polymorpha*, a dominant Hawaiian tree species, along an altitudinal gradient: the role of phenotypic plasticity. – *Oecologica, 113*: 188-196.

Coyne, J.A. Barton, N.H. and Turelli, M. 1997. Perspective; A critique of Seawall Wright's shifting balance theory of evolution. – *Evolution 51:* 643-671.

Coyne, J.A. and Orr, H.A. 1998 The evolutionary genetics of speciation – *Phil. Trans. Roy. Soc. Lond. 353:* 287-305.

Cracraft, J 1990. *Speciation and its ontogeny.* In Speciation and its consequences (eds. Otte, and Endler) pp28-59. Sinaur, Massachusetts.

Cunningham, C.W., Omland, K.E. and Oakley, T.H. 1998. Reconstructing ancestral animal states: a critical appraisal. – *TREE 13:* 361-366.

Darwin, C. 1871 (reprint 1874) *The decent of man, and selection in relation to sex.* Murray; London.

Daltry, J., Wuster, W. and Thorpe, R.S. 1996. Diet and snake venom evolution. – *Nature, 379:537-540.*

Day, T. and Schulter, D. 1995. The fitness of hybrids. - *Trends Ecol. Evol. 10:* 288.

Diaz, J.A., Bauwens, D., and Asensio, B. 1996 A comparative study of the relation between heating rates and ambient temperatures in lacertid lizards. – *Phys. Zoo. 69:* 1359-1383.

Dixon, W.J. (Ed.) 1992. *BMDP statistical software manual.* –Vol.1. University of California Press.

Dodd, C.K. and Seigel, R.A. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: are they conservation strategies that work? - *Herpetologica, 47:* 336-350.

Downhower, J.F., Bulmer, L.S. and Brown, L. 1987. Opportunity for selection: an appropriate measure for evaluating variation in the potential for selection? – *Evolution 41:* 1395-1400.

Edwards, M. and Dunn, D. 1991 *The forests of Dominica Ed. A. James,* Environmental Education Unit, Dominica.

Endler, J.A. 1977. *Geographic variation, speciation and clines.* Princeton Uni. Press.

Endler, J.A. 1980. Natural selection in colour patterns in *Poecilia reticulata.* – *Evolution,* 34: 76-91.

Endler, J.A. 1985. *Natural selection in the wild.* Princeton Uni. Press, Princeton, NJ.

Endler, J.A. 1991 Variation in the appearance of guppy colour patterns to guppies and their predators under different visual conditions. *Vision res 31*: 587-648.

Fairbairn, D. and Preziosi, R.F. 1994. Sexual selection and the evolution of allometry for sexual size dimorphism in the water strider, *Aquarius remigis.* – *Am. Nat. 144*: 101-118.

Felsenstein, J. 1982. How can we infer geography and history from gene frequencies? – *J. Theor. Biol. 96:* 9-20.

Felsenstein, J. 1985. Pylogenies and the comparative method. – *Am. Nat. 125*: 1-15.

Fleming, T.H. and Hooker, R.S. 1975 *Anolis cupreus*: the response of a lizard to tropical seasonality. – *Ecology 56:* 1243-1261.

Forsman, A. 1991. Variation in sexual size dimorphism and maximum body size among adder populations – effect of prey size. *J. Animal Ecology Vol.60, No.1*: 253-267.

Forsman, A. and Shine, R. 1995 The adaptive significance of colour pattern polymorphism in the Australian Scincid *lizard Lampropholis delicata.* – *Bio. J. Linn. Soc. Lond. 55:* 273-291

Foster, S.A.; Scott,R.J. and Williams, A.C. 1998 Nested biological variation and speciation. – *Phil. Trans. Roy. Soc. Lond. 353:* 207-218.

Futuyma, D.J. 1986. *Evolutionary Biology.* Second edition, Sinaur, Massachusetts.

Garland, T., jr., Harvey, P.A. and Ives, A.R. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrast. – *Sys. Bio. 41*: 18-32.

Gianassi, N.C. 1997. Molecular, morphological and behavioural variation of the *Anolis roquet* species group. *Ph.D. thesis University of Wales, Bangor.*

Gibbs, P.E. 1993 Phenotypic changes in the progeny of *Nucella lapillus* transplanted from an exposed shore to a sheltered inlet. – *J. Moll. Stud. 59:* 187-194.

Grant, P.R. 1998. *Evolution on islands* Oxford University press

Grant, B.R. and Grant, P.R. 1993 Evolution of Darwin's finches caused by a rare climatic event. – *Proc. R. Soc. Lond. 251:* 111-117.

Gray, D.A. and Cade, W.H. 1999. Sex, death and genetic variation: natural and sexual selection on cricket song. – *Proc. R. Soc. Lond. 266:* 707-709.

Greene, H.W. 1983 Dietary correlates of the origin and radiation of snakes. – *Amer. Zool. 23:* 431-441.

Griffiths, B., Scott, J.M., Carpenter, J.W. and Reed, C. 1989. Translocation as a species conservation tool: Status and stratergy. – *Science, 245:* 477-480.

Haily, A., and Coulson, I.M. 1996 Temperature and the tropical tortoise *Kinixys spekii*: tests of thermoregulation. – *J. Zoo. Lond. 240:* 537-549.

Halkka, O., Halkka, I. And Raatikainen, M. 1975 Transfer of individuals as a means of investigating natural selection in operation. *Hereditas 80*: 27-34.

Harvey, P.H., and Pagel, M.D. 1991. *The comparative method in evolutionary biology*. Oxford Uni. Press.

Hedrick, P.W. 1986. Genetic polymorphism in heterogeneous environments: a decade later. – *Ann. Rev. Ecol. Syst. 17:* 535-566.

Hertz, P.E., Huey, R.B. and Stevenson, R.D. 1993 Evaluating temperature regulation by field-active ecotherms: the fallacy of the

Hughs, D.J. 1992 Genotype-environment interactions and relative clonal fitness in a marine bryozoan. – *J. Anim. Ecol. 61*: 291-306.

Hodge, W.H. 1943 The vegetation of Dominica – *The Geographical Review, 33:* 349-375.

Hoffmann, R.J. 1981 Evolutionary genetics of *Metridium senile*. I. Kinetic differences in the phosphoglucos isomerase allozyme. *Biochem. Gen. 19:* 129-144.

Holopainen, I.J.J., Aho, M., Vornanen, H., and Huuskonen, H. 1997 Phenotypic plasticity and predator effect on morphology and physiology of crucian carp in nature and in the laboratory. – *J. Fish Biol. 50:* 781-798.

Janson, K. 1983. Selection and migration in two distinct phenotypes of *Littorina saxatilis* in Sweden, - *Oecologica, 59:* 58-61.

Jenssen, T.A. 1970. Female response to filmed displays of *Anolis nebulosa* (Sauria: Iguanidae) – *Anim. Behav. 18:* 640-647.

Jenssen, T.A. and Gladson, N.L. 1984. A comparative display analysis of the *Anolis websteri* and *Anolis caudalis* in Hiati. –*J. Herpetology 18*:217-230.

Johannesson, K., Kautsky, N. and Tedengren, M. 1990. Genotypic and phenotypic differences between Baltic and North Sea populations of *Mytilus edulis* evaluated through reciprocal transplantation. II. Genetic variation. *Marine Eco. 59*: 211-219.

Johnstone, R.A. 1997. *The evolution of animal signals*. P155-178 *in* Krebs and Davies; Behavioural Ecology. 4th edition. Blackwell Sci. Press Oxford

Johnston, R.F. and James, F.C. 1981. Over winter mortality and sexual size dimorphism in the house sparrow. – *Auk, 98:* 503-511.

Johnston, R.F., and Sealander, R.K. 1971 Evolution in the house sparrow,II. Adaptive differentiation in North American populations. – *Evolution 28:* 1-28.

Jockusch, E.L. 1997 Geographic variation and phenotypic plasticity of a number of trunk vertebrae in slender salamanders, *Batrachoseps* (Caudata: Plethodontidae) – *Evolution, 51:* 1966-1982.

Katsikaros, K.and Shine, R. 1997. Sexual dimorphism in the tusked frog, *Adelotus brevis* (Anura: Myobatrachidae): the roles of natural and sexual selection. – *Bio. J. Linn. Soc. 60*; 39-51.

Korn, E.L. and Graubard, B.I. 1990. Simultaneous testing of regression coefficients with complex survey data – use of Bonferroni statistics. – *Am. Statistician, 44*: 270-276.

Lack, D. 1954. *The natural regulation of animal numbers*. Oxford: Clarendon Press.

Lande, R. 1975 Natural selection and randon genetic drift in phenotypic evolution. – *Evolution 30:* 314-334.

Lande, R. 1979. Quantitative genetic analysis of multivariate evolution applied to brain:body size allometry. – *Evolution 33*: 402-416.

Lande, R. and Arnold, S.J. 1983 Measuring selection on correlated characters. – *Evolution 37:* 1210-1226.

Lande, R. 1995 Mutation and Conservation. –*Conservation Biol. 9:* 782-791.

Lang, D.M. 1967. *Soil and land use surveys, No.21, Dominica*. University of the West Indies, Trinidad.

Langley, R. 1970 *Practical statistics*. – Pan Books Ltd., London

Lawler, S.H., Sussman, R.W. and Taylor, L.L. 1995 Mitochondrial-DNA of the Mauritian macaque (*Macaca fascicularis*) – an example of founder effect. – *Amer. J. Physical Anthropology, 96:* 133-141.

Lecompte, O., Madec, L., and Daguzan, J. 1998 Temperature and phenotypic plasticity in the shell colour and banding of the land snail *Helix aspersa.* – *Comptes Rendus de L Academie des Science Seire. 321:* 649-654.

Lennington, S. 1980. Female choise and polygyny in the redwinged black bird. *Anim. Behav. 28:* 347-361.

Losos, J.B. 1990. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards:an evolutionary analysis. – *Ecological Mon. 60:* 369-388.

Losos J.B. 1994. An approach to the analysis of comparative data when a phylogeny is unavailable or incomplete. – *Sys. Zoo. 43*: 117-123.

Losos, J.B. 1995. Community evolution in greater Antillean Anolis lizards: phylogenetic patterns and experimental tests. – *Phil. Trans. R. Soc. Lond., 349:* 69-75.

Losos, J.B. 1996 Ecological and evolutionary determinants of the species area relation in Caribbean anoline lizards. – *Phil. Trans. R. Soc. 351:* 847-853.

Losos, J.B. and De Queiroz, K. 1997. Evolutionary consequences of ecological release in Caribbean *Anolis* lizards. – *Biol. J. Linn. Soc. 61:* 459-483.

Losos, J.B., Irschick, D.J. and Schoener, T.W. 1994 Adaptation and constraint in the evolution of speciation of Bahamian Anolis lizards. – *Evolution 48:* 1786-1798.

Losos, J.B., Warhelt, K.I. and Schoener, T.W. 1997 Adaptive differentiation following experimental island colonisation in *Anolis* lizards. – *Nature 387*: 70-73.

Luiselli, L., Capula, M. and Shine, R. 1997. Food habits, growth rates, and reproductive biology of grass snakes, *Natrix natrix* (Colubridae) in the Italian Alps. – *J. Zoo. 241*: 371-380.

MacArthur, R.H. and Wilson, E.O. 1967. *The theory of Island biogeography* - Princeton Uni. Press

Macedonia, J.M., Evans,C.S. and Losos, J.B. 1994. Male *Anolis* lizards discriminate video recorded conspecific and heterospecific displays – *Anim. Behav. 47:*1220-1223.

Madsen, T. 1983. Growth rates, maturation and sexual size dimorphism in a population of grass snakes, *Natrix natrix*, in southern Sweden. – *Oikos, 40*: 277-282

Maddison, W.P. 1991. Squared change parsimony reconstruction of ancestral states for continuous-valued characters on a phylogenetic tree. – *Sys. Zoo. 40*: 303-314.

Magurran, A.E. 1998 Population differentiation without speciation. – *Phil. Trans. Roy. Soc. Lond. 353:* 275-286.

Malhotra, A. 1992 What causes geographic variation: a case study of *Anolis oculatus*. *Ph.D. thesis. Uni of Aberdeen*

Malhotra, A and Thorpe, R.S. 1991. Experimental detection of rapid evolutionary response in natural lizard populations. – *Nature, 353*: 341-343.

Malhotra, A and Thorpe, R.S. 1991b. Microgeographic variation *in Anolis oculatus*, on the island of Dominica, West Indies. – *J. Evol. Biol. 4:* 321-335.

Malhotra and Thorpe 1992. An experimental field study on a eurytopic anole, *Anolis oculatus*. – *J. Zool. Lond.*

Malhotra and Thorpe 1992b *Anolis oculatus* (Cope) Dominican anole. – *Catalogue of American Amphibians and Reptiles. Soc. Stud. Amphib. Rep*. 540.1-540.4.

Malhotra, A. and Thorpe, R.S. 1997. Size and shape variation in a Lesser Antillean anole, *Anolis oculatus* (Sauria: Iguanidae) in relation to habitat. – *J. Linn. Soc. 60*: 53-72.

Malhotra, A. and Thorpe, R.S. 1997b. Microgeographic variation in scalation of *Anolis oculatus* : A multivariate analysis. – *Herp. 53*: 49-62.

Malhotra, A. and Thorpe, R.S. *in press.* The dynamics of natural selection and vicarience in the Dominican anole: patterns of within-island molecular and morphological divergence. *In Press.*

Manly, B. F. J. 1991 *Randomisation and Monte Carlo methods in biology*. Chapman and Hall, London.

McNamara, J.M. 1998 Phenotypic plasticity in fluctuating environments: consequences of the lack of individual optimisation. – *Behavioural Ecology, 9:* 642-648.

Miles, D.B. and Dunham, A.E. 1993. Historical perspectives in ecology and evolution: the use of phylogenetic comparative analysis. – *Ann. Rev. Eco. Sys. 24*: 587-619.

Mlot, C. 1989. The science of saving endangered species. – *BioSciences 39:* 68-70.

Moore, W.S. and Price, J.T. 1993. Nature of selection in the northern flicker hybrid zone and its implications for speciation theory. *In* R.G. Harrison ed. *Hybrid zones and evolutionary process*. Ox. Uni. Press.

Morris, A.E.L.I., Taner, I., Meyerhoff, H.A. and Meyerhoff, A.A. 1990 Tectonic evolution of the Caribbean region. – *The Geology of North America. Vol. H. Geol. Soc. Amer.*

Orr, M.R. and Smith, T.B. 1998. Ecology and speciation. – *Trends in Ecol. Evol. 13:* 502-506.

Pagel, M.D. 1992. A method for the analysis of comparative data. - *J. Theo. Bio. 156:* 431-442.

Palmer, A.R. 1990 Effect of crab effluent and sent of damaged conspecifers on feeding, growth, and shell morphology of the atlantic dogwelk, *Nucella lapillus (L.) Hydrobiologica, 193;* 155-182.

Pearson, K. 1903. Mathematical contribution to the theory of evolution. XI On the influence of natural selection on variability and correlation of organs. – *Phil. Trans. Roy. Soc. Lond. 200:* 1-66.

Perry, G. 1996. The evolution of sexual dimorphism in the lizard *Anolis polylepis* (Iguanidae): Evidence for intraspecific variation in the foraging behaviour and diet. – *Can. J. Zoo. 74:* 1238-1245.

Perezmellado, V. and Delariva, I. 1993. Sexual size dimorphism and ecology-the case of a tropical lizard, *Tropidurus melanopleurus* (Sauria, Tropiduridae) – *Copia 4*: 969-976.

Pindell, J.L. and Barrett, S.F. 1990 Geological evolution of the Caribbean region: a plate tectonic perspective. – *The Geology of North America. Vol. H. Geol. Soc. Amer.*

Pough, F.H., Andrews, R.M., Cadle, J.E., Cemp, M.L., Savitzky, A.H., and Wells, K.D. 1998. *Herpetology* – Prentice Hall Press.

Pounds, J.A. 1988. Ecomorphology,locomotion and microhabitat structure: patterns in a tropical mainland *Anolis* community. – *Eco. Mon. 58:*229-320.

Preest, M.R. 1994. Sexual size dimorphism and feeding energetic in *Anolis carolinensis* – why do females take smaller prey than males? – *J. Herp. 28*: 292-298.

Preziosi, R.F. and Fairbairn, D.J. 1997 Sexual size dimorphism and selection in the wild in the water strider *Aquarius remigis*: lifetime fecundity selection on female total length and its components. – *Evolution, 51:* 467-474.

Purvis, A. 1991. *Comparative analysis by independent contrast, version 1.2: user's guide*. Oxford: Oxford Uni.

Pyron, M. 1996. Sexual size dimorphism and phylogeny in North American minnows. – *Bio. J Linn. Soc. 57:* 327-341.

Qualls, F.J., and Shine, R. 1998 Geographic variation in lizard phenotypes: importance of the incubation environment. – *Biol. J. Linn. Soc. 64:* 477-491.

Rand, A.S. 1967. Ecology and social organisation in *Anolis lineatopus*. – *Proc. U.S. Nat. Mus. 122:* 1-79.

Rand, A.S. and Williams, E.E. 1969 The anoles of La Palma: aspects of their ecological relaionships. – *Brevoria, 327:* 1-17.

Ranta, E., Laurila, A. and Elmberg, J. 1994. Reinventing the wheel: analysis of sexual size dimorphism in body size. – *Oikos 71:* 313-321.

Rhen, T., and Lang, J.W. 1995 Phenotypic plasticity for growth in the common snapping turtle – effects of incubation-temperature, clutch, and their interaction. – *Amer. Nat. 146:* 726-747.

Robertson, A. 1966. A mathematical model of the culling process in dairy cattle. – *Anim. Prod. 8:* 93-108.

Rohwer, S., Langston, N. and Gori, D. 1996. Body size and harem size in male red-winged blackbirds: manipulating selection with sex-specific feeders. – *Evolution, 50*: 2049-2065.

Roughgarden, J.D. 1972. Evolution of niche width. –*Am. Nat. 106:* 683-718.

Roughgarden, J.D. 1974. Niche width: biogeographic patterns among *Anolis* lizard populations - *Am. Nat. 108:* 429-442.

Roughgarden, J.D. 1995. *Anolis lizards of the Caribbean: ecology, evolution, and plate tectonics.* – Oxford Uni. Press. New York.

Roughgarden, J.D. and Fuentes, E. 1977. The environmental determinants of size in solitary populations of West Indian Anolis lizards. – *Oikos 29:* 44-51.

Ruibal, R. and Philibosian, R. 1970 Eurythermy and niche expansion in lizards. – *Copeia 1970:* 645-653.

Scheiner, S.M. 1993 Genetics and evolution of phenotypic plasticity. – *Annual Rev. Ecol. Systematics. 24:* 35-68.

Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. – *Evolution, 42:* 849-860.

Schulter, D. and Smith, J.N.M. 1986 Natural selection on beak and body size in the song sparrow. – *Evolution 40:* 221-231

Schoener, T.W. 1969. Size patterns in West Indian *Anolis* lizards. I. Size and species diversity. – *Sys. Zoo. 18:* 386-401.

Schoener, T.W. 1970 Size patterns of West Indian *Anolis* lizards. II.Correlations with the size of particular sympatric species-displacement and convergence. – *Amer. Nat. 140:* 85-108.

Schoener, T.W. 1977. Competition and the niche. *Biology of the Reptilia Vol.7*, Academic Press, New York.

Schoener, T.W. and Gorman, G.C. 1968. Some niche differences in three lesser Antillian lizards of the genus *Anolis*. – *Ecology, 49*: 819-830.

Scott, J.M., and Carpenter, J.W. 1987. Release of captive reared or translocated endangered birds: What do we need to know? – *Auk, 104:* 544-545.

Selander R.K. 1966. Sexual dimorphism and differential niche utilisation in birds. – *Condor, 68:* 113-151.

Sherbrooke, W.C., Castrucci, A.M.D. , and Hadley, M.E. 1994 Temperature effects on in-vitro skin darkening in the mountain spiny lizards, *Sceloporus jarrovii* – A thermoregulatory adaptation. – *Physiologial Zool.. 67:* 659-672.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. – *Q. Rev. Biol. 64*: 419-461.

Shine, R. 1988. The evolution of large body size in females: a critique of Darwin's "fecundity advantage" model. – *Am. Nat. 131;* 124-131.

Shine, R., Harlow, P.S., Keogh, J.S. and Boeadi 1998. The influence of sex and body size on food habits of a giant tropical snake, *Python reticulatus*. – *Func. Ecol. 12*: 248-258.

Soares, A.G., Callahan, R.K., and DeRuyck, A.M.C. 1998 Microevolution and phenotypic plasticity in *Donax serra roding* (Bivalvia: Donacidae) on high energy sandy beaches. – *J. Molluscan Studies, 64:* 407-421.

Sorci, G., Clobert, J., and Belichon, S. 1996 Phenotypic plasticity of growth and survival in the common lizard, *Lacerta vivipara*. – *J. Anim. Ecol. 65:* 781-790.

Spitze, K., and Sadler, T.D. 1996 Evolution of a generalist genotype: multivariate analysis of the adaptivness of phenotypic plasticity. – *American Naturalist, 148:* 108-123.

Stamps, J.A. 1983. *Sexual selection, sexual dimorphism and territoriality*. Lizard ecology: Study of a model organism. 169-204. Harvard Uni. Press

Stamps, J.A. 1993. *Territoriality and the non-passive female*. – in prep.

Stamps, J.A. and Andrews, R,M. 1992. Estimating asymptotic size using the largest individual per sample. – *Oecologica (Berlin) 92*: 503-512.

Stamps, J.A. and Krishnan, V.V. 1994a. Territory acquisition in lizards: I. First encounters. – *Anim. Behav. 47:* 1375-1385.

Stamps, J.A. and Krishnan, V.V. 1994b. Territory acquisition in lizards: II. Establishing social and spatial relationships. – *Anim. Behav. 47:* 1387-1400.

Stamps , J.A., Losos, J.B. and Andrews, R.M. 1997. A comparative study of population density and sexual size dimorphism in lizards. – *Am. Nat. 149*: 64-90 .

Stevenson, R.D. 1985. Body size and limits to the daily range of body temperature in terrestrial ectotherms. – *Am. Nat. 125*: 102-117.

Stuhsaker, J.W. 1986. Selection mechanisms associated with intraspecific shell variation in *Littorina picta* (Prosobranchia : mesogastropoda) – *Evolution, 22:* 459-480.

Tasse, J. 1989. Translocation as a strategy for preserving endangered species. – *Endangered Species Update, 6:* 6.

Taylor, E.B. and McPhail. 1999. Evolutionary history of an adaptive radiation in species pairs of threespine sticklebacks (*Gasterosteus*): insight from mitochondrial DNA. – *Bio. J. Linn. Soc. 66:* 271-291.

Thompson, D.B. 1999 Genotype-environment interaction and the ontogeny of diet – induced phenotypic plasticity in size and shape of *Melanoplus femurrubrum* (Orthoptera: Acaridae) – *J. Evol. Biol. 12:* 38-48.

Thompson, J.D. 1991 Phenotypic plasticity as a component of evolutionary change. – *Trend. Ecol. Evol. 6:* 246-249.

Thorpe, R.S. 1984 Primary and secondary transition zones in speciation and population differentiation: a phylogenetic analysis of range expansion. – *Evolution, 38:* 233-243.

Thorpe, R.S. 1987. Geographic variation: a synthesis of cause, data, pattern and congruence in relation to sub-species, multivariate analysis and phylogenesis. – *Boll. Zool. 54:* 3-11.

Thorpe, R.S. 1996. The use of DNA divergence to help determine the correlates of evolution of morphological characters. - *Evolution, 50*: 524-531.

Thorpe, R.S. and Brown, R.P. 1989. Microgeographic variation in the colour pattern of the lizard *Gallotia gallotia*, within the island of Tenerife. Distribution, pattern and hypothesis testing. – *Biol. J. Linn. Soc. 38:* 303-322.

Thorpe, R.S. and Brown, R.P. 1991. Microgeographic clines in the size of mature male *Gallotia gallotia* on Tenerife: Causal hypothesis. – *Herpetologica, 47:* 23-37.

Thorpe, R.S., Brown, R.P., Malhotra, A., Day, M., McGregor, D.M., and Wuster, W. 1994. Testing ecological and phylogenetic hypotheses in microevolutionary studies. In Eggleton, P.J. and Vane-Wright (Eds.) *Phylogeny and ecology*. – Accademic Press, London.

Thorpe, R.S. and Malhotra 1996 Molecular and morphological evolution within small islands. – *Phil. Trans. R. Soc. Lond. 351*: 815-822.

Thorpe, R.S., Black, H. and Malhotra, A. 1996. Matrix correspondence tests on the DNA phylogeny of the Tenerife Lacertid elucidates both historical causes and morphological adaptation. – *Sys. Bio. 45*:335-345.

Tinkle, D.W. 1965 Population structure and effective size of a lizard population – *Evolution, 19*:569-573.

Tokarz, R.R. 1985. Body size as a factor determining dominance in staged agonistic encounters between male brown Anoles. *Anim. Behav. 33:* 746-753.

Tosini, G. and Avery, R. 1993 Intraspecific variation in lizard thermoregulatory set points-a thermographic study of *Podarcis muralis*. – *J. Thermo. Bio. 18:* 19-23.

Trivers R.L. 1972. *Parental investment and sexual selection*. 136-179 in Biology, Cambell, ed. Heinemann, London.

Trivers, R.L. 1976. Sexual selection and resource accruing ability in *Anolis garmani*. – *Evolution 340:* 253-269.

Tudge, C. 1992. *Last animal in the zoo*. Oxford press

Tudge, C. 1993. *The engineer in the garden*. Oxford Press

Underwood, G. 1959. The anoles of the eastern Caribbean. Part III. Revisionary notes. – *Bull. Mus. Comp. Zool. 37:* 209-215.

Underwood, H. 1981. Parietalectomy affects phototropic responsiveness in thermoregulating lizards (*Anolis carolinensis*) – *Comp. Biochem. And Physiol., 69:* 575-578.

VanBuskirk, J. and Relya, R.A. 1998 Selection for phenotypic plasticity in *Rana sylvatica* tadpoles. – *Biol. J. Linn. Soc. 65:* 301-328.

VanDamme, R., Bauwens, D., and Verheyen, R.F. 1991 The thermal dependence of feeding behaviour, food consumption, and gut passage time in *Lacerta vivipara jacques*. – *Func. Ecol. 5:* 507-517.

Via, S. 1991 The genetic structure of native plant adaptation in a spatial patchwork: demographic variability amongreciprocal transplanted pea aphid clones. *Evolution 45*: 827-852.

Vitt, L.J., Caldwell, J.P., Zani, P.A. and Titus, T.A. 1997. The role of habitat shift in the evolution of lizard morphology: Evidence from tropical *Tropidurus*. – *Proc. National Acad. Sci. U.S.A. 94:* 3828-3832.

Wade, M.J. and Kalisz, S. 1990 The causes of natural selection – *Evolution. 44*: 1947-1955.

Wagner, A. 1996. Does evolutionary plasticity evolve? *Evolution, 50:* 1008-1023.

Wallace, A.R. 1865 On the phenomena of variation and geographical distribution as illustrated by the Papilionidae of the Malayan region. – *Trans. Linn. Soc. 25:* 1-71.

Wainwright, G., Webster, S.G., Wilkinson, M.L., and Sook Chung, J. 1996. Mandibular organ-inhibiting hormone in the crab, *Cancer pagurus*. – *J. Biol. Chem. 271:* 12749-12754.

Webster, T.P., and Burns, J.M. 1973. Dewlap colour variation and electrophoretically detected sibling species in a Hatian lizard, *Anolis breviorstris*. – *Evolution, 27:* 368-377.

Wedell, N. 1997. Ejaculate size in bushcrickets: the importance of being large. – *J. Evol. Bio. 10*: 315-325.

White, M. and Kolb, J.A. 1974. A preliminary study of *Thamonphis* near Sagehagen Creek, California. – *Copia,* 126-136.

Whitlock, M.C. 1996 The red queen beats the jack-of-all-trades: the limitations on the evolution of phenotypic plasticity and niche breadth. – *Amer. Nat. 148:* 65-77.

Wikelski, M. and Trillmich, F. 1997. Body size and sexual dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: an island comparison. – *Evolution 51*: 922-936.

Williams, E.E. 1969. The ecology of colonisation as seen in the zoogeography of anoline lizards on small islands. – *Q. Rev. Biol. 44:* 245-289.

Williams, E.E. 1972. The origins of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. – *Evol. Biol. 44:* 245-289.

Williams, E.E. 1983 Ecomorphs, faunas, island size and diverse end points in island radiations of *Anolis*. *Lizard Ecology, Harvard Uni. Press* 326-370

Williams, E.E., and Rand, A.S. 1977 Species recognition, dewlap function and faunal size. – Amer. Zool. 17:261-270

Womble, W.H. 1951. Differential systematics. – *Science 114:* 315-322.

Wright, S. 1935. The analysis of variance and the correlation between relatives with respect to deviations from an optimum. *J. Gen. 30:* 243-256.

APPENDICES.

A roost of free-tailed bats, situated in the eves of the authors house, on the Balvine Estate, Dominica.

Appendix 2.1

MANOVA results of Male Survivor/non-survivor Biomtrics against Experimental Population Ecotype at Wet and Dry Season Experiment Step 3.		
Character set	**Frequency (F)**	**P - Value**
Snout to vent length	**6.72**	**0.0101****
Femur length	0.01	0.9209
Tibial length	0.03	0.8633
Toe length	0.03	0.8569
Toe width	1.17	0.2803
Head width	1.96	0.1630
Head length	0.94	0.3341
Around body scale count	0.48	0.4872
Lamellar scale count	0.18	0.6721
Scale size index	3.15	0.0771
Ventral scale count	1.27	0.2611
Eye ring yellow	0.09	0.7696
Eye ring magenta	0.71	0.4015
Eye ring cyan	0.17	0.6846
Dorsal yellow	0.02	0.8919
Dorsal magenta	0.17	0.6806
Dorsal cyan	0.01	0.9169
Transect 1	0.82	0.3659
Transect 2	0.16	0.6920
Transect 3	1.00	0.3188
Multivariate Probabilities		
Survivorship/Ecotype	3.95	0.0000***

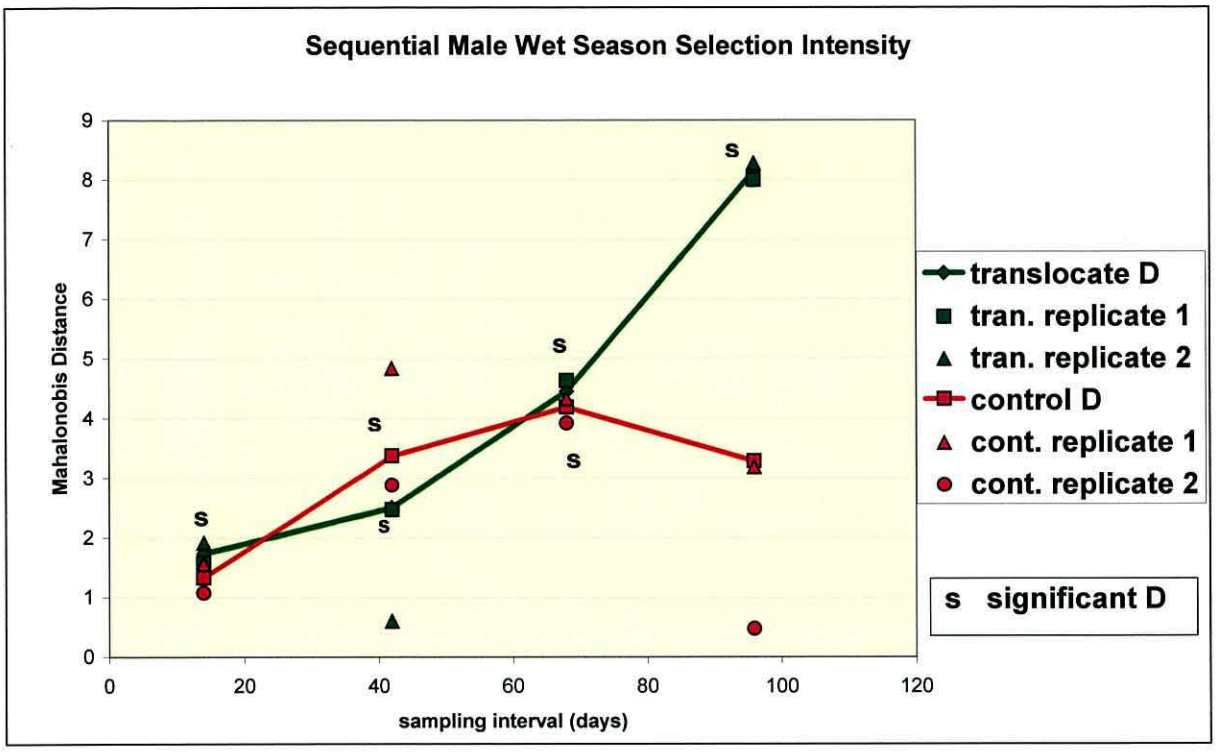
Key – Degrees of Freedom = 1,256; ** = significant to 0.05; *** = significant to 0.005.

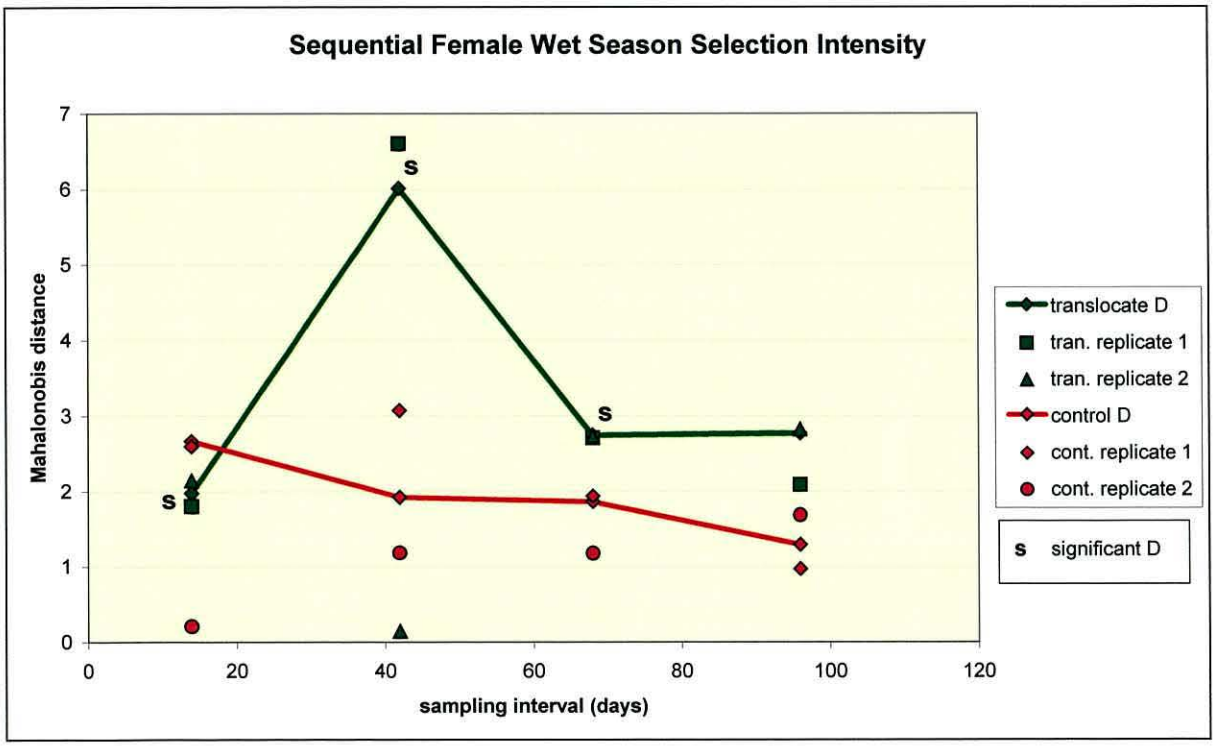
Appendix 2.2

MANOVA results of Female Survivor/non-survivor Biomtrics against Experimental Population Ecotype at Wet and Dry Season Experiment Step 3.		
Character set	**Frequency (F)**	**P - Value**
Snout to vent length	2.07	0.1516
Femur length	0.05	0.8278
Tibial length	1.99	0.1600
Toe length	0.59	0.4440
Toe width	1.14	0.2860
Head width	1.23	0.2687
Head length	**4.63**	**0.0324****
Around body scale count	1.66	0.1981
Lamellar scale count	1.14	0.2876
Scale size index	2.98	0.0855
Ventral scale count	0.14	0.7075
Eye ring yellow	1.18	0.2792
Eye ring magenta	**6.14**	**0.0139****
Eye ring cyan	1.37	0.2433
Dorsal yellow	0.03	0.8650
Dorsal magenta	0.00	0.9859
Dorsal cyan	1.04	0.3098
Transect 1	2.74	0.0996
Transect 2	0.05	0.8184
Transect 3	0.53	0.4680
Multivariate Probabilities		
Survivorship/Ecotype	5.55	0.0000***

Key – Degrees of Freedom = 1, 254; ** = significant to 0.05; *** = significant to 0.005.

Appendix 2.3


Sequential Male Wet Season Selection Intensity
Mahalonobis Distance
sampling interval (days)
translocate D
tran. replicate 1
tran. replicate 2
control D
cont. replicate 1
cont. replicate 2
s significant D


Sequential Female Wet Season Selection Intensity
Mahalonobis distance
sampling interval (days)
translocate D
tran. replicate 1
tran. replicate 2
control D
cont. replicate 1
cont. replicate 2
s significant D

Appendix 2.4 Sequential Logistical Regression of Wet Season Male Survival against Phenotype

Population	Control	Control	Control	Control	Trans	Trans	Trans	Trans
Analysis interval	14 days	42 days	70 days	98 days	14 days	42 days	70 days	98 days
Snout to vent length	0.8039	0.6571	0.9233	0.8456	0.0801	**0.0325****	0.0900	0.2492
Upper leg length	0.8570	0.3149	0.3511	0.5196	0.1243	0.0733	0.1817	0.3012
Lower leg length	0.6997	0.3659	0.6031	0.8817	0.1536	0.1073	0.2302	0.3090
Toe length	0.3343	0.0999	0.2270	0.4939	0.2179	0.1175	0.2020	0.2495
Toe width	0.8248	0.7539	0.9236	0.9318	0.3862	0.2845	0.5644	0.7633
Head width	0.9109	0.8005	0.9057	0.8087	0.1132	0.0482	0.0942	0.3126
Head length	0.7091	0.9838	0.7096	0.6180	0.1429	0.0809	0.1648	0.3578
Around body scale count	0.9985	0.3940	0.6652	0.7432	0.5588	0.7749	0.9224	0.6117
Lamellae scale count	0.0634	0.3571	0.6760	0.4389	0.3721	0.7369	0.8214	0.8074
Scale size	0.9498	0.5676	0.8079	0.5676	0.9170	0.5887	0.3702	0.4874
Ventral scale count	0.5061	0.7199	0.9899	0.6923	0.1247	0.1439	0.1027	0.8698
% eye yellow	0.7174	0.5870	0.6516	0.9810	0.9823	0.6511	0.7037	0.2092
% eye magenta	0.6091	0.5592	0.5804	0.6116	0.2313	0.7973	0.8451	0.8911
% eye cyan	0.4504	0.9282	0.5543	0.7864	0.1081	0.4863	0.9038	0.8976
% dorsal yellow	0.2146	0.3460	0.7426	0.6275	0.0977	0.1378	0.0899	0.3504
% dorsal magenta	0.9891	0.7631	0.6598	0.6185	0.2084	0.3798	0.2913	0.7383
% dorsal cyan	0.4765	0.8357	0.4983	0.5125	0.2792	0.4058	0.5546	0.7317
Black marking width	0.4872	0.3157	0.7342	0.8308	0.4010	0.9271	0.8577	0.5039
% anterior white marking	0.0328	0.1293	0.6466	0.5277	0.2103	0.4187	0.6463	0.4478
% mid-body white marking	0.1101	0.2194	0.2873	0.1167	0.5053	0.2146	0.0983	0.2134
% posterior white marking	0.4468	0.8217	0.5485	0.5670	0.8024	0.6080	0.8942	0.6674
Degrees of freedom	56	56	56	56	49	49	49	49
P-VALUE	**0.046*****	**0.027*****	**0.024*****	**0.027*****	**0.030*****	**0.042*****	**0.072*****	**0.194*****

Appendix 2.4 illustrates the character trait coefficients generated by a logistical regression for wet season male experimental *Anolis oculatus*.

Appendix 2.5 Sequential Logistical Regression of Wet Season Female Survival against Phenotype

Population	Control	Control	Control	Control	Trans	Trans	Trans	Trans
Analysis interval	14 days	42 days	70 days	98 days	14 days	42 days	70 days	98 days
Snout to vent length	**0.8785****	**0.7163****	0.3204	0.1161	0.4999	0.4637	0.8644	0.5745
Upper leg length	**0.2814****	0.9440	0.3448	0.6347	0.6287	0.6464	0.9963	0.6153
Lower leg length	**0.1303****	**0.4407****	0.2694	0.2549	0.4382	0.3244	0.5377	0.3115
Toe length	**0.2782****	**0.2288****	**0.0167****	0.0423	0.1931	0.1357	0.3063	0.1824
Toe width	**0.0896****	**0.0283****	**0.0401****	0.0868	0.2358	0.2747	0.5134	0.2554
Head width	**0.4280****	**0.6984****	0.7405	0.8031	0.4947	0.3947	0.6811	0.4139
Head length	**0.8208****	0.8452	0.4455	0.3899	0.3552	0.2862	0.5278	0.3297
Around body scale count	**0.5697****	**0.4163****	0.4457	**0.0187****	0.1269	0.1128	0.3151	0.7526
Lamellae scale count	**0.9945****	0.7258	0.4933	0.9812	0.5662	0.9335	0.8950	0.8302
Scale size	**0.6875****	0.9417	0.7604	0.3838	0.1361	0.1176	0.4020	0.3231
Ventral scale count	**0.1102****	**0.2701****	0.2152	0.6971	0.0587	0.0756	0.0516	0.0741
% eye yellow	**0.6124****	**0.4678****	0.9484	0.7471	**0.0050****	0.1896	0.3593	0.3248
% eye magenta	**0.5731****	0.7237	0.7746	0.8193	**0.0007****	0.0056	**0.0377****	**0.0219****
% eye cyan	**0.9606****	0.7869	0.4897	0.4894	**0.0221****	0.1718	0.4003	0.3478
% dorsal yellow	**0.5029****	**0.5254****	0.6973	0.3682	**0.0199****	0.0691	**0.0347****	0.1608
% dorsal magenta	**0.6469****	0.9939	0.6736	0.8755	**0.0185****	0.1447	0.2977	0.2320
% dorsal cyan	**0.3639****	**0.7256****	0.6697	0.4773	0.1430	0.2654	0.7225	0.7629
Black marking width	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
% anterior white marking	**0.8007****	**0.3762****	0.5900	0.2833	0.7031	0.5475	0.7908	0.9342
% mid-body white marking	**0.1680****	0.9111	0.8023	0.5633	**0.0397****	**0.0210****	**0.0136****	0.1302
% posterior white marking	**0.6844****	**0.3959****	0.6298	0.1520	0.8370	0.7832	0.4403	0.3454
Degrees of freedom	60	60	60	60	49	49	49	49
P-VALUE	**1.000****	**0.788****	**0.173****	**0.022****	**0.042****	**0.031****	**0.039****	**0.042****

Appendix 2.6 Sequential Logistical Regression of Dry Season Male Survival against Phenotype

Population	Control	Control	Control	Control	Trans	Trans	Trans	Trans
Analysis interval	14 days	42 days	70 days	98 days	14 days	42 days	70 days	98 days
Snout to vent length	0.1877	0.1902	0.4407	0.4448	0.2513	0.1962	0.1200	0.2115
Upper leg length	0.5103	0.5460	0.5087	0.7402	0.2111	0.1359	0.0922	0.1441
Lower leg length	0.3345	0.2981	0.2594	0.4088	0.1683	0.1107	**0.0692****	0.1502
Toe length	0.4364	0.3421	0.3413	0.4103	0.0841	**0.0524****	**0.0309****	**0.0780****
Toe width	0.9014	0.9211	0.8841	0.8805	0.4549	0.3367	0.1743	0.2414
Head width	0.2847	0.3261	0.3751	0.4980	0.2804	0.1992	0.1381	0.2016
Head length	0.7848	0.7464	0.7139	0.8022	0.1786	0.1309	0.0942	0.1628
Around body scale count	0.3252	0.2948	0.3559	0.4809	**0.0100****	**0.0153****	0.0865	**0.0476****
Lamellae scale count	0.0707	0.0578	0.0926	0.0625	0.6057	0.9401	0.8090	0.6125
Scale size	0.8520	0.9517	0.7569	0.8544	0.4952	0.4330	0.3164	0.9196
Ventral scale count	0.3108	0.3776	0.4122	0.6012	0.2955	0.2925	0.7230	0.7179
% eye yellow	0.5804	0.6475	0.7175	0.4112	0.9353	0.8678	0.4652	0.9670
% eye magenta	0.9233	0.9779	0.9675	0.9129	0.7791	0.3645	0.1289	0.2638
% eye cyan	0.9055	0.7780	0.7460	0.8087	0.6059	0.6944	0.4214	0.7256
% dorsal yellow	0.7214	0.7422	0.5101	0.1770	0.8420	0.8137	0.7916	0.8741
% dorsal magenta	0.4675	0.3936	0.5721	0.7816	0.1965	0.3467	0.4225	0.4615
% dorsal cyan	0.7472	0.7761	0.7280	0.6448	0.3346	0.2995	0.2313	0.3329
Black marking width	0.6411	0.5442	0.5431	0.5581	0.3145	0.6876	0.8748	0.5972
% anterior white marking	0.2101	0.1539	0.2026	0.3094	0.8663	0.8936	0.7494	0.9553
% mid-body white marking	0.7186	0.6619	0.7513	0.9194	0.8222	0.9264	0.7335	0.9823
% posterior white marking	0.1766	0.0700	0.0864	0.1341	0.9250	0.8384	0.8051	0.8909
Degrees of freedom	115	115	115	115	35	35	35	35
P-VALUE	**0.003****	**0.003****	**0.003****	**0.003****	**0.050****	**0.053****	**0.069****	**0.083****

Appendix 2.7 Sequential Logistical Regression of Dry Season Female Survival against Phenotype

Population	Control	Control	Control	Control	Trans	Trans	Trans	Trans
Analysis interval	14 days	42 days	70 days	98 days	14 days	42 days	70 days	98 days
Snout to vent length	0.4176	0.4176	0.6651	0.7282	0.0988	0.0988	0.0672	0.0672
Upper leg length	0.3765	0.3765	0.4435	0.4137	0.1961	0.1961	0.1549	0.1549
Lower leg length	0.8252	0.8252	0.6381	0.7358	0.1338	0.1338	0.1238	0.1238
Toe length	0.3811	0.3811	0.4737	0.6323	0.1526	0.1526	0.1155	0.1155
Toe width	0.7303	0.7303	0.4175	0.5301	0.1630	0.1630	0.1139	0.1139
Head width	0.6473	0.6473	0.5638	0.5753	0.1446	0.1446	0.1031	0.1031
Head length	0.4866	0.4866	0.6922	0.5788	0.2200	0.2200	0.2071	0.2071
Around body scale count	0.9585	0.9585	0.9685	0.7739	0.3314	0.3314	0.0992	0.0992
Lamellae scale count	0.1187	0.1187	0.1958	0.5141	0.9597	0.9597	0.5969	0.5969
Scale size	0.4430	0.4430	0.6820	0.6475	0.6708	0.6708	0.4551	0.4551
Ventral scale count	0.4760	0.4760	0.4922	0.4094	0.0941	0.0941	0.1845	0.1845
% eye yellow	0.2029	0.2029	0.2801	0.3717	0.2667	0.2667	0.6812	0.6812
% eye magenta	0.1971	0.1971	0.2810	0.6809	0.8021	0.8021	0.9708	0.9708
% eye cyan	0.6673	0.6673	0.9202	0.8241	0.3537	0.3537	0.5932	0.5932
% dorsal yellow	0.1169	0.1169	0.1637	0.2217	0.4464	0.4464	0.4209	0.4209
% dorsal magenta	0.4852	0.4852	0.3127	0.4318	**0.0182****	**0.0182****	0.0925	0.0925
% dorsal cyan	0.2421	0.2421	0.3533	0.3223	0.7446	0.7446	0.8593	0.8593
Black marking width	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
% anterior white marking	0.1298	0.1298	0.0596	0.0544	0.8085	0.8085	0.3917	0.3917
% mid-body white marking	0.5539	0.5539	0.4796	0.5164	0.8166	0.8166	0.6931	0.6931
% posterior white marking	0.4321	0.4321	0.2841	0.4296	0.4807	0.4807	0.6406	0.6406
Degrees of freedom	104	104	104	104	43	43	43	43
P-VALUE	**0.018****	**0.018****	**0.013****	**0.010****	**0.039****	**0.039****	**0.056****	**0.056****

APPENDIX 2.8

Wet Season Mahalonobis (D) Distances Between Survivor and Nonsurvivor Groups						
Experimental Pop^{n}.	**days**	**D**	**Replicate 1 D**	**Replicate 2 D**	**Survivor/ Nonsurv.**	**F-Stat.**
Cmw 0-1	14	1.32473	1.55667	1.07627	39:20	1.954
Cmw 0-2	42	1.32338	1.395	1.2535	35:24	1.825
Cmw 0-3	68	1.11663	1.346186	1.17818	30:29	1.548
Cmw 0-4	96	0.94869	0.672	1.13984	27:32	1.11
Smw 0-1	**14**	**1.72772**	**1.56757**	**1.913633**	**26:24**	**3.027****
Smw 0-2	**42**	**1.90988**	**1.5537**	**2.17928**	**20:30**	**3.528****
Smw 0-3	**68**	**1.94226**	**1.89972**	**2.01725**	**17:33**	**3.439****
Smw 0-4	96	1.62137	1.522105	1.73458	13:37	2.055
Cfw 0-1	14	2.65933	2.594079	0.20444	58:3	1.71
Cfw 0-2	42	1.58608	2.323034	0.53375	53:8	1.482
Cfw 0-3	68	1.42222	1.44244	1.356429	46:15	1.939
Cfw 0-4	96	1.165557	1.117594	1.258958	35:36	1.718
Sfw 0-1	**14**	**1.96962**	**1.795143**	**2.13925**	**30:20**	**3.782****
Sfw 0-2	**42**	**1.98055**	**2.15727**	**1.900857**	**27:23**	**3.958****
Sfw 0-3	**68**	**1.89248**	**1.986143**	**1.827143**	**24:26**	**3.632****
Sfw 0-4	**96**	**1.78772**	**1.62263**	**1.938782**	**20:30**	**3.116****

Key – Cmw = Cabrits Male Wet season population; Smw = Syndicate Male Wet season population; Cfw = Cabrits Female Wet season population; Sfw = Syndicate Female Wet season population.
** = Significant to 0.05.

Dry Season Mahalonobis (D) Distances Between Survivor and Nonsurvivor Groups						
Experimental Pop^{n}.	**days**	**D**	**Replicate 1 D**	**Replicate 2 D**	**Survivor/ Nonsurv.**	**F-Stat.**
Cmd 0-1	**14**	**0.88942**	**0.981655**	**0.7961**	**66:52**	**2.122****
Cmd 0-2	42	0.91783	1.015025	0.82274	65:53	1.938
Cmd 0-3	68	0.85763	0.934602	0.77953	64:54	1.987
Cmd 0-4	96	0.85763	0.934602	0.77953	64:54	1.987
Smd 0-1	**14**	**2.29096**	**2.308**	**1.529**	**17:19**	**3.463****
Smd 0-2	**42**	**2.39835**	**2.2636**	**1.8755**	**16:20**	**3.76****
Smd 0-3	**68**	**2.42725**	**2.3407**	**1.9405**	**14:22**	**3.706****
Smd 0-4	**96**	**2.0469**	**2.0928**	**1.50125**	**13:23**	**2.559****
Cfd 0-1	14	1.00143	1.56066	0.45692	69:37	1.829
Cfd 0-2	42	1.00143	1.56066	0.45692	69:37	1.829
Cfd 0-3	68	1.08664	1.56066	0.226629	67:39	1.859
Cfd 0-4	96	1.08664	1.56066	0.226629	67:39	1.859
Sfd 0-1	**14**	**1.69079**	**1.795143**	**1.41526**	**20:24**	**2.45****
Sfd 0-2	**42**	**1.69079**	**2.15727**	**1.41526**	**20:24**	**2.45****
Sfd 0-3	**68**	**2.13337**	**1.986143**	**2.236944**	**17:27**	**3.73****
Sfd 0-4	**96**	**2.13337**	**1.62263**	**2.236944**	**17:27**	**3.73****

Key – Cmd = Cabrits Male Dry season population; Smd = Syndicate Male Dry season population; Cfd = Cabrits Female Dry season population; Sfd = Syndicate Female Dry season population.
** = Significant to 0.05.

Appendix 2.9a, b.

Appendix 2.9a illustrates how, during the wet season, the enclosures have an insignificant effect on gravidity in the control experimental populations, when comparing native to enclosure data, but have a significant and considerable effect on the translocated montane females.

Chi-Square Results of Gravidity Levels Between Wet Season Experimental Populations

Experimental interval	Populations tested	Chi-Square Value	Probability (P)
0 days	Enc. Controls – Native Controls	0.025	0.874
	Enc. Controls – Enc. Montane	0.381	0.537
	Enc. Montane – Native montane	0.025	0.023
	Native Control – Native Montane	0.857	0.335
14 days	Enc. Controls – Native Controls	0.029	0.866
	Enc. Controls – Enc. Montane	27.001	0.000
	Enc. Montane – Native montane	10.264	0.001
	Native Control – Native Montane	3.475	0.061
42 days	Enc. Controls – Native Controls	0.002	0.958
	Enc. Controls – Enc. Montane	35.636	0.000
	Enc. Montane – Native montane	38.969	0.000
	Native Control – Native Montane	0.090	0.746
68 days	Enc. Controls – Native Controls	0.026	0.873
	Enc. Controls – Enc. Montane	60.785	0.000
	Enc. Montane – Native montane	45.197	0.000
	Native Control – Native Montane	0.084	0.772
96 days	Enc. Controls – Native Controls	0.027	0.869
	Enc. Controls – Enc. Montane	58.413	0.000
	Enc. Montane – Native montane	37.831	0.000
	Native Control – Native Montane	3.429	0.064

Appendix 2.9a illustrates how, during the dry season, the enclosures have an insignificant effect on gravidity in the control experimental populations, when comparing native to enclosure data, but have a significant and considerable effect on the translocated montane females

Chi-Square Results of Gravidity Levels Between Dry Season Experimental Populations

Experimental interval	Populations tested	Chi-Square Value	Probability (P)
0 days	Enc. Controls – Native Controls	0.328	0.567
	Enc. Controls – Enc. Montane	3.056	0.080
	Enc. Montane – Native montane	2.031	0.154
	Native Control – Native Montane	6.697	0.010
14 days	Enc. Controls – Native Controls	0.083	0.774
	Enc. Controls – Enc. Montane	11.598	0.001
	Enc. Montane – Native montane	39.286	0.000
	Native Control – Native Montane	7.574	0.006
42 days	Enc. Controls – Native Controls	0.019	0.892
	Enc. Controls – Enc. Montane	38.022	0.000
	Enc. Montane – Native montane	79.597	0.000
	Native Control – Native Montane	6.948	0.008
68 days	Enc. Controls – Native Controls	0.021	0.885
	Enc. Controls – Enc. Montane	37.074	0.000
	Enc. Montane – Native montane	67.523	0.000
	Native Control – Native Montane	9.750	0.002
96 days	Enc. Controls – Native Controls	0.185	0.667
	Enc. Controls – Enc. Montane	40.376	0.000
	Enc. Montane – Native montane	77.657	0.000
	Native Control – Native Montane	5.882	0.015

Appendix 2.10a,b.

Appendix 2.10a illustrates that at all stages of analysis, there were significantly different numbers of hatchlings between the control Cabrits and translocated Montane populations throughout the wet season experiment.

Chi-Square Results of Hatchlings in Enclosures Between Control and Translocated Montane Populations During Wet Season			
Experimental interval	Populations	Chi-Squred Value	Probability (P)
14 days	Montane - Control	15.6	0.000
42 days	Montane - Control	17.3	0.000
68 days	Montane - Control	16.7	0.000
96 days	Montane - Control	15.1	0.000

Appendix 2.10b illustrates that at all stages of analysis, there were significantly different numbers of hatchlings between the control Cabrits and translocated Montane populations throughout the dry season experiment.

Chi-Square Results of Hatchlings in Enclosures Between Control and Translocated Montane Populations During Dry Season			
Experimental interval	Populations	Chi-Squred Value	Probability (P)
14 days	Montane - Control	9.9	0.041
42 days	Montane - Control	16.4	0.000
68 days	Montane - Control	14.4	0.001
96 days	Montane - Control	7.6	0.000

Appendix 2.11a,b.

Appendix 2.11a illustrates the largely significant difference in the level of mortality during the wet season, between the experimental groups, and even where significance is not gained, one may observe from figure 2.18, that the overall trend is still observed.

Chi-Squared Results of Mortality between Experimental Populations During Wet Season Experiment			
Experimental interval	populations	Chi-Square Value	Probability (P)
14 days	Control males – Montane males	3.48	0.062
	Control females – Montane females	32.75	0.000
42 days	Control males – Montane males	6.48	0.011
	Control females – Montane females	24.38	0.000
68 days	Control males – Montane males	2.95	0.086
	Control females – Montane females	16.65	0.000
96 days	Control males – Montane males	15.90	0.000
	Control females – Montane females	4.51	0.034

Appendix 2.11b illustrates the largely significant difference in the level of mortality between the experimental groups during the dry season, considering the female groups,and even where significance is not gained between the males, one may observe from figure 2.20, that the overall trend is still observed.

Chi-Squared Results of Mortality between Experimental Populations During Dry Season Experiment			
Experimental interval	populations	Chi-Square Value	Probability (P)
14 days	Control males – Montane males	0.08	0.777
	Control females – Montane females	8.97	0.003
42 days	Control males – Montane males	0.50	0.497
	Control females – Montane females	8.97	0.003
68 days	Control males – Montane males	2.02	0.154
	Control females – Montane females	13.54	0.000
96 days	Control males – Montane males	2.74	0.116
	Control females – Montane females	10.58	0.001

Appendix 5.0 Environmental Data

Sites	Altitude	Temp	Humidity	Xeric	Intermediate	Montane
Cabrits	075.0	026.8	061.3	1	0	0
Batali	010.0	028.2	066.3	1	0	0
Rosalie	036.0	025.4	082.4	0.5	0.5	0
Eden	018.0	026.1	076.1	0.5	0.5	0
Portsmouth	150.0	028.7	071.4	0	1	0
Bornes	247.0	026.0	070.3	0	1	0
Hampstead ridge	154.0	026.6	077.2	0	0.5	0.5
Bense	532.0	021.9	088.9	0	0	1
Palmist ridge	280.0	024.8	080.7	0	0	1
Emerald pool	393.0	022.3	078.2	0	0	1
Syndicate	547.0	023.3	083.0	0	0	1
Freash water lake	756.0	021.4	089.6	0	0	1

Appendix 5.0 illustrates the environmental variables recorded at each experimental site. Temperature was taken from extrapolations made by Malhotra (1992).