Chapter 1
General Introduction

Unisexuality in Vertebrates

Unisexuality has frequently been reported in a range of plant and invertebrate taxa. Unisexuality in vertebrates was first recognised in 1932 when an all-female fish, *Poecilia formosa*, was described (Hubbs and Hubbs 1932). Now approximately 70 unisexual vertebrate taxa have been identified including fish, amphibians, and squamate reptiles. The majority of these unisexual vertebrates are known to have arisen via hybridization between two or more sexual species.

There are three identified modes of unisexuality, parthenogenesis, gynogenesis, and hybridogenesis. Parthenogenesis requires no investment by males. Eggs are produced without genetic recombination or reduction in ploidy and develop without sperm into viable genetically identical offspring (Dawley 1989). The first evidence of parthenogenesis was the observation of the lack of males in several genera of lizards including *Lepidodactylus* (Taylor 1918), *Rhampholeon* (Schmidt 1919), *Lacerta* (Lantz and Cyren 1936, Darevsky 1957) and *Cnemidophorus* (Minton 1959, Tinkle 1959, Duellman and Zweifel 1962, Maslin 1962, Zweifel 1965, Maslin 1966). Since then parthenogenesis has been observed in seven of the 17 families of lizard and in one species of blind snake (reviewed by Cole 1975 and Darevsky et al. 1985).

The remaining two modes of unisexuality are sperm-dependent. In gynogenesis sperm from males of a related sexual species is needed to activate embryogenesis, but paternal genetic material is not incorporated or expressed (Vrijenhoek 1994). Therefore, the offspring again are genetically identical. Hybridogenesis differs from the first two modes in showing some features of sexual reproduction. In hybridogenetic systems, only the ancestral maternal lineage is clonal and the paternal complement is replaced each generation by sperm from a related sexual species (Schultz 1969, 1977, Vrijenhoek 1984a, 1984b). Sperm-dependent modes

of unisexuality have been recorded for several species of fish and amphibians (reviewed by Schulz, 1969, White 1978 and Bell 1982).

The discovery of unisexuality in vertebrates prompted two major approaches to explaining the evolution and maintenance of sexual reproduction. The first approach, a group-selectionist one, highlighted the long-term advantage of sexual reproduction. It was first suggested by Weismann (1889) and later elaborated by Fisher (1930) and Muller (1932) that due to genetic variation populations reproducing sexually evolve more rapidly than do asexual populations, and therefore are able to survive environmental changes and effectively clear deleterious mutations (Muller 1964) which may cause unisexual forms to go extinct. Goddard et al. (2005) recently presented the results of an experiment with yeast, which showed asexual clonal lines had lower persistence in varying conditions. This, in addition to their taxonomic rarity (Vrijenhoek 1989), has lead to the labeling of unisexual animals as evolutionary "dead ends" (Maynard Smith 1978, White 1978).

Despite these evolutionary limitations, many all female 'species' are ecologically very successful (Schultz 1977, Vrijenhoek 1979, Bell 1982, Lynch 1984, Moore 1984, Vrijenhoek 1989, Vrijenhoek 1998). The importance of explaining the maintenance of sexual reproduction through short-term advantages to the individual within populations of vertebrates was first recognised by Williams (1971, 1975) and Maynard Smith (1971). These authors suggest that "all-else equal", sexual reproduction entails a two-fold reproductive cost. This is either due to a cost of meiosis because an asexual female transmits all her genes to her offspring, while a sexual female only passes on half (Williams 1975), or due to the cost of males since an asexual female has double the reproductive potential in any generation, as only female progeny are produced (Maynard Smith 1971). A further benefit associated with asexual reproduction, is that it allows the conservation and repetition of well adapted genotypes that would be broken up by the process of sexual reproduction (Zweifel 1965, Barton and Charlesworth 1998). Other disadvantages that accrue to sexual reproduction include the expenditure of resources in locating mates and courtship and mating behaviour, the increased opportunity for sexually transmitted diseases, the increased risk of predation

during sexual displays, the damage inflicted by males during mating sessions, and the risk that an individual may fail to find a mate (Ghiselin 1974, Williams 1975, Maynard Smith 1978, Lloyd 1980, Bell 1982).

Given the two-fold demographic advantage, clones should rapidly outgrow their sexual counterparts (Case and Taper 1986). For instance, it has been shown that an asexual lineage beginning with a single individual could replace a sexual population of 105 individuals and a sex ratio of 1:1 in less than 50 generations (Lively 1996). However, all female lineages have not completely replaced their bisexual ancestors on broad geographical scales (Case 1990, Stewart 1993). One explanation for this is that asexual lineages are newcomers on the scene and have not been around long enough to displace their sexual competitors (Blanchard 1996). Alternatively, it is suggested that the "all-else-equal" assumption must be incorrect, in that there must be reproductive, ecological or genetic advantages to sex (Maynard Smith 1978) that allow sexually reproducing organisms to overcome this two-fold cost.

The assumption that "all else is equal" between sexual and asexual individuals suggests the two forms are equivalent in reproduction, survivorship and niche requirements. This assumption is central to the two-fold cost of sex theory and to most of the models designed to assess the costs and benefits of sexual vs. asexual reproduction (Williams 1975, Maynard Smith 1978). Some evidence of at least a two-fold reproductive advantage of asexuals and a cost of males for sexuals has been found when comparing reproductive potential and characteristics between sexual and asexual *Ambystoma* (salamanders) (Licht 1989), *Cnemidophorus* (lizards) (Echternacht 1967, Christiansen et al. 1971, Schall 1978), and *Potamopyrgus antipodarum* (freshwater snails) (Jokela et al. 1997b). However, this is not a common characteristic of all sexual / asexual systems. It is generally accepted that unisexual organisms face developmental constraints due to factors directly related to asexuality. For instance, hybridization, often the basis of asexuality, can disrupt normal developmental processes. Moritz *et al*. (1989a) termed this the "balance hypothesis" stating that hybridising entities must be dissimilar enough to disrupt meiosis, but not so dissimilar that somatic development of hybrids is also disrupted (Vrijenhoek et al. 1989). Lower

reproductive success, as measured by the number of successful offspring per female, has been found in asexual forms when compared with sexual forms of *Heteronotia* (lizards) (Kearney and Shine 2005), *Lacerta* (lizards) (Darevsky 1960), *Poeciliopsis* (fish) (Wetherington et al. 1987), and *Ambystoma* (Uzzell 1964, Bogart 1989). Thus, the assumption of a two-fold reproductive advantage is not valid in these systems (reviewed in Suomalainen et al. 1987).

Other studies have identified ecologically relevant differences between sexual and asexual species (Lynch 1984, Schenck and Vrijenhoek 1986b, Schultz and Fielding 1989, Wetherington et al. 1989, Case 1990), suggesting that the all-else equal assumption is seldom met, and therefore the advantage to asexually producing organisms may not be two-fold.

Elucidating the nature of the short-term advantages to sexual reproduction has become one of the major challenges of evolutionary biology. Many hypotheses have been developed proposing either sufficiently large short-term advantages for sex to offset the two-fold cost, or alternatively, disadvantages to asexual reproduction that outweigh the potential fitness benefits (see Ghilsen 1974, Williams 1975, Maynard Smith 1978, Lloyd 1980, Bell 1982 and Kondrashov 1993 for reviews). These theories can be broadly classified into environmental (or ecological) and mutation-based models and most focus on the possible advantages gained by genetic diversity and the production of variable offspring in a sexual population. A selection of the major environmental and mutation-based hypotheses are discussed below. Where possible I have used examples of experiments on vertebrates. However, in some cases examples of studies on invertebrates and plants have been included.

Environmental (Ecological) Hypotheses

Weed Hypothesis

Examining possible short-term advantages of sexual reproduction prompted much interest in the ecological relationships and geographical distributions of closely related sexual and asexual species. A frequently observed pattern from these studies, termed “geographical parthenogenesis” (Vandel 1928), is that the

ecological and geographic trends of parthenogen organisms and their sexual relatives differ. In general, parthenogenesis is predominant in more extreme conditions, at higher latitudes and altitudes, in habitats that are farther south or north, in habitats that are warmer-drier or colder-wetter, in xeric environments, on islands or in island-like habitats, and in habitats variously described as disturbed, transient, ecotonal and marginal (Wright and Lowe 1968, Ghiselin 1974, Levin 1975, Cueller 1977, Glesner and Tilman 1978, Bell 1982, Lynch 1984, Peck et al. 1998). This observation encouraged theories that not only attempt to explain the maintenance of sex, but also the differences in the distributions of sexual and parthenogen animals.

One of the best known hypotheses, the Weed Hypothesis, was developed by Wright and Lowe (1968) to explain the distribution of parthenogenetic *Cnemidophorus*. They regarded parthenogenetic species of *Cnemidophorus* as geographic and ecological weeds that are successful only in disturbed areas which are unsuitable to sexual species. Similarly, Cueller (1977) suggested parthenogen *Cnemidophorus* occur in habitats where natural disturbances periodically eliminate lizard populations and Maslin (1968) added that parthenogens are opportunistic, and only able to succeed in areas where competition is weak or absent. Both Levin (1975) and Glesner and Tilman (1978) suggest that asexual species are restricted to sparsely populated areas where biotic interactions, with competitors, parasites and predators are weak. They suggest asexuals are unable to counteradapt to such forces. The implication of these hypotheses is that parthenogens are inferior competitors within the natural habitats of the parental species, and thus the successful establishment of parthenogen species depends on the availability of disturbed or marginal habitats in which they can move in to and escape from competition with their sexual relatives (Cueller 1977). Their high rate of increase and ability to colonise new habitats (Maslin 1971, Cueller 1977, Bell 1982, Moore 1984, Case and Taper 1986) assists in their success in these disclimax habitats. All of these theories propose that without isolation from closely related sexual species, parthenogens would be eliminated.

There is some support for the Weed Hypothesis in the distribution of parthenogenetic *Lacerta* (Darevsky 1962), *Cnemidophorus* (Walker et al. 1989)

and *Heteronotia* (Kearney et al.) which occupy more extreme, disturbed or harsher environments than sexual forms. A superior competitive ability of sexual over asexual forms has also been shown (Browne 1980).

In contrast, Schall (1977, 1978, and 1993) tested three predictions of the Weed Hypothesis using data on reproduction, diet, thermal relations and microhabitat use for several species of *Cnemidophorus*, but only found weak support for the hypothesis. Similarly, Serena (1984) and Price et al. (1993) found no major differences in geographical areas occupied by parthenogenetic and sexual taxa.

Intermediate Niche Hypothesis

A variant of the Weed Hypothesis that also predicts the inferior competitive ability of asexual animals, is the intermediate niche hypothesis (Schultz 1977, Moore 1984). This hypothesis suggests that newly arisen hybrid lineages may escape direct competition with their sexual relatives by having ecological requirements intermediate between those of their sexual parents. This restricts them to occupy intermediate niche space in which the parental species are inferior competitors (Schultz 1977, Moore 1984, Schlosser et al. 1998). Thus unisexuals should be most abundant in areas of overlap between geographical ranges of the sexual progenitors.

There is some support for this hypothesis. For example, gynogenetic *Phoxinus eos-neogaeus* has feeding structures intermediate to its parental species (Schlosser et al. 1998), parthenogenetic *Lacerta* occupy habitat that is intermediate between the parental habitats with respect to humidity, tree cover and elevational range (Uzzell and Darevsky 1975), and three unisexual species of *Poeciliopsis* were found to have ecological conditions intermediate between those of the parental species (Thibault 1978). However, most studies have failed to support this theory. For instance, although some lab-synthesised hybridogenetic strains of *Poeciliopsis monacha-lucida* were broadly intermediate to their sexual progenitors for most quantitative traits, several strains possessed phenotypes that deviated greatly from the intermediate mean (Wetherington et al. 1989, Lima and Vrijenhoek 1996). And although the intermediate niche hypothesis is consistent with the broad ecological patterns of *P. monacha occidentalis*, it fails to explain the local

ecological distributions of *P. monacha, P. lucida* and their diploid and triploid hybrids (Vrijenhoek 1994). Studies have also revealed ecological and behavioural differences among asexuals. This shows that asexuals are not constrained to express 'intermediate' phenotypes (Vrijenhoek 1979, 1984a, Schenck and Vrijenhoek 1989, Weeks et al. 1992). For example, asexual *Poeciliopsis* can be either more extreme than both sexuals, as in the case of predator efficiency (Weeks et al. 1992), or well within the range of a coexisting sexual, as in the case of growth, reproduction and offspring size at birth (Weeks and Gaggiotti 1993).

Sib Competition, "Lottery" Models

The Sib competition "Lottery" models suggest a different form of competitive superiority in sexually reproducing organisms. In these models the environment is divided into spatial patches, each of which can support at most one individual (Williams 1975). When groups of both sexual and asexual offspring occur in patches, sexually reproducing parents would be at an advantage because their offspring would be genetically more diverse, and therefore would have a greater probability of producing the best adapted genotype in a given patch (Williams and Mitton 1973, Koella 1988). In these models, there is no advantage in diversity per se just more chance of including the winner. Maynard Smith (1976, 1978) presented a computer simulation of this situation showing that sexuals can have an advantage over asexuals. However, there are numerous studies that fail to support this model of sib competition (Lively 1987, Schmitt and Ehrardt 1987, Kelley 1989, Garcia and Toro 1992).

Destabilising Hybridization

A further theory predicting that coexistence between sexual and parthenogen animals is unlikely was developed by Cueller (1977) who stated that parthenogen forms will be most successful in isolation. When they co-occur with sexual forms a parthenogen may lose its genetic identity through hybridization, a phenomenon termed 'destabilising hybridization' (Lynch 1984). This occurs if parthenogens mate with males of a sexual species to produce hybrid progeny of a higher ploidy level that are either males, that are usually non viable and deformed (Cueller and McKinney 1876, Zweifel 1965, Taylor et al. 1967, Lowe et al. 1970, Darevsky et al. 1978, Darevsky et al. 1985), sterile (McKay 1971) or new parthenogen forms

(Uzzell 1964, Neaves 1969, Maslin 1971, Schultz 1977, Lynch 1984, Serena 1984, Vrijenhoek 1989). In the latter case, the replacement of the original parthenogen by the higher ploidy form can occur (Paulissen et al. 1992). Thus, the frequent association of parthenogens with marginal habitats where sexuals are uncommon may be more a consequence of their inability to block genetic interference by their sexual relatives (Lynch 1984) in habitats occupied by sexual ancestors. This theory predicts that coexistence only becomes possible when interference mechanisms that result from hybridization are absent.

Evidence for the mating of parthenogens by sexual males has been seen in *Heteronotia binoei*, where sperm has been found in the oviducts of wild-caught parthenogen females (Whittier et al. 1994) and there are occasional cases of apparently sterile tetraploid parthenogens resulting from matings with sexual males (Moritz 1984). Darevsky and Danielyan (1968) experimentally demonstrated the significance of destabilising hybridization and concluded that genomic interference mechanisms prevent the coexistence of parthenogen and sexual *Lacerta*.

The hypotheses discussed above assume one or more of the following;

- That the sexuals are superior competitors in their 'niche space'
- That asexual lineages contain very little if any genetic diversity
- That coexistence between sexual and asexual lineages is unlikely

More recent descriptions of the ecological and distributional relationships between syntopic sexual and parthenogen forms and the availability of more advanced genetic methods imply that these hypotheses are perhaps over simplified.

Firstly, coexistence between sexual and asexual forms is not as rare as once thought. All sperm-dependent unisexual vertebrates must coexist with a closely related sexual species to survive, as they rely on males of sexual species for insemination (Graf and Pelaz 1989, Rasch and Balsano 1989). Furthermore, even though parthenogens can escape geographically from competition with closely related sexual forms, there are numerous examples of coexistence between sexual and parthenogen forms, suggesting that parthenogen forms do not require

isolation to persist. Examples include three lizard genera, *Cnemidophorus* (Milstead 1957, Zweifel 1965, Echternacht 1967, Medica 1967, Wright 1968, Christiansen et al. 1971, Schall 1976, Cueller 1977, Schall 1978, Cueller 1979, Mitchell 1979, Walker 1987, Walker et al. 1989, Case 1990, Paulissen et al. 1992, Casas-Andreu and Gurrola-Hidalgo 1993, Schall 1993), *Lacerta* (Darevsky et al. 1985), and *Heteronotia* (Moritz 1983).

Secondly, a large number of asexual lineages have been found to contain high levels of genetic diversity, either through genotypic diversity (multiple clones) or individual heterozygosity (identical clones, but with heteroygote genotypes). This coupled with their higher rate of increase provides these asexual lineages with a strong competitive ability against sexual relatives.

This has lead to the production of a further set of hypotheses attempting to explain the maintenance of sex, in systems where sexuals and asexuals coexist or in systems where clones exhibit genetic diversity. To allow this observed coexistence, it is suggested that there is neither competitive displacement nor destabilizing hybridization. For instance, competition may never be severe if the ecological resources shared by the various parthenogen and sexual forms are never limiting or if predation maintains populations below carrying capacity level (Moore 1984). Alternative hypotheses suggest there is competition or destabilising hybridization, but some other factor counteracts their effects.

There are two views about how the ecological adaptations of unisexual vertebrates permit their coexistence with sexual forms. Each is based on the type of genetic diversity present. One view is that each unisexual lineage may have a broad generalist niche as a result of heterosis (Spontaneous Heterosis Hypothesis) (Schultz 1977, Bulger and Schultz 1979), or the possession of a general purpose genotype (GPG hypothesis) (Lynch 1984). The second view is that the unisexual taxon may consist of several lineages, each with a distinct narrow niche (Frozen Niche Variation and Tangled Bank models) (Vrijenhoek 1979, Bell 1982, Vrijenhoek 1984a, Bell 1985). These two groups of models are discussed in more detail below.

Generalist Niche Models

The generalist niche models predict that unisexuals have broader environmental tolerances and thus occupy a broader range of environments than their sexual relatives, either through heterosis resulting from hybridization (Bulger and Schultz 1979, Cullum 1997, Schlosser et al. 1998), through the evolution of polyploidy (Suomalainen 1962, Soltis and Soltis 2000) or simply through selection over time for generalist clones (Lynch 1984). It is suggested that competitive interactions would frequently confine their success to underutilised resources and areas where their sexual hosts are poorly adapted (Moore 1984, Schlosser et al. 1998). Unlike views of Wright and Lowe (1968), Cueller (1977) and Maslin (1968), the generalist model suggests that the exclusive use of these extreme environments by parthenogens is a byproduct of physiological or morphological adaptations acquired through selection for generalism rather than a simple consequence of enhanced colonising ability of unisexuals or a competitive superiority of sexuals (Lynch 1984). The possession of a broadly adapted genotype allows the unisexuals wide ecological expansion in many environments and competitiveness with parental bisexual species (Darevsky 1992). These advantages may offset, in part, the inability of parthenogens to track environmental change genetically.

One generalist model is the Spontaneous Heterosis Hypothesis (Wetherington et al. 1987). The hybrid nature of most unisexual vertebrates is well documented (Neaves and Gerald 1968, Neaves 1969, Uzzell and Darevsky 1975, White 1978, Moritz 1983, Parker and Selander 1984, Moritz and King 1985, Moritz 1987, Vrijenhoek et al. 1989), and can involve as many as three sexual species (Wright and Lowe 1967). This results in many asexual animals having high levels of heterozygosity (Bulger and Schultz 1979, Moore 1984, Dawley 1989, Dessauer and Cole 1989, Bullini 1994), often several fold the levels seen in closely related sexual species (Cullum 1997). This has lead to the suggestion that at least part of the reason for the success of asexuals may be that they exhibit some degree of hybrid ‘vigour’ or heterosis (superior performance in a variety of traits) (Neaves and Gerald 1968, Neaves 1969, Schultz 1969, McKay 1971, Schultz 1971, Mitton and Grant 1984, Bullini 1994).

Another version of the generalist model was described by Lynch (1984), who refined the generalist view with respect to temporal variation, and termed it the General Purpose Genotype (GPG) Hypothesis. The GPG model predicts that over time environmental fluctuations should eliminate all narrowly adapted clones, resulting in an erosion of clonal diversity and persistence only of those clones with broad ecological tolerances. Thus the GPG predicts that inter-clonal selection will result in clonal assemblages with both broad tolerance ranges and low fitness variance across relevant physical, chemical and biotic gradients (Lynch 1984).

In support of the generalist view, many studies have noted the widespread distributions achieved by various unisexual vertebrates (Maslin 1968, Wright and Lowe 1968, Maslin 1971, Ghiselin 1974, Uzzell and Darevsky 1975, Parker and Selander 1976, Cueller 1977, Parker et al. 1977, Jaenike et al. 1980, Lynch 1984, Schlosser et al. 1998, Van Doninck et al. 2002). In addition, a number of experimental tests have shown broader tolerances to physiological stress in asexual forms than either of their parental species. Examples include, wider altitudinal range, and greater tolerance to egg desiccation (Uzzell and Darevsky 1975), broader thermal tolerances (Bulger and Schultz 1979, Tunner and Nopp 1979, Vrijenhoek 1994), enhanced physiological performance (Tunner and Nopp 1979, Mitton and Grant 1984), differing life history traits (Mitton and Grant 1984, Gutman et al. 1994), and broader ecological tolerance (Hanley et al. 1994). In examining the *Phoxinus eosneogaeus* complex, Schlosser et al. (1998) found that each drainage system contained only a single asexual clone of this fish, and that the gynogens survived longer and had greater physiological tolerance to oxygen stress than sexuals. Similarly, Hanley et al. (1994) found that in *Lepidodactylus* geckos a single genetic clone, major clone 2NA, had greater diet and habitat breadth than the sexual species. Some more recent studies provide strong support for the GPG model (Jacobsen and Forbes 1997, Jaenike and Dombeck 1998, Schlosser et al. 1998, Van Doninck et al. 2002). For example, Van Doninck *et al.* (2002) found that a parthenogen ostracod species (*Darwinula stevensoni*) had a wider tolerance range for both salinity and temperature than a sexual species (*Heterocypris incogruens*), which coincided with the wider geographic and ecological distribution of the parthenogen. These studies indicate that the GPG

model may be an appropriate description of evolution of clonal assemblages in some specific systems.

In contrast, studies of other asexual lineages have failed to show broad environmental tolerances. Examples include studies on asexual *Poeciliopsis* (Bulger and Schultz 1979, Bulger and Schultz 1982, Moore 1984, Wetherington et al. 1987, Schultz and Fielding 1989) and parthenogen *Cnemidophorus* (Cullum 1997). And several studies on geographic parthenogenesis have failed to demonstrate the existence of a genuine GPG in asexuals (Weider 1993, Parker and Niklasson 1995, Kenny 1996, Semlitsch et al. 1997, Browne and Wanigasekera 2000).

Specialised Niche Models

While the generalist model provides a sufficient explanation for unisexual-bisexual coexistence and is generally consistent with the geographical distributions of many asexual taxa, development of this generalist model occurred prior to the discovery of clonal diversity within many asexual populations. Although parthenogenetic complexes may vary widely in the amount of genetic diversity (Moritz et al. 1989b), extensive genetic analyses have usually revealed multiple clonal genotypes within these complexes. In these cases it is suggested the asexual taxa originated from multiple hybridization events. Multiple origins have been documented for *Heteronotia* (Moritz 1984, Moritz et al. 1989a), *Cnemidophorus* (Zweifel 1965, Scudday 1973, Parker and Selander 1976, Parker 1979a, 1979b, Dessauer and Cole 1989, Parker et al. 1989), *Lepidodactylus* (Bolger and Case 1994), *Poeciliopsis* (Thibault 1978, Vrijenhoek 1978, Vrijenhoek 1979, 1984a), and *Phoxinus* (Goddard et al. 1989).

Two hypotheses that are derived from the multiple clonal forms and that explain stable coexistence of multiple clonal lineages with their sexual ancestors are the Tangled Bank (Bell 1982) and Frozen Niche Variation (Vrijenhoek 1979, 1984a) hypotheses. These hypotheses are conceptually similar, predicting that a population of genetically diverse sexual individuals can utilise a broader range of resources than any single clone and hence is buffered from competitive exclusion (Ghiselin 1974, Vrijenhoek 1979, Bell 1982, Vrijenhoek 1984a, Case and Taper

1986). The Frozen Niche Variaiton hypothesis is more focused on the maintenance of clonal diversity than sex per se (Jokela et al. 2003).

The Tangled Bank (TB) Hypothesis is analogous to the concept of sib-competition, but different from the lottery models. It predicts that sex would be favoured in multiple resource environments where competition for resources is intense, since the genetically uniform progeny of an asexual female can utilise and compete for only a limited portion of the available resources. In contrast, the genetically diverse offspring of a sexual parent can utilise a broader range of the resources as its members will have different ecological requirements. Therefore, it is a contest between a clone which has the greater reproductive efficiency but a narrow ecological competence and a reproductively inefficient, but broadly competent sexual population. The clone cannot displace the sexual from its entire ecological range, whilst the sexual population cannot eliminate the clone from its favoured niches. The result is coexistence (Ghiselin 1974, Maynard Smith 1976, Bulmer 1980, Bell 1982, Koella 1988). Bell (1982), Case and Taper (1986) and Koella (1988) have studied the TB hypothesis through simulation. All three studies showed that sexuals can overcome their intrinsic disadvantage due to the cost of sex, and can persist with asexuals in a heterogeneous habitat.

Identification of ecological differences among coexisting clones in the *Poeciliopsis monacha-lucida* complex led Vrijenhoek (1979, 1984a) to develop the Frozen Niche Variation (FNV) model. This model is composed of two parts. Firstly, it assumes that coexisting clones had multiple, independent origins from genetically variable sexual ancestors, that allowed them to effectively 'freeze' and replicate different genotypic combinations of their parental species. Thus the first prediction of the model is that each clone has a lower phenotypic variance than the ancestral sexual population (Jokela et al. 2003). During the second stage, clones compete with the sexual population, replacing the overlapping sexual phenotypes, because of their two-fold reproductive advantage. Clones also compete with each other, leading to selection that produces an assemblage of ecologically differentiated and specialised clones that effectively subdivide resources (Williams 1975, Vrijenhoek 1979). The FNV thus predicts that clones form stable, genotypically diverse populations. These processes permit

coexistence among clones, as well as facilitate coexistence with the broad-niched sexual species from which the clone arose (Maynard Smith 1978, Vrijenhoek 1979, Bell 1982, Case and Taper 1986).

In both the TB and FNV hypotheses, the sexual lineage is expected to persist provided that the total niche width of the sexual population is greater than that of the entire array of clones (Vrijenhoek 1978, Bell 1982, Case and Taper 1986). As the number of different clones increases, the relative success of the sexual population declines.

In support of these hypotheses, there is evidence of parthenogens being more specialised than their sexual relatives in thermal tolerance (Bulger and Schultz 1979), feeding preferences (Vrijenhoek 1978, Schenck and Vrijenhoek 1989, Case 1990, Weeks et al. 1992), morphological variation and general niche breadth (Parker 1979a, Vrijenhoek 1984a, Bolger and Case 1994, Radtkey et al. 1995, Dybdhal and Lively 1995b). And, investigations comparing ecology among vertebrate clones have provided evidence of the freezing of phenotypic variation in clonal fish (*Poeciliopsis*) (Wetherington et al. 1989, Lima and Vrijenhoek 1996), frogs (*Rana esculenta*) (Semlitsch et al. 1997) and snails (*Potamopyrgus antipodarum*) (Jokela et al. 1997a). Studies of naturally occurring unisexual animals have also revealed evidence for ecological diversification among coexisting clones including differences in distribution (Wright 1968, Vrijenhoek 1978, Parker et al. 1989, Bolger and Case 1994, Radtkey et al. 1995), diets, and microhabitat and macrohabitat use (Scudday 1973, Vrijenhoek 1978, Schenck and Vrijenhoek 1986b, Paulissen et al. 1988a, Parker et al. 1989, Schenck and Vrijenhoek 1989, Weeks et al. 1992), activity time (Paulissen et al. 1988a), growth rate and fecundity (Schulz 1982), aggressive behaviour and mate selection (Keegan-Rogers and Schultz 1984), thermal preferences and tolerance (Bulger and Schultz 1979, Bulger and Schultz 1982, Keegan-Rogers and Schultz 1984, Keegan-Rogers and Schultz 1988, Bolger and Case 1994), size at birth and juvenile growth rate (Wetherington et al. 1989), and morphology (Zweifel 1965, Parker 1979a).

These models also predict a higher average fitness of clonal mixtures relative to single clones in spatially heterogeneous environments, because clonal mixtures can utilise a broader range of resources (Vrijenhoek 1979, 1984a, Case and Taper 1986, Weeks and Gaggiotti 1993). Some studies have supported this prediction (Vrijenhoek 1979, 1984a, 1984b).

Conversely, other studies on *Poeciliopsis* (Weeks 1995), and *Potamopyrgus* (Jokela et al. 1997a) have found mixed support for the FNV and TB models. Furthermore, interclonal niche diversification is not a universal phenomenon (Jaenike et al. 1980, Lynch 1984, Bolger and Case 1992) and the niche of asexuals is not always confined within the niche space of sexuals (Schenck and Vrijenhoek 1986b, Case 1990, Bolger and Case 1992, Hanley et al. 1995, Radtkey et al. 1995). For example, *Artemia parthenogenetica* were found to have large among-clone differences in key life history traits (Browne and Hoops 1990), but they differed as a group from the coexisting sexual species (*A. tunisiana*) (Browne et al. 1988). Other tests have failed to identify increased productivity in genetically variable populations of asexual clones (Weeks and Sassaman 1990).

The FNV and GPG models (a specialist niche vs. a generalist niche model) are not necessarily mutually exclusive (Semlitsch et al. 1997), as the former focuses on spatial heterogeneity and the latter on temporal variation. It is conceivable that coexisting clones might segregate according to food or spatial resources, and yet have corresponding broad tolerances for seasonal changes (Vrijenhoek and Pfeiler 1997). For example, Michaels and Bazzazz (1989) found that when compared to sexuals, asexual *Antennaria parlinii* appeared to be ecological generalists with respect to their allocation to vegetative growth, but they appeared specialists with respect to their allocation to reproductive function. Similarly parthenogen LAR-A and LAR-B of the *Cnemidophorus laredoensis* complex show phenotypic flexibility (seasonal changes in diet) predicted by the GPG hypothesis; but the niche characteristics of the two clonal complexes differ as predicted by the FNV model (see Vrijenhoek 1998 and Parker and Niklasson 1999 for a review).

Some other models have been derived to explain coexistence of sexual and asexual forms.

Sib Competition, the "Elbow Room Model"

Different to the sib-competition "Lottery" models discussed earlier, the Elbow-room model involves the more familiar form of density-dependent competition involving common use of a limiting resource (Young 1981, Bell 1982) seen in the TB and FNV models discussed above.

In the Elbow-room model, when groups of siblings compete, sexual females may be favoured because the intensity of competition amongst sexual siblings will be lower, compared to competition between asexual siblings (Williams and Mitton 1973, Maynard Smith 1976, 1978, Young 1981). This is because the intensity of competition is thought to increase with the genetic similarity of the competitors (Maynard Smith 1978, Bell 1982). Therefore, in this model, the advantage to the sexual species is a reduction in intraspecific competition, and genetic diversity leads to ecological diversity, so that a sexually-produced sibship can exploit the environment more fully (Young 1981).

Several studies have supported the elbow-room model, including those on *Drosophila* (Pérez-Tomé and Toro 1982) and the grass *Anthoxanthium odoratum* (Ellstrand and Antonovics 1985, Kelley et al. 1988, Kelley 1989). In these studies an increase in genetic variability resulted in a decrease in competition intensity. In contrast with the predictions of the elbow-room model, however, competitive superiority did not increase with planting density (Kelley 1989). However, the majority of tests have failed to support sib-competition (Bell 1982, Schmitt and Ehrardt 1987, Kelley 1989, Garcia and Toro 1992, Jokela et al. 2003).

Interspecific Competition Models

Similar in concept to the FNV and TB Hypothesis are the models of interspecific competition which predict coexistence of sexual and asexual lineages due to differences in niche utilisation and an advantage to sexual populations of a reduction in interspecific competition with asexual lineages and a wider range of available niches due to increased genetic diversity.

Several ecological studies on the patterns of resource partitioning and utilisation between sexual species and related asexual forms have been undertaken to

determine what factors combine to allow co-existence. In *Cnemidophorus*, differences in daily activity patterns and foraging behaviour (Echternacht 1967, Casas-Andreu and Gurrola-Hidalgo 1993), diet (Case 1990, Paulissen et al. 1992), habitats, (Medica 1967, Wright 1968, Christiansen et al. 1971, Schall 1976), behaviour (Milstead 1957, Schall and Pianka 1980, Leuck 1985, Bolger and Case 1992, Price 1992), and morphology (Wright 1968) have been identified. Similarly, Echelle et al. (1989) determined that in the asexual *Menidia clarkhubbsi* complex, competition with the sexual form functions to dampen its overall abundance, while resource partitioning allows it to persist. And spatial segregation has been found to be important in reducing competition between sexual and asexual *Poeciliopsis* (Vrijenhoek 1978) and *Poecilia* (Balsano et al. 1981). All of these examples suggest levels of competitive release that allow coexistence.

However, the majority of studies comparing the ecology of sexual and parthenogen *Cnemidophorus*, have shown little or no, ecological differences in thermal requirements, habitat use, diets, activity, or reproduction (Milstead 1957, Zweifel 1965, Echternacht 1967, Medica 1967, Christiansen et al. 1971, Scudday 1973, Schall 1976, 1977, Congdon et al. 1978, Mitchell 1978, Cueller 1979, Mitchell 1979, Walker 1987, Anderson and Karasov 1988, Case 1990, Casas-Andreu and Gurrola-Hidalgo 1993, Cueller 1993, Price et al. 1993, Schall 1993). Thus there is still debate about how these species coexist.

Recent theoretical studies by Doncaster et al. (2000) and Pound et al. (2002 and 2004) have addressed the ability of an asexual lineage to invade and eliminate its sexual ancestor. Simulations are set in a purely ecological context involving competition between similar species for common resources using classic Lotka-Volterra equations. Success of invasion depends on how well the asexual lineage manages the trade-off between its superior growth capacity and its inferior ability to compete with a more genetically variable sexual species. The studies show that small advantages in competitive ability for the sexual population can be enough to compensate fully for its two-fold reproductive disadvantage and stop the invasion of asexual forms. This advantage can be small because the asexual individuals are competing amongst themselves for common resources as well as competing against sexual individuals (Case and Taper 1986, Doncaster et al. 2000, Pound et

al. 2002), thus reducing inter-specific competition between sexuals and asexuals. This will allow coexistence over an ecological time scale. Sex then has time to express its longer-term advantages of genetic variation in meeting environmental change, resulting in the eventual displacement of asexuals (e.g. Kondrashov 1993, Pound et al. 2004). Tagg et al. (2005) tested the principal assumption of the Lotka volterra dynamics theory using sexual and asexual *Daphnia* and found support for the theory. Although these studies explain the coexistence of sexual and asexuals in the short-term, they predict that coexistence is not stable in the long-term, and that the sexuals will eventually displace the asexuals.

Support for competition within asexual lineages has come from studies that have found high aggression levels and dominance hierarchies within asexual species (or taxa) (Gustafson and Crews 1981, Leuck 1985, Grassman and Crews 1987, Brown and Sakai 1988, Brown et al. 1991, Ryhorchuk 2002). But in contrast to tis theory, other parthenogenetic lineages studied demonstrate very little aggression towards conspecifics (Frankenberg 1982). High levels of aggression have also been found within sexual species (Hardy 1962, Brackin 1978), and asexual animals in general have been found to be less aggressive than closely related sexual species (Milstead 1957, Echternacht 1967, Schall 1976, Leuck 1985, Bolger and Case 1992).

The few studies that have directly compared competition between sexual and asexual groups show mixed results, with some showing a superior competitive ability of asexuals, others showing a superior competitive ability of sexuals and still others failing to detect competition.

For example, it is suggested that along the Grande Valley in Southern New Mexico, *Cnemidohporus uniparens* (parthenogen) is excluding *C. tigris* (sexual) directly by competition (Cueller 1993), *Poeciliopsis clones* have been shown to out compete their closely related sexual counterparts (Schultz 1977, Schenck and Vrijenhoek 1986b) and asexual *Artemia* are competitively superior to Old World sexual populations (Browne and Halanych 1989). Similarly, in a population manipulation experiment, Cueller (1979) found that the sexual *Cnemidophorus marmoratus* invaded the habitat of the parthenogenetic *C. uniparens* only after the

local population of *C. uniparens* had been partially removed over a four year period, suggesting the competitive superiority of the parthenogen. However, other population manipulation experiments undertaken in the field over several years have failed to detect competition between syntopic parthenogenetic and sexual *Cnemidophorus* species (Price 1986, Cueller 1993, Price et al. 1993). In these experiments, the population responses of one species to removal of the other varied from weak to absent.

And in contrast, results from salamanders (*Ambystoma*) (Wilbur 1971), the perennial herb *Antennaria* (Michaels and Bazzaz 1986), the grass *Anthoxanthum* (Ellstrand and Antonovics 1984, Ellstrand and Antonovics 1985) and from New World populations of the brine shrimp *Artemia* (Browne 1980) demonstrate that sexual populations out compete their asexual counterparts. In addition an example of successful competitive exclusion (through exploitation of insect resources) is that of the native asexual gecko, *Lepidodactylus lugubris*, by the sexual gecko *Hemidactylus frenatus* throughout the Pacific (Case et al. 1994, Petren and Case 1996).

Red Queen Hypothesis

It has been suggested that novel (Levin 1975, Glesner and Tilman 1978) or more recently, rare (Jaenike 1978b) genotypes generated by sexual reproduction may provide a substantial advantage in the face of biotic-based frequency dependent selection (Jaenike 1978b, Hamilton 1980, Lloyd 1980). Studies have shown an advantage to sex under such frequency-dependent selection including, predator-prey interaction (Glesner 1979), pathogen pressure and resistance (Bremermann 1980, Hamilton 1980), and competition (Antonovics and Ellstrand 1984).

One of the favoured ecological hypotheses for the maintenance of sex and genetic diversity in vertebrates is the frequency dependent selection imposed by parasites. This has been termed the Red Queen Hypothesis (Van Valen 1973), and provides both an advantage to sexual reproduction and an alternative (to FNV and TB hypotheses) explanation for the coexistence of multiple clones (Hamilton et al. 1990, Howard and Lively 1994).

The idea behind the Red Queen Hypothesis is that parasites will be under strong selection to infect the most common host genotypes. This kind of frequency-dependent selection will favour rare host genotypes, which should increase in frequency over time, eventually becoming common. The parasite is then under selection to infect these previously rare, but now common host genotypes (Jaenike 1978a, Hamilton 1980, Hamilton 1982, Hamilton et al. 1990, Howard and Lively 1994, 1998). This leads to oscillations in genotypic frequencies in both the host and the parasites. Under the Red Queen Hypothesis, sexual reproduction is selected over asexual reproduction as a mechanism to produce variable progeny, some of which may have relatively rare genotypes, which escape infection (Lively 1987). Alternatively, an asexual clone can gain a new allele only by mutation and cannot rapidly readapt. This process provides an advantage to sex and prevents clones from becoming fixed and eliminating the sexual form, thus promoting coexistence between asexual and sexual forms.

Several clonal genotypes may also coexist under this model, even if the competing clones do not specialise on different resources, as long as the clones differ in their resistance genotypes (Jokela et al. 2003). The model predicts temporal dynamics in the clonal composition, where the most common clones alternate depending on the differences in the relative parasite pressure, (Antonovics and Ellstrand 1984), preventing the long term dominance of a single clone.

Numerous studies on the freshwater snail (*Potamopyrgus antipodarum*) have confirmed the predictions of the Red Queen Hypothesis (Lively 1987, Lively et al. 1990, Dybdahl and Lively 1995a, Lively and Dybdhal 2000a). Support has also come from other studies (Moritz et al. 1991, Johnson 2000, Sa Martins 2000). Contrary to the Red Queen, however; Brown et al. (1995) and Hanley et al. (1995) found that parasite rates were lower in parthenogenetic (*Lepidodactylus lugubris*) than sexual (*Hemidactylus frenatus*) gecko species and that the parthenogen gecko exhibits more parasite avoidance behaviours than the bisexual gecko (Brown et al. 1998).

Mutation-based Models

All of the models discussed so far have been based on ecological differences between sexual and asexual populations. Genetic processes also need to be considered in assessing the relative fitness of the two forms. In particular, all forms, sexual or asexual, will accumulate mutations, some of which will be deleterious.

The accumulation of deleterious mutations provides a final challenge to the persistence of asexuals. Two hypotheses propose that sexual reproduction is advantageous as it facilitates the elimination of deleterious mutations.

Muller's Ratchet

In the original model, Muller's ratchet (Muller 1964, Felsenstein 1974) it is suggested that mutations accumulate like a 'ratchet mechanism' in asexual lineages until they are driven to extinction. Sexual lineages, due to recombination, can produce offspring with higher and lower mutational loads than the parents, and selection effectively maintains a low load. In contrast, an asexual population cannot reduce its load below that of the 'least loaded' clone. If by chance that clone is lost through stochastic mechanisms (e.g. all progeny of the least loaded individuals receive at least one additional mutation, or all individuals in the least loaded class fail to reproduce) the load has increased one step ("ratchet" clicks one notch) (Howard and Lively 1998). Excluding back mutations, the mutation load can not be reduced. The ratchet mechanism is based on finite populations only and provides a long-term (rather than short-term) advantage to sexual reproduction.

There is now abundant evidence to suggest that Muller's ratchet does operate (Leslie and Vrijenhoek 1980, Bell 1988, Graf and Pelaz 1989, Chao 1990, Lynch and Gabriel 1990, Rice 1994, Moran 1996, Charlesworth and Charlesworth 1997, Vorburger 2001), but at present it seems that the process does not operate fast enough (except in very small populations) to be a sufficient explanation for the evolutionary persistence of sex. Other tests on *Cnemidophorus* lizards have

suggested the ratchet may have only minor effects (Dessauer and Cole 1989, Cullum 1997).

Mutational deterministic (MD) Model

More recent studies have extended Muller's basic idea to include cases where an advantage to sex can accrue even in infinitely large populations (Kondrashov 1988, Charlesworth 1990, Howard and Lively 1994). The Mutational Deterministic hypothesis, suggests there is an advantage to sex because recombination maintains a higher variance in mutation number and enhances the efficiency of selection against deleterious mutations (Kondrashov 1988). In an asexual population, unless the rate of mutation is very high, the variance in the number of mutations will be low, and most individuals that are eliminated by selection will have only one mutation in excess of the critical number. As a result more individuals will have to die than in a sexual population to eliminate the same number of deleterious mutations (Hurst and Peck 1996). For a mutation rate per-genome-per-generation greater than one, a decrease in the population mutation load of a sexual population can offset the inherent two-fold reproductive advantage of invading clones, provided there is a synergism among mutations such that such that, at some point, each mutation reduces fitness more than the previous mutation (Kondrashov 1988).

Based on the idea that mutations might have a more negative effect on fitness as the level of competition increases, Lively et al. (1998) examined mortality rates in a freshwater snail (*Potamopyrgus antipodarum*) from New Zealand. They found that asexuals and sexuals had similar mortality rates, suggesting that the Mutational Deterministic theory is an insufficient explanation for maintenance of sex in this system. These results are consistent with a study of desiccation stress in sexual and asexual cockroaches (Gade and Parker 1997). Results of other studies are inconsistent with the conditions of the degree of synergisms and rate of mutation being high (Keightley 1996, Elena and Lenski 1997, Peters and Keightley 2000).

Polyploid asexual lineages may be buffered to some extent against deleterious recessive mutations (Kondrashov and Houle 1994). Both Muller's Ratchet and the

Mutation Deterministic Model have a weaker effect on polyploid animals, as the greater the ploidy level, the slower the rate at which deleterious recessive mutations will accumulate (Judson 1997, Lively et al. 1998).

Pluralist approach

The majority of the hypotheses presented require either extreme assumptions in order to explain adequately the maintenance of sex or they have problems associated with them. For example, the mutation accumulation theories operate too slowly (Maynard Smith 1978, Howard and Lively 1998), require high rates of mutation (Kondrashov 1988, Charlesworth 1990), or do not explain the distribution of parthenogens. The Red Queen Hypothesis requires that parasites have severe fitness effects on their hosts (May and Anderson 1983, Howard and Lively 1994) and it is unlikely that frequency-dependent selection, by itself, can eliminate asexual clones (Lively and Howard 1994, Judson 1997, Lythgoe 2000). In addition, since parasites do not select for sexual reproduction per se, but for diversity, they could equally well select for the accumulation of clonal diversity; leading to the elimination of a sexual population by a diverse set of clonal genotypes (Lively and Howard 1994). For example, Lively et al (1990) showed that recently inbred sexual populations of *Poeciliopsis* had higher levels of trematodes than syntopic asexuals, and that the introduction of new genetic material into these populations caused a reversal in the pattern of parasitism.

Further to this, Doncaster et al. (2000) stated that the problem with sex is that its evolutionary advantage(s) have very little time to express themselves if an asexual invasion can seep through a sexual population in just a few generations. Asexual species may not outlast environmental change, but they could wipe out sexual ancestors before their own demise.

West et al. (1999) suggested that a pluralistic view, for example by combining the Red Queen hypothesis with a mutation-based hypothesis may offer a better explanation than any one of the different opposing hypotheses. This approach may overcome the problems mentioned above. A pluralist approach has been used by several authors. For example, Howard and Lively (1994) constructed a simulation

model which assessed the interaction between mutation accumulation (through Muller's Ratchet) and host-parasite coevolution. They found that in the short term, parasites prevented the fixation of clones and the elimination of sex, while in the long term, mutation accumulation led to the eventual extinction of clones (Howard and Lively 1994, 1998). Similarly, Hamilton et al. (1990) suggested that parasites may exacerbate the effects of intraspecific competition to produce a severe effect on the fitness of infected hosts (Hamilton et al. 1990). Computer simulations supported this idea, showing that the extra constraint of competing for shared resources may eventually cause either the sexual or asexual population to collapse. Also in a similar vein, Peck et al (1999) have shown how spatial structuring in a sexual population can delay migration through it by an asexual invader for a sufficient time to allow deleterious mutations to accumulate in the asexual population.

The merits and drawbacks of the various hypotheses put forward to explain the maintenance of sex continue to be investigated in a number of asexual / sexual systems. It is understood that the ecological and genetic constraints placed on one set of organisms is potentially different from that placed on another. Therefore different mechanisms may regulate the incidence of asexuality in different groups, and in addition more than one mechanism may be involved in any one system (i.e. the pluralist approach). It is with great interest, therefore, that I too delve in to the mysteries of why there is sex.

Asexuality in Australia

Kearney et al. (2003) noted that the Australian arid zone harbours a diverse collection of parthenogenetic taxa, with at least four well documented systems including the grasshopper *Warramaba virgo* (White et al. 1963), the gecko *Heteronotia binoei* (Moritz 1983), stick insects of the genus *Sipyloidea* (John et al. 1987), and trees of the *Acacia aneura* complex (Andrew et al. in press, as cited in Kearney et al. 2003). A study of geographical parthenogenesis in the first three of these complexes, found that in general there has been a strong tendency for parthenogens to originate via hybridization in the western part of the arid zone with subsequent eastward spread (Kearney et al. 2003).

Recently, a new case of vertebrate parthenogenesis was reported in the Australian arid zone in the lizard genus *Menetia*. Until recently, one widespread taxon, *Menetia greyii* was recognised. Indications of parthenogenetic lineages within *Menetia* first surfaced during a general herpetofaunal study in Western Australia, where several distinct taxa were identified within *M. greyii*, including apparent F1 hybrids (Alpin and Adams 1998). Parthenogenesis was formally described in 2003 after investigation of karyotypes, allozymes, mitochondrial DNA, cytology and sex ratios of populations in south-central Australia (Adams et al. 2003). These studies confirmed a clonal reproductive mode by comparing mulitlocus genotypes among mothers and offspring. Seven genetically distinct lineages were recognised in this region (Figure 1.1 shows their distribution) including; three sexual diploid lineages, SAN (SA (South Australian) north), SAS (SA south), SAR (SA "RP parent"), three parthenogenetic lineages, WP (widespread parthenogen), RPa (Riverland parthenogen "a"), RPb (Riverland parthenogen "b"), and one individual of uncertain status, PP ("putative" parthenogen) (Adams et al. 2003). The parthenogen forms of *Menetia* all appear to be triploid and all have high heterozygosity compared with the diploid sexual forms. This strongly suggests a hybrid origin of the parthenogens. Of the three sexual lineages identified, at least two (SAN and SAR) are distinct biological and evolutionary species (Avise 1994). The mtDNA and allozyme data suggest that the RPa and RPb parthenogens originated via hybridization between maternal SAR X paternal SAS ancestors. The mtDNA data were unable to identify a possible maternal ancestor for WP, but the allozyme data were most consistent with an origin involving SAN and one or both of SAR and SAS (Adams et al. 2003). Subsequently, and in this thesis, the RPa form has been called RP3 (Adams, pers. comm.). There is also considerable clonal diversity within the asexual lineages of *Menetia*, with 35 unique clones detected among 52 individuals (Adams et al. 2003). The total geographical distribution of the parthenogen and sexual lineages is yet to be determined, but the occurrence of apparent triploid individuals in the Carnarvon Basin region on the coast of Western Australia indicates that the parthenogens may be very widespread.

During collection, some areas were found where parthenogens and sexuals of the *M. greyii* complex occurred in sympatry (Adams et al. 2003). One of those areas was the Riverland area of South Australia.

These findings represent the first case of parthenogenesis recorded within the Scincidae, a successful and diverse lizard family, and only the second unequivocal example of unisexuality among the endemic Australian vertebrates. The first case was parthenogenesis in the gecko, *Heteronotia binoei* (Moritz 1983). They also break a world-wide discovery drought of parthenogen reptile genera (Adams et al. 2003), being the first new report for 20 years.

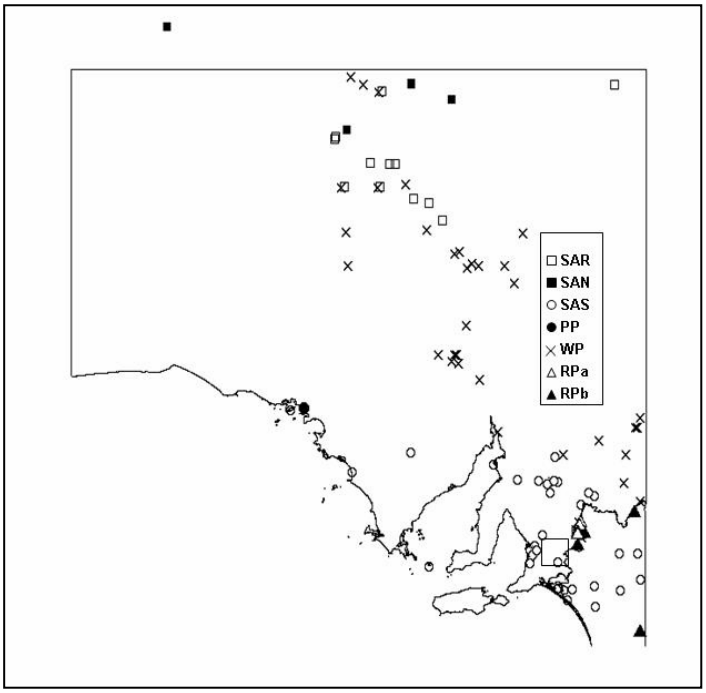

Figure 1.1. The distribution of parthenogenetic and sexual lineages identified within the M. greyii *complex in south-central Australia.*

Diagnostic Features for M. greyii (as taken from Adams et al. 2003)

In *M. greyii*, there are no obvious morphological features to either diagnose between different parthenogen forms or to distinguish between parthenogen and sexual forms. Therefore, a combination of mitochondrial DNA (mtDNA) and allozyme electrophoresis were used to determine the different taxa and their status.

Firstly, mtDNA in concert with allozyme overview data (obtained from frozen liver, or tail muscle) were used to identify the seven major evolutionary lineages present. Figure 1.2. represents the mtDNA gene tree obtained from the 92 *M. greyii* sequenced (Adams, 2003 #331). The comparative allozyme loci suggested that; SAN, SAS, and SAR are sexual, RPa, RPb, and WP are likely parthenogens, and the status of PP is unresolved.

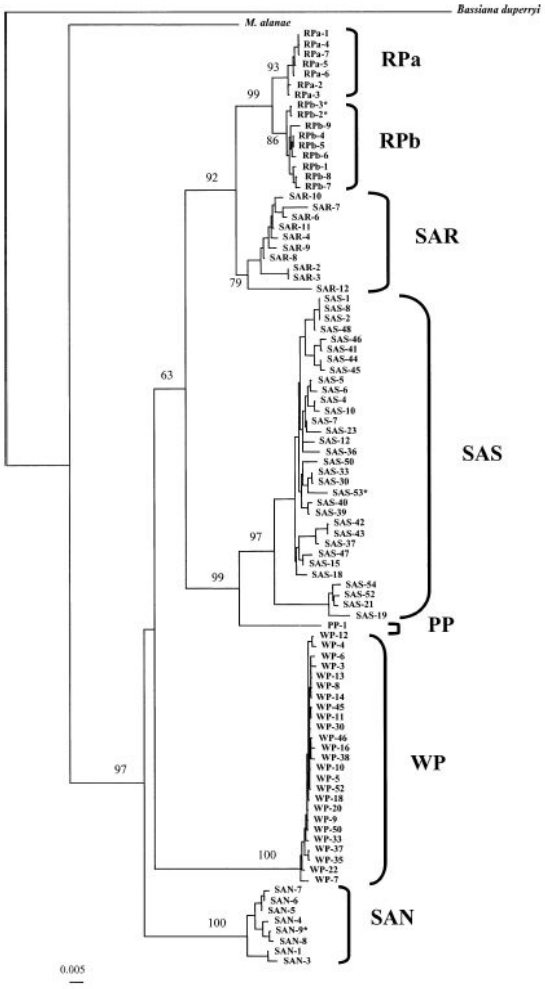

Figure 1.2. Neighbour-joining tree, based on Kimura 2-parameter distances, among mitochondrial nucleotide sequences of Menetia*, rooted using Bassiana duperreyi. Bootstrap proportions (above 70%) from 10000 pseudo-replications are indicated for the deeper nodes only. *= mitochondrial enrichment procedures used. Scale represents 0.005 substitutions per site (Adams et al. 2003).*

A principal coordinate analysis (PCA) of the genetic distance between individuals indicted that SAN, WP (as two distinct groups) and RPb represent three separate clusters and are distinguishable from a fourth cluster comprising SAS, PP, SAR, and RPa (Figure 1.3). Discrimination among these groups was largely due to allelic differences at eight key loci.

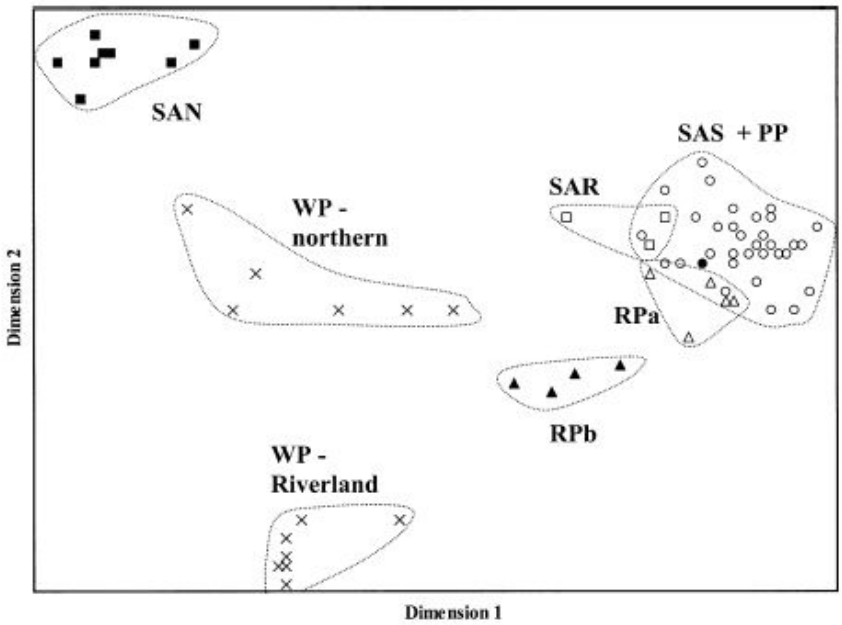

Figure 1.3. Principal coordinate analysis of the allozyme data from the overview study. The relative PCA scores have been plotted for the first and second dimensions, which individually explained 34% and 13% respectively, of the total multivariate variation.

Animals were readily classified into one of the seven existing lineages on the basis of using diagnostic allozyme profiles and geographic distribution data. For example, in areas of sympatry RPa individuals were distinguishable in sympatry from SAS by being highly heterozygous for differing suites of loci (Acon2, Enol2, Est2, G6pd, Glo, Pgm1, and Pgm2). Differences at the eight key loci also allowed WP parthenogens to be clearly distinguished from RPa parthenogens. For more details refer to Adams *et al.* (2003).

Other information supported the results determined by the mtDNA and allozyme data and the PCA, including;

- All suspected parthenogens were female, in contrast to SAN, SAS and SAR where males were as abundant as females.
- Karyotype analysis indicated that SAS display the standard 2N=30 karyotype found by Donnellan (1985) for *M. greyii*, whereas both WP and RPb animals are triploid 3N=45 (Figure 1.4).
- Parthenogenetic lineages displayed some allozyme phenotypes typical of triploids, and multi-locus "clones" were present whenever sample sizes allowed their detection (Table 1.1)

- In comparison with SAS, WP and RP3 displayed higher levels of heterozygosity for Allozyme loci and considerably lower levels of mtDNA nucleotide diversity.

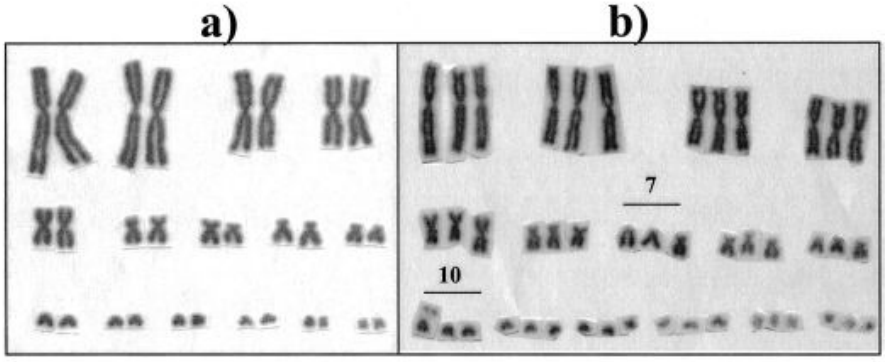

Figure 1.4. Representative karyotypes of diploid and triploid M. greyii. a) diploid male (from Donnellan 1985); b) triploid female WP. Heteromorphy is evident for chromosomes 7 and 10 in the triploid (Adams et al. 2003).

Table 1.1. Summary of some key biological attributes of each lineage. Data from the overview study were used to determine diagnostic allozyme profiles (i.e. the combination of alleles or genotypes which best diagnose the mtDNA lineages, using SAS as a reference profile) and observed heterozygosity levels (Ho; direct count). Sex ratio, females:males (Adams, 2003).

Taxa	Diagnostic Allozyme profiles (vs. SAS)	*Ho* (+/-SE)	Pi	Sex ratio	Ploidy	Inheritance data	Multilocus clonality	Allozyme phenotypes
SAN	*Adh2*; *G6pd; Gpi; Idh1; Sordh*	0.073± 0.027	0.0104	5:5	?	-	No	Diploid
SAS	Not applicable	0.119± 0.035	0.0190	26:23	2*N* (n=3)	Mendelian (n=1)	No	Diploid
SAR	No diagnostic differences; allele frequency differences at *Acon2, Me2, Pgm1*	0.119± 0.039	0.0157	5:6	?	-	No	Diploid
PP	None	0.179± 0.074	-	1:0	?	-	-	3 Alleles at Acon2
RPa	Many heterozygotes at *Acon2, Enol2, Est2, G6pd, Glo, Pgm1, Pgm2*	0.239± 0.072	0.0015	7:0	?	-	Yes (3 clones)	Dosage at *Acon2, Glo, Pgm1*
RPb	Many heterozygotes at *Adh2, G6pd, Idh1, Me2, Pep-B, Pgm1*	0.256± 0.079	0.0035	7:0	3N (n=2)	Clonal (n=2)	Yes (4 clones)	3 alleles at *Pgm1*; dosage at *Idh1, Pep-B, Pgm1*
WP	Many heterozygotes at *Acon2, Adh2, Ak2, Dia, Est2, Fum, Glo, G6pd, Gpi, Idh1, Me2, Pep-B, Pgm1, Sordh*	0.457± 0.077	0.0020	47:0	3N (n=3)		Yes (35 clones)	3 alleles at *Adh2, Gpi, Pgm1;* dosage at *Acon2, Glo, Gpi, Idh1, Pgm1*

The diagnostic (genetic and biological) features for the seven lineages identified by Adams et al (2003) are summarised in Table 1.1. The same methods were used to identify and distinguish between sexual and parthenogen lineages in the current study. This was undertaken at the South Australian Museum by Mark Adams and Ralph Foster. In the current study RP3 individuals are equivalent to RPa individuals in the above description.

The study system*: Menetia greyii*

The original taxon, *Menetia greyii* Gray 1845. is described as a small (average snout-vent =30mm), brown-grey, diurnal, terrestrial skink that is widely distributed throughout mainland Australia (Figure 1.5). It is found in a wide variety of habitats from dry sclerophyll forest and temperate and tropical woodlands, to mallee, and other arid scrubs and hummock grasslands (Cogger 2000).

Figure 1.5. Menetia greyii.

Little is known of the general biology and niche requirements of *M. greyii*. Some basic work has been done on its critical thermal maxima (Greer 1980) and natural history (Smyth and Smith 1974). These studies showed that four *Menetia* individuals where able to tolerate temperatures between 44.4 and 45.2 ^{o}C for 30 minutes, and they displayed panting behaviour. However, it is not known if the lizards used in these studies were sexuals or parthenogens. No no ecological or behavioural study has been carried out since the discovery of parthenogenesis in this lizard. I present the first descriptions of the niche characteristics, reproduction, physiology, competitive interactions and parasite susceptibility of a single assemblage of sexual and parthenogen *Menetia greyii*. My prime aim was

to determine and quantify any ecological differences between the reproductive modes that might reduce competition and allow coexistence.

The Study Population

The study population occurs near Bundey Bore station in the semi-arid region of South Australia (approximately 160km north east of Adelaide, Figure 1.6). The area has vegetation dominated by chenopod shrubland, and is characterised by a number of abandoned farm buildings now in ruins. The area is similar in habitat and climate to other sites in the region where both sexual and parthenogenetic *Menetia greyii* have been found previously (Adams et al. 2003). Annual rainfall in the region (measured at Bower 25km south of the study area) averaged 310mm over 1990-2000, with a mean of 92mm in the spring months Sept-Nov when the liards appear to be most active. In the study years 2001, 2002, and 2003 annual rainfall was 261mm, 114mm, and 273mm with 110mm, 24mm, and 81mm falling in the study months Sept-Nov. In 2002 the study area had the lowest rainfall recorded since recording started at Bundey Bore in 1927. Average daily maximum temperatures for the months the study was conducted in (measured at Eudunda 30km west of the study area) were 19°C (2001), 22°C (2002), and 20.5°C (2003).

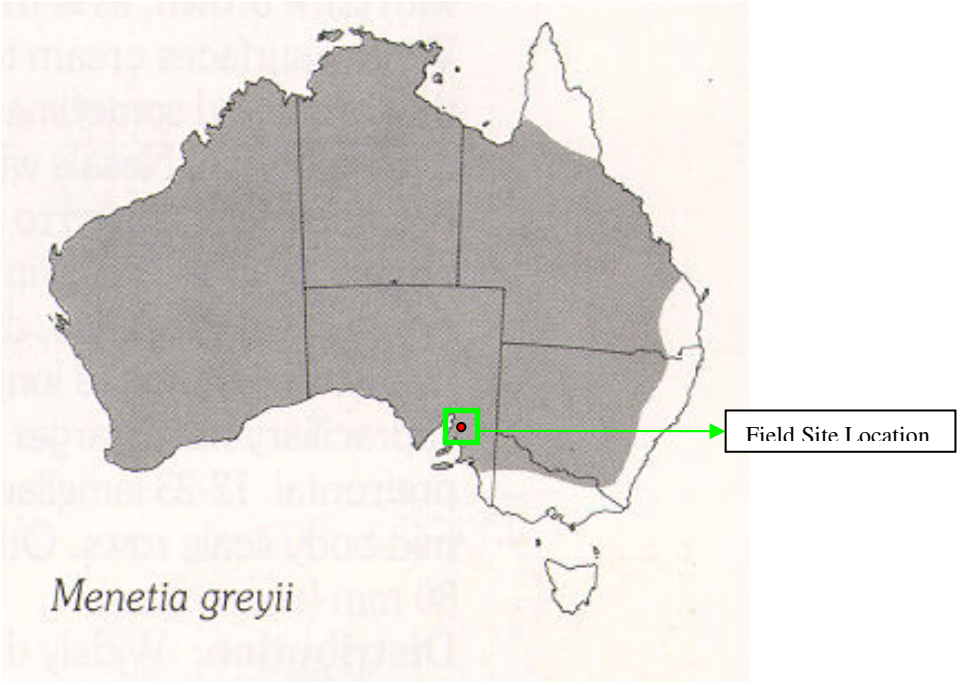

Figure 1.6. Distribution of Menetia greyii *within Australia (shaded area), and the location of the field site (Bundey Bore) for the current study.*

Chapter 2

General Methods

The methods for each experiment are explained within the relevant chapters. Described below is some of the general information that was applicable in more than one chapter.

Definitions

SAS	Sexual taxon (males and females)
SASm	Sexual males
SASf	Sexual females
WP	WP parthenogens
RP3	RP3 parthenogens
SASmt	Tetraploid males

Statistical Analyses

All statistical analyses were undertaken using the Statistical Package for the Social Sciences (SPSS).

For data that did not conform to the assumptions of the relevant statistical test, a series of transformations of the data were undertaken in order to attempt to get the data to comply with the assumptions. The transformation used, was the one that best met the assumptions. If a successful transformation could not be found, non-parametric tests were used. Table 2.1 below outlines the assumptions for each of the tests utilised in this thesis, the methods used to test that these assumptions are met, and the non-parametric equivalents for situations were transformations were not found to be suitable.

The specific tests used are explained in more detail throughout the results section of each of the chapters.

Table 2.1. Summary of the statistical tests used.

Statistical Test	**Assumptions**	**Methods of testing assumptions**	**Non-parametric Equivalent**	**Post-hoc tests**
ANOVA (analyses of variance)	Homogeneity of Variance Normality of residuals	observing QQ plots, skewness & kurtosis values.	Kruskal Wallis	For comparisons with equal sample sizes = Tukey For comparisons with unequal sample sizes = Bonfferoni If a significant difference was found using Kruskal Wallis, Mann-Whitney U tests were used to compare between each pair
ANCOVA(analyses of variance with covariate)	Homogeneity of Variance	Levene's test,		
Repeated Measures ANOVA	Normality of data	observing QQ plots, skewness & kurtosis values.		
	Sphericity condition	Mauchley's test		
Paired t-tests	Normality of data	Observing QQ plots		-
Independent t-tests			Mann-Whitney U test	-
Pearsons Correlation	Linearity	Plot of the residuals		-
	Homogeneity of Variance			
	normality	Observing QQ plot		

Proportions or frequencies were compared using a Contingency Chi-square test (X^2). In situations were cells had a value less than five, a Fisher's exact test was used.

Intact Tails

Where I refer to the lizards having 'intact' tails for experimental trials, this means that the tails have regenerated to full length (after the tip being removed for genetic typing).

Chapter 3

Ecology of sexual and parthenogenetic *Menetia greyii* at Bundey Bore

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Introduction

There are three modes of unisexuality; gynogenesis, hybridogenesis, and parthenogenesis. Gynogens and hybridogens must coexist with their sexual congeners as they rely on sperm from a closely related sexual species to reproduce. Parthenogens on the other hand can survive isolated from sexual taxa, and several theories predict that parthenogens and sexuals should rarely persist in sympatry, either because of reproductive advantages to parthenogens or superior competitive abilities of sexuals. The weed hypothesis put forward by Wright and Lowe (Wright and Lowe 1968), and theories established by Maslin (1968, 1971) and Cueller (1977) predict that parthenogens are competitively inferior and thus can only persist in novel and/or highly disturbed habitats where sexual forms do not occur. Studies have shown that the geographical distribution of parthenogens and sexuals can differ, with the parthenogens being predominant at higher altitudes, on islands, or in island-like habitats and in more disturbed habitats (Glesner and Tilman 1978, Bell 1982). The distribution of parthenogenetic *C. laredoensis*, (Walker et al. 1989) and of sexual and parthenogenetic lineages of *Heteronotia binoei* in Australia (Kearney 2003) support these theories. Another theory is that sex is favoured over parthenogens in environments of high biotic uncertainty since recombination is necessary for effective coevolution with predators, parasites and competitors (Jaenike 1978a, Hamilton et al. 1990, Lively et al. 1990) resulting in parthenogens being restricted to sparsely populated environments were biotic interactions are weak (Glesner and Tilman 1978, Hamilton et al. 1990). In addition the proposed disruptive effects of hybridization (Cueller 1977, Lynch 1984), lead to a prediction that parthenogens should only persist where sexual species are absent.

However, there are numerous published examples of coexistence of parthenogenetic and sexual lizards (Zweifel 1965, Echternacht 1967, Case 1990, Paulissen et al. 1992, Casas-Andreu and Gurrola-Hidalgo 1993, Cueller 1993, Price et al. 1993, Bolger and Case 1994, Paulissen 2001). The commonly reported coexistence of parthenogens and sexuals has promoted many researchers to compare the ecology of both sexual and parthenogenetic lizards, as well as coexisting clonal lineages with a prediction of ecological differences allowing coexistence. The majority of this work has been done with parthenogenetic and sexual lizards of the *Cnemidophorus* group (whiptail lizards). From these studies some ecological differences have been recognised although the results are varied and sometimes contradictory.

Sexuals and parthenogens have been found to differ in their microhabitat use (Cueller 1993), and parthenogens have been found to occupy a greater variety of habitats than sexuals (Hanley et al. 1994). Differences in diet have also been found with some studies showing that parthenogenetic *Cnemidophorus* have broader diets (Paulissen et al. 1992, Hanley et al. 1994), while in another study sexuals were found to possess wider diet niches than parthenogens (Case 1990). In other studies subtle differences have been discovered in macrohabitat and microhabitat use (Mitchell 1979), foraging behaviour (Echternacht 1967), and prey choice (Paulissen et al. 1988a). However in these latter studies, high niche overlaps were noted and ecological differences between sexual and parthenogenetic species were determined to be minimal (Echternacht 1967, Mitchell 1979, Paulissen et al. 1988a).

There are also studies where differences in ecology between sexual and parthenogenetic lizards were not found, including no differences in activity time (Medica 1967, Casas-Andreu and Gurrola-Hidalgo 1993, Paulissen 2001), microhabitat use (Casas-Andreu and Gurrola-Hidalgo 1993, Paulissen 2001), body temperature (Casas-Andreu and Gurrola-Hidalgo 1993) and diet (Echternacht 1967, Medica 1967).

The general conclusion, particularly for *Cnemidophorus* lizards, is that parthenogenetic and sexual taxa occupy very similar ecological niches (Price

1992, Price et al. 1993). Thus, the question of how parthenogenetic and sexual taxa coexist is still largely in debate, and a subject that continues to be investigated.

Two main and contrasting hypotheses have been put forward to explain what factors combine to allow this observed coexistence of sexuals and parthenogens. The 'frozen niche variation model' (FNV) (Vrijenhoek 1984a) suggests that multiple hybrid origins can produce a variety of coexisting clones with individually narrow but collectively diverse niches. Each clone should successfully compete with sexuals in its narrow niche, but the sexuals should persist due to their wider niche breadth and hence ability to use resources not used by the parthenogens. In contrast, the 'general purpose genotype' model (GPG) (Lynch 1984) predicts that parthenogens possess a broad ecological niche and are capable of exploiting a wide range of habitats and conditions. Thus, even though they may compete with sexuals, this broader range serves as a refugium. The GPG model suggests the presence of only a single clonal lineage coexisting with one or more sexual lineages. Several of the studies comparing the ecology of sexual and asexual forms have addressed the predictions of these contrasting hypotheses, with some finding support for the FNV model (Bulger and Schultz 1979, Vrijenhoek 1979, 1984a, Case and Taper 1986, Paulissen et al. 1988a, Schenck and Vrijenhoek 1989, Case 1990, Weeks et al. 1992, Bolger and Case 1994), while others found support for the GPG model (Uzzell and Darevsky 1975, Hanley et al. 1994, Vrijenhoek 1994, Jacobsen and Forbes 1997, Jaenike and Dombeck 1998, Schlosser et al. 1998).

Since the discovery of parthenogenetic lineages within the *Menetia greyii* complex (Alpin and Adams 1998), seven genetically distinct lineages have been recognised in south-central Australia , including; three sexual diploid lineages, and four triploid parthenogenetic lineages (Adams et al. 2003). During collection some areas were found where parthenogens and sexuals occurred in sympatry (Adams et al. 2003), suggesting that this complex could be valuable for testing theories on the maintenance of sex and the factors that allow coexistence between sexual and asexual organisms.

Hypotheses, Aims and Predictions

The current study investigated the ecology and distribution of a mixed population of sexual and parthenogen *M. greyii*. Since few details have been published of the ecological requirements of the taxa of *M. greyii*, and because the genetics of the complex as a whole are still in early development, the first aim was to identify an area within south-central Australia where genetically recognised forms of *M. greyii* can be found, and where sexual and parthenogenetic lineages both occur. Subsequent aims were:

1) to determine how many distinct genetic lineages existed within this area
2) to determine if the different lineages occur in local sympatry or allopatry
3) to describe the morphology and ecological characteristics of each lineage including, micro and macrohabitat requirements, and incidence of predation.
4) to compare the morphology and ecological requirements;
    a. between sexuals and parthenogens
    b. between parthenogenetic lineages
5) To discuss the results in context of the competing theories put forward explaining either a) the lack of coexistence, or b) the occurrence of coexistence.

It is predicted that if the principles of the Weed Hypothesis apply to this complex, there should be evidence of the parthenogens and sexuals partitioning resources at the macrohabitat level and thus occurring in local allopatry. The parthenogens would inhabit the more modified and disturbed habitats.

If local sympatry occurs with sexuals and parthenogens sharing macrohabitats, then it would be expected that habitat partitioning at the microhabitat level would occur in order to reduce competition. In this case, the FNV model would predict that more than one parthenogenetic lineage would occur in the area, and that the distinct parthenogens would possess different habitat niches that are narrower than, and encompassed within, the habitat niche of the sexuals. The GPG model would predict there to be a single broadly adapted parthenogen, with a habitat niche wider than that of the sexuals.

Methods

The study area

The study of the ecology of *M. greyii* was conducted during spring and early summer (Sept-Nov) over three consecutive years (2001-2003) in an approximately 1400 ha area located in semi-arid South Australia, 160km north east of Adelaide, near to Bundey Bore homestead. The area has vegetation dominated by chenopod shrubland, and is characterised by a number of abandoned farm buildings now in ruins. The area is similar in habitat and climate to other sites in the region where both sexual and parthenogenetic *Menetia greyii* have been found previously (Adams et al. 2003). Annual rainfall in the region (measured at Bower 25km south of the study area) averaged 310mm over 1990-2000, with a mean of 92mm in the months Sept-Nov. In the study years 2001, 2002, and 2003 annual rainfall was 261mm, 114mm, and 273mm with 110mm, 24mm, and 81mm falling in the study months Sept-Nov. Average daily maximum temperatures for the months the study was conducted in (measured at Eudunda 30km west of the study area) were 19^{o}C (2001), 22^{o}C (2002), and 20.5^{o}C (2003).

A total of 13 sites were actively searched within this area (Figure 3.1), across six different habitat types (Figure 3.2), reflecting the heterogeneous habitat use recorded for *Menetia greyii* (Cogger 2000). These sites represent the total range of major habitat types available in the area. Two or three sites of each habitat type were searched, usually greater than 1km apart. The alternate habitat types potentially provide a wide array of available habitats differing in structural aspects, ground cover percentage and sun exposure. The study area is characterised by a flat topography and elevation of all the sites was approximately the same. The sites and habitats used in this study are described below;

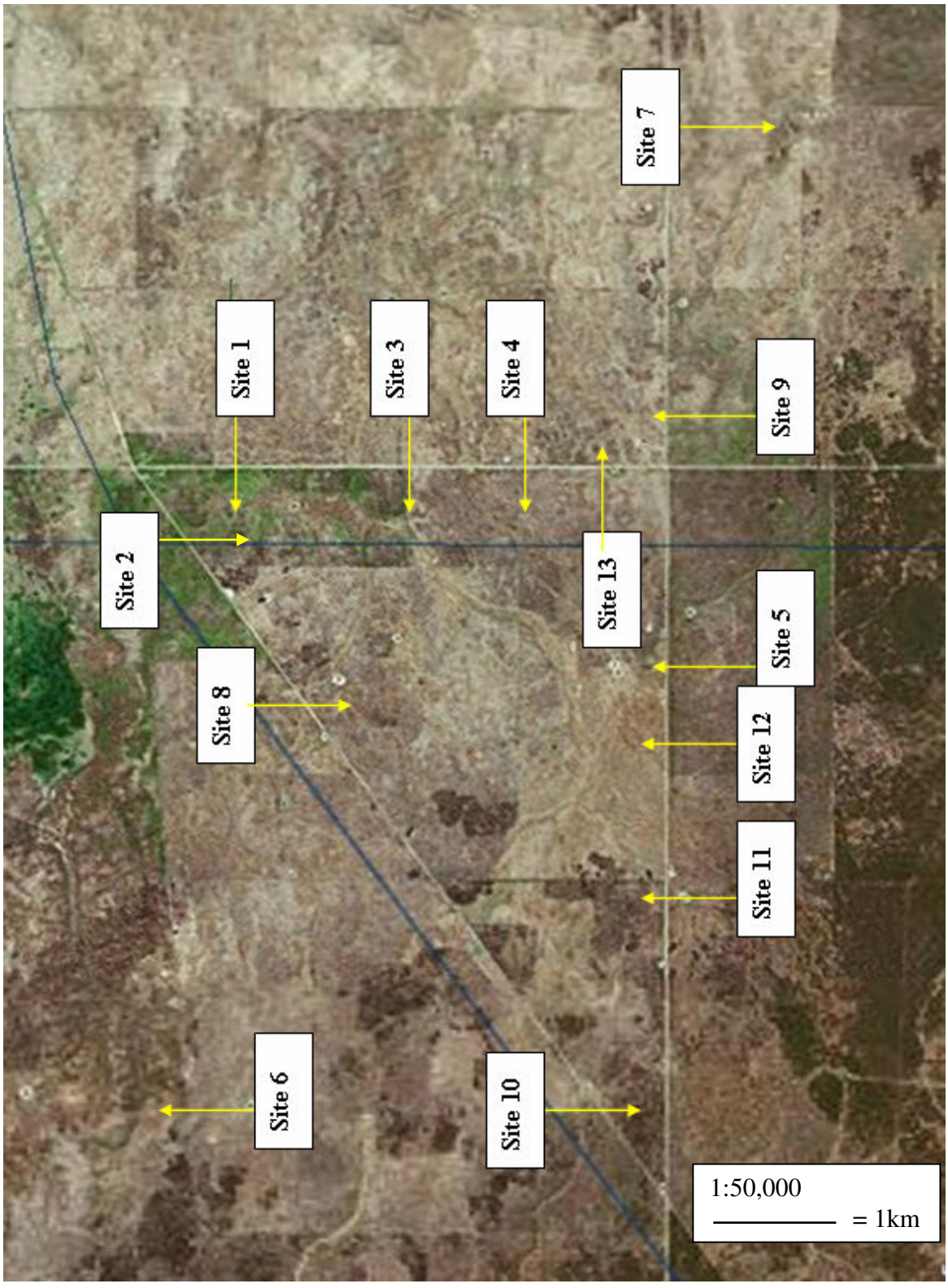


Figure 3.1. The locations of the 13 sites actively searched for Menetia greyii.

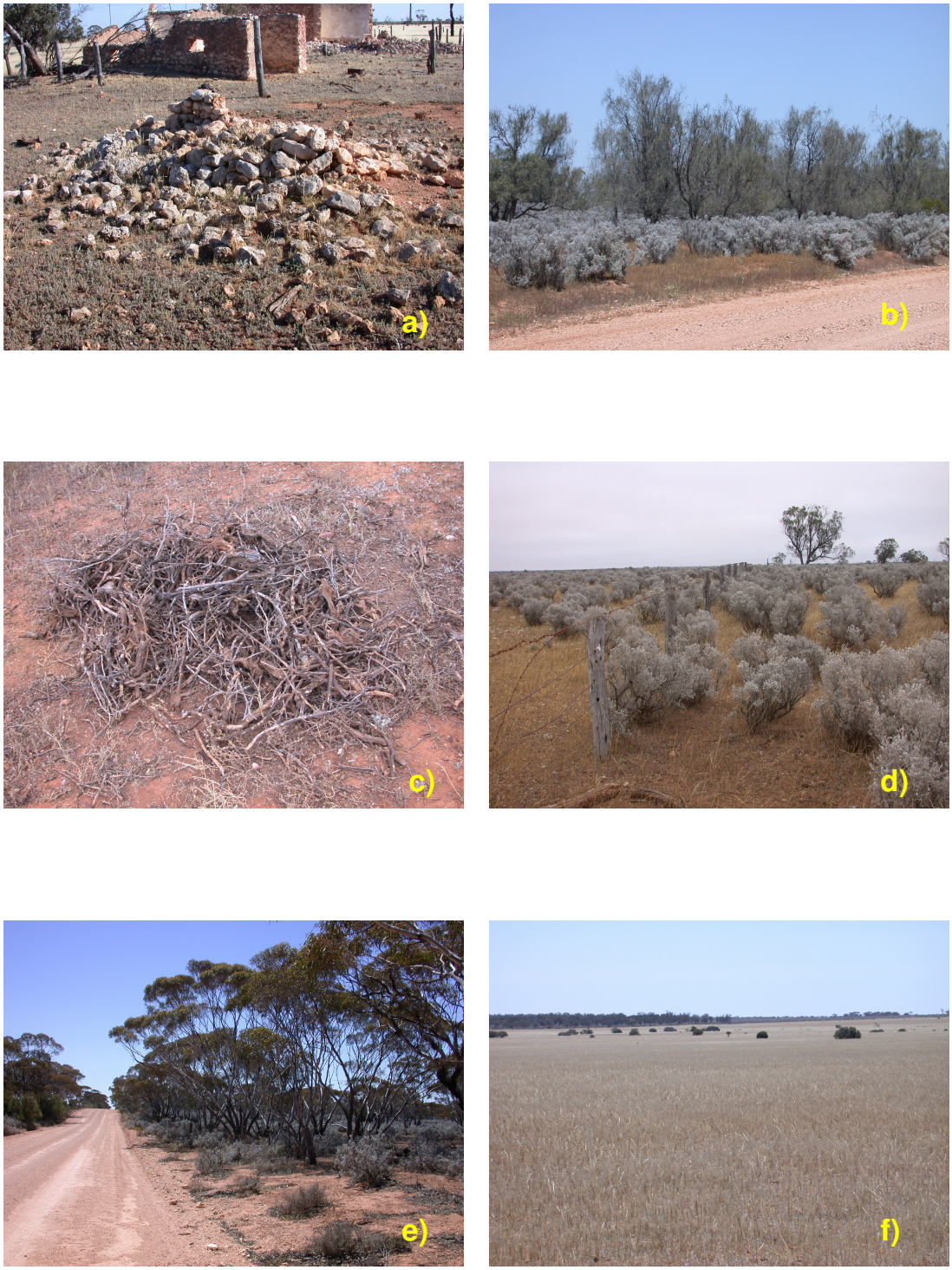


Figure 3.2. The six different macrohabitat types actively searched for Menetia greyii. *Where a) ruins, b) sheoak, c) dfob, d) blue bush, e) mallee, f) grassland*

Habitat Types

Bluebush, (Sites 1 & 2)

These sites occurred in chenopod woodland dominated by blue bush (*Maireana sedifolia*). The area of each bush averaged 2.89m^2 (SE=0.63) (Kerr et al. 2003), and were spaced approximately 3-4m apart at both sites. Open ground constituted 70% of the area between the bushes, while the other 30% was made up of several daisies (including; variable daisy (*Brachycome ciliaris var ciliaris*), dwarf brachycome (*Brachycome lineariloba*), and the minny daisy (*Minuria leptophyla*)), and introduced annual plants including wards weed (*Carrichtera annua*), Salvation Jane (*Echium plantagium*), and sow thistle (*Sonchus oleraceous*). All of these plants provide visual cover for lizards. There were no large trees at these sites. The area searched in each site was approximately 50mX40m.

Bluebush with dead bushes, (BB&db) (Sites 3 & 4)

Sites 3 and 4 were similar to sites 1 and 2 except they each included a fence separating two paddocks. Along the fence line dead blue bushes occurred approximately 45m apart (mean= 44.30m; SE= 4.30). These plants had been destroyed when the fence lines had been installed roughly 60 years ago. Now they represent piles of debris covering 1m^2 close to the ground and provide lizard shelter. The sites were surveyed by walking 520m (site 3) or 1.2km (site 4) along the fence lines and inspecting each dead bush by lifting the branches and raking through the soil and debris underneath. Fourteen bushes were sampled at site 3 and twenty three bushes at site 4. The dead bushes were numbered and permanent markers were attached for easy identification within and between seasons.

Ruins (Sites 5, 6 & 7)

The open ruins sites consisted of piles of rocks, sheets of tin, tree debris, fallen logs and old fence posts. Vegetation was scarce, only covering approximately 20% of the ground, with primary plants being grasses and wards weed. Two *Eucalyptus oleosa* trees occurred at site 5, and one at each of sites 6 and 7. Sites 5 & 6 were small areas approximately 20mX15m and site 7 was larger, 50mX40m.

Sheoak (Sites 8 & 9)

These sites were dominated by Sheoak trees (*Casuarina cristata pauper*) with scattered blue bush (approx. 10m apart). Tree debris (bark and leaf litter) covered approximately 75% of the ground and fallen branches were common. The area searched in each site was 40mX40m.

Mallee (Sites 10 & 11)

The mallee habitat consisted of several species of Eucalypt (*Eucalyptus gracillis, E. oleosa, and E. socialis*), over scattered bluebush (approx. 15m apart). There was a dense ground cover (approx. 80%) of tree debris and fallen branches were common. Search area was approximately 40m X 40m at both sites.

Grazed grassland (Sites 12 & 13)

The open grass areas had recently been grazed by sheep, and contained many small rocks and fallen logs. No vegetation other than exotic grasses and other weed species occurred within these areas, and the height of vegetation never exceeded 4cm. An area of 20m X 20m was searched at site 12 and 30m X 20m at site 13.

Table 3.1 shows the number of lizards caught each day via active searching (within the habitats described above) in each of the nine field trips (three per year). The number of lizards caught varied greatly across days, with a minimum of zero lizards and a maximum of 19 lizards caught on any day. This suggests that despite our intensive searching within all of the described habitats, lizards potentially occur in the areas that were searched, but in which lizards were not observed and caught. These areas may represent differences in habitat use. We can only assess data for areas where lizards were found and this may not represent the true distribution of *M. greyii* at Bundey Bore.

Table 3.1. Number of M. greyii *caught on each day of the nine field trips undertaken.*

Trip #	Date	# lizards caught	Trip #	Date	# lizards caught	Trip #	Date	# lizards caught
1	15.09.01	5	**4**	18.09.02	0	**7**	17.09.03	0
	16.09.01	15		19.09.02	2		18.09.03	2
	17.09.01	1		20.09.02	3		19.09.03	4
	18.09.01	6		21.09.02	11		20.09.03	12
	19.09.01	9		22.09.02	6		21.09.03	2
2	08.10.01	2	**5**	14.10.02	1	**8**	25.10.03	1
	09.10.01	0		15.10.02	1		26.10.03	0
	10.10.01	2		16.10.02	10		27.10.03	0
	11.10.01	1		17.10.02	8		28.10.03	6
	12.10.01	1		18.10.02	0		29.10.03	7
3	08.11.01	4	**6**	10.11.02	3	**9**	09.11.03	4
	09.11.01	17		11.11.02	5		10.11.03	7
	10.11.01	3		12.11.02	19		11.11.03	0
	11.11.01	4		13.11.02	10		12.11.03	0
	12.11.01	4		14.11.02	2		13.11.03	3

In conjunction with active searching, drift-fence pitfall trapping was utilised as it has been a successful method of capturing *M. greyii* in the past (Braithwaite 1983). A pitfall line was established adjacent to one of the sites within each of the habitat types described above. Therefore, a total of six pitfall lines were installed across the area. The traps used were plastic buckets 20cm deep and 14cm in diameter. Ten traps were used for each pitfall line and were placed in the ground so that the lip of the bucket was level with the soil surface. A plastic drift fence (0.4m x 33m) was used and was laid in a straight line and straddled the traps which were spaced at 3m intervals. The traps were left open for four consecutive days in each of the months September, October and November, 2001. Traps were checked in the early morning (between 0530hrs and 0630hrs), mid afternoon (between 1200hrs and 1300hrs) and late evening (between 1800 and 1900hrs) on each day. This trapping method was not employed in the 2002 and 2003 seasons, since it proved to be an ineffective means of capturing *M. greyii* at Bundey Bore. In the 2001 season a total of 12 trapping days were undertaken without a single capture of *M. greyii*.

Data collection

Taxa present, abundance, morphology, habitat use

In each of the three field years, all sites were searched twice in each of the months September, October and November, giving a total of 18 search sessions per site over the course of the study. Equal searching time of approximately four person-hours (2hrs x2 people) per search session was spent in blue bush, BB&db, ruins and sheoak habitats. Thus these sites were searched for eight person-hours per month, 24 person-hours per season and 72 person-hours overall. About half that time (2 person-hours per search session) was spent searching in Mallee and grassland habitats.

Lizards were captured by hand usually during the first four - five hours of sunlight and late evening when the temperature was lower and the lizards were slower and easier to catch. In all the sites, searching involved walking through the habitat looking under any possible retreat sites including logs, dead bark and debris, tin, rocks, and old fence posts. In addition in the mallee and sheoak habitats dense leaf litter was searched using a hand rake, and in the BB&db habitat the dead bushes were pulled apart by hand and the soft sand underneath was raked. All refuge material was replaced after searching.

Upon capture the lizards were assigned a number and placed in individual containers. The date, time, sex, status (adult or non-adult), macrohabitat, microhabitat, and whether found alone or with other lizard(s) were noted. If found under a dead bush in the BB&db habitat, the bush identification number was recorded. Sex was determined via ventral colouring, with females displaying a white-cream and males yellow-orange ventral colour (Figure 3.3). Lizards were considered to be adult if their SVL exceeded 29mm, the size of the smallest reproductive lizard detected. There were six possible macrohabitat classes corresponding to the six habitat types present within the study area. Microhabitat classes were identified for the ruins sites only, as this was the only habitat in which a variety of microhabitats was recognised. The microhabitats were 1)fence post (included old fence posts and pieces of wood of approximately the same size), 2)tin, 3)rock, 4)leaf litter (included all tree debris), 5)log (very large fallen tree trunks).

Collected lizards were transported to the Animal Care Unit at Flinders University of South Australia where weight (nearest 0.001g on a Mettler scale), snout-vent length (SVL) (to nearest 0.5mm), tail length (to nearest 0.5mm), and tail condition (complete, regenerated, or broken) were recorded. Possible gravid females were also noted.

Figure 3.3. Yellow-orange underbelly colouring of male Menetia greyii.

Genetic Identification of taxa

Tips of the tails were removed by manually inducing autotomy by pressing down on the tail approximately 10-15mm from tip. Each tail tip was placed in an ephindorph tube marked with the lizard number and date. The tubes were then stored in liquid nitrogen for transportation to the South Australian Museum. Allozyme and mitochondrial DNA analyses were then performed on the tail muscle by Mark Adams in the Evolutionary Biology Unit of the museum to identify the lineages present within the study area. The procedure was the same as that in Adams et al (2003). For further details on the diagnostic features refer to pages 26 –31 in the introduction.

Spatial Niche breadth & overlap

Data from habitats (macro and micro)were used to estimate niche breadth and overlap for each type. Niche breadth was calculated using Simpson's (1949) index of diversity

$$1/\sum P i^2$$

where *pi* is the proportion of the *i*th habitat category used. Niche breadth was then standardised by dividing by the number of different habitat categories, *n*.

Niche overlap values were determined using the formula (Pianka 1973),

$$\frac{\sum P_{ij} P_{ik}}{\sqrt{\sum P_{ij}^2 \sum P_{ik}^2}}$$

where P*ij* and P*ik* are proportions of the *i*th habitat used by the *j*th and *k*th species, respectively. Overlap values obtained from this equation vary from zero (no overlap) to one (complete overlap).

Four macrohabitat types were used in the analysis, bluebush, bluebush with dead bushes (BB&db), sheoak and ruins. Mallee and grassland habitats were omitted from niche breadth & overlap calculations because no *Menetia* were found there.

Microhabitat niche breadth and overlap were only calculated for lizards captured in the ruins. Five microhabitat types were used in the analysis, fence post, tin, leaf litter, rock and log (Figure 3.4).

Statistical Analyses

Statistical procedures used are explained throughout the results section.

Figure 3.4. The five different macrohabitat types utilised by Menetia greyii *within ruins. Where a) tin, b) log, c) rock, d) fence posts, e) leaf litter.*

Results

Lineages present and abundance

Three genetically distinct lineages were found in the study area. All three taxa were reported by Adams et al (2003) in their study of *M. greyii* in South Central Australia. There was one sexual taxon (SAS – South Australian sexual) consisting of diploid males and females, and two all female triploid parthenogenetic taxa; WP (the widespread parthenogen) and RP3 (the Riverland parthenogen, RPa). In the 2003 season five tetraploid SAS males (constituting 2.5% of total lizards caught) were also found. Microsatellite profiles suggest that these males probably arose from hybridization between a WP parthenogen and a SAS male. These five males were not included in any of the analyses. The sexual taxon (SAS) is unlikely to be the direct ancestor of the WP parthenogen, but is potentially the paternal ancestor of the RP3 parthenogen (Adams et al. 2003).

In analyses sexual males and females were treated separately to determine any sexual differences, and to allow direct comparison between parthenogenetic and sexual females. Thus there were four types; sexual males (SASm), sexual females (SASf), and the two parthenogens (WP & RP3).

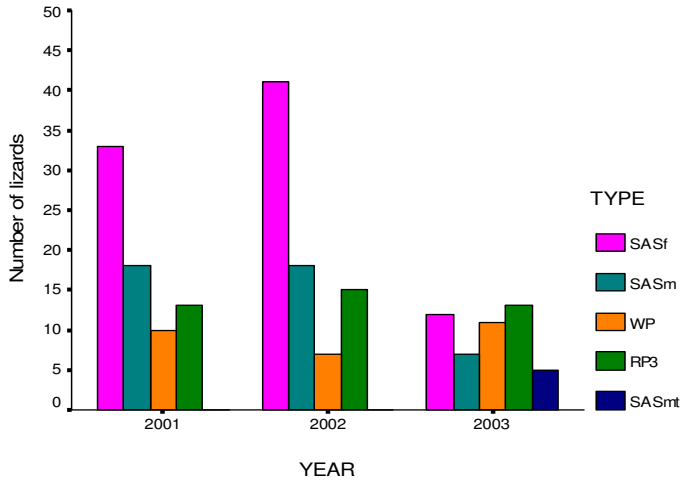


Figure 3.5. The number of sexual females (SASf) and males (SASm), tetraploid males (SASmt), and parthenogens (WP & RP3) caught in each season.

The number of captures of each type in each year is shown in Figure 3.5. A total of 203 *M. greyii* were caught over the three years and the order of abundance was sexual females (86 individuals) > sexual males (43 individuals) > RP3

parthenogens (41 individuals) > WP parthenogens (28 individuals) > tetraploid males (5 individuals). Sex-ratio bias is evaluated in Chapter 4, page 70.

When considering the years separately, numbers of each parthenogenetic lineage remained about the same in all three years, whereas the abundance of SAS males and females were considerably lower in 2003 than in the previous two years.

Relative abundances were similar between 2001 and 2002, with SAS females being by far the most abundant form (44.6% & 50.6%), followed by SAS males (24.3% & 22.2%), RP3 clones (17.6% & 18.5%) and lastly WP clones (13.5% & 8.6%). In 2003 the relative proportions changed due to the lower numbers of sexual males and females caught. In 2003 RP3 parthenogens were the most abundant (30.2%), followed by SAS females (27.9%), WP parthenogens (25.6%), and SAS males were the least abundant (21.7%).

Macrohabitat

Distribution & niche breadth- No *Menetia greyii* were found in mallee or grazed grassland in any year. The distribution of each type in the four other macrohabitats for each season and pooled over all years is shown in Figure 3.6 and Figure 3.7 respectively.

Sexual males and females had very similar distributions in 2001 and 2002. In 2001 both were found in all four habitats, with the majority being found in the BB&db, and in 2002 both were found in all habitats except for sheoak, with the greatest numbers being found in ruins. In 2003, sexual females were again found in all habitats except sheoak, with most being in BB&db and ruins, whereas males were only found in BB&db and ruins with the majority being found in the former. RP3 parthenogens were never found in the sheoak habitat. Apart from this they were found in the same habitats as males in each season, and numbers were always greatest in BB&db. WP parthenogens were only ever found in BB&db. Thus, in general, the SAS and RP3 taxa occurred over the same range of habitats, with the exception that no parthenogens were found in the sheoak sites. The WP parthenogens showed a much more restricted distribution.

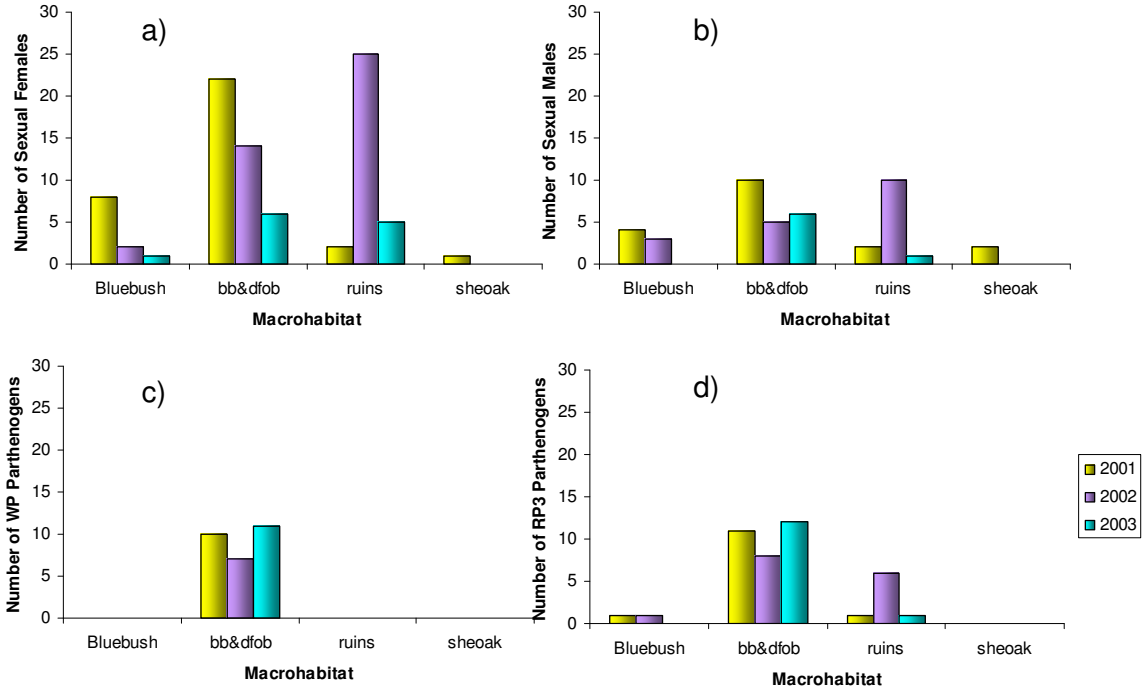


Figure 3.6. Number of a)sexual females, b) males, c) WP parthenogens and d) RP3 parthenogens collected in bluebush, BB&db, ruins and sheoak macrohabitat, in each year of the study.

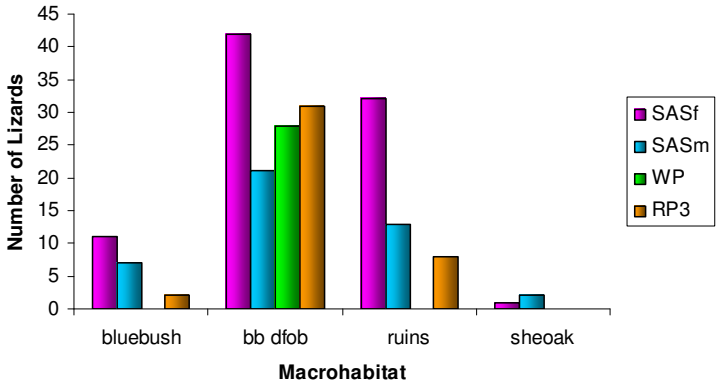


Figure 3.7. Number of each type collected in bluebush, BB&db, ruins and sheoak macrohabitat pooled over all years.

The proportion of captured lizards of each type, occupying each macrohabitat (pooled over all years) was compared using contingency chi-squared test. It was also necessary to pool data for the bluebush and sheoak habitats due to the small number of captures in these habitats. Macrohabitat comparisons could not be made statistically among years because many expected values were less than five. This overall difference in macrohabitat utilisation among the four types was significant (X^2=31.885, *df*=6, p<0.001).

The above distributions are reflected in the niche breadth of each type (Table 3.2). SAS females possessed a broad macrohabitat niche in all three years of the study, SAS males generally exhibited higher niche breadth than RP3 parthenogens, and both types had broad niches in 2001 & 2002, and a narrower niche in season 2003. WP parthenogens displayed the narrowest niche breadth in each year. Overall the macrohabitat niche breadth was broad for sexuals, and narrower for parthenogens.

Table 3.2. Macrohabitat niche breadth values for each year and overall (years pooled)

YEAR	SASf	SASm	WP	RP3
2001	0.492	0.653	0.250	0.344
2002	0.509	0.603	0.250	0.557
2003	0.5803	0.331	0.250	0.291
overall	**0.636**	**0.698**	**0.250**	**0.409**

Coexistence & niche overlap- The preferred habitat (that habitat where the largest numbers were found) was the same for both the sexuals and parthenogens and was the blue bush with dead bushes (BB&db) habitat.

The parthenogens always occurred in sympatry with the sexuals. Furthermore, the WP parthenogen was only found in habitats that were also inhabited by the RP3 parthenogen, whereas the RP3 parthenogen was found in two habitats without the WP parthenogen. Thus the sexuals were found in sympatry with at least one parthenogen in three of the four habitats but also occurred in the sheoak habitat where no parthenogens were found. However, they were only found in sheoak in the first year, and only in small numbers.

The high occurrence of sympatry of the different types and the overall preference for the same macrohabitat is reflected in the niche overlap values (Table 3.3). In 2002 sexuals (males and females) and WP parthenogens showed a reduced overlap in macrohabitat use, however the values are still considered to be high (0.487 and 0.432). All other overlap values were very high (all >0.76), and would suggest very little segregation among the different types by macrohabitat use.

Table 3.3. Macrohabitat niche values for each year and overall (years pooled).

YEAR	SASf & SASm	SASf & WP	SASf & RP3	SASm & WP	SASm & RP3	WP & RP3
2001	0.985	0.936	0.959	0.898	0.940	0.992
2002	0.980	0.487	0.914	0.432	0.886	0.796
2003	0.856	0.762	0.812	0.986	0.997	0.997
overall	**0.991**	**0.778**	**0.913**	**0.816**	**0.931**	**0.966**

Microhabitat use within ruins

Distribution & niche breadth- Microhabitat utilisation by the three different types (SAS males, SAS females and RP3 parthenogens) within ruins for each year and all years pooled is shown in Figure 3.8 and Figure 3.9 respectively.

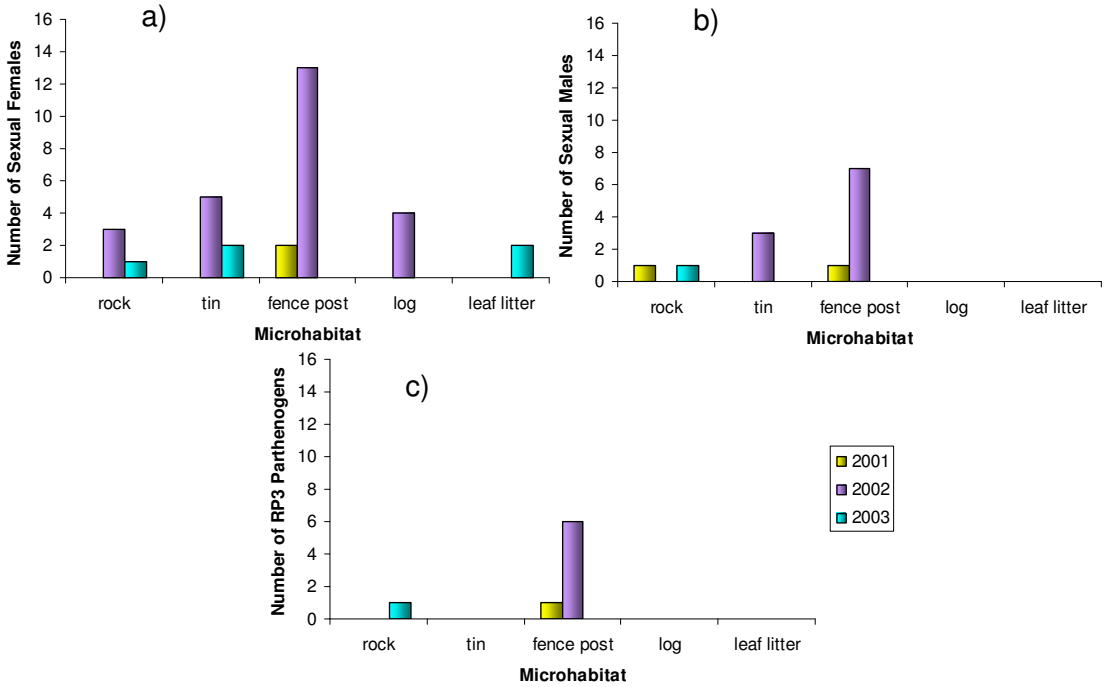


Figure 3.8. The number of a) sexuals females, b) males and c) RP3 parthenogens caught under each microhabitat within ruins for each year.

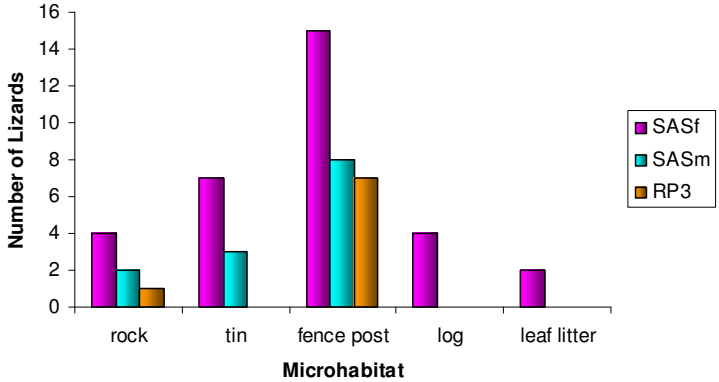


Figure 3.9. The number of sexuals females, males and RP3 parthenogens caught under each microhabitat within ruins for all years pooled.

Sexual females utilised the most microhabitats, being found in all five available microhabitat types over the study period. In 2001 when four lizards were found in ruins, they were only found under fence posts, but in the next two years when numbers found in ruins increased they utilised four habitats in 2002 (all, except leaf litter), and three in 2003 (rock, tin and leaf litter). Sexual males were more limited in their microhabitat use. They were found under two retreat types in the first two seasons (rock & fence posts in 2001, tin & fence posts in 2002), and only one male was found in 2003 under a rock. Thus, over the period of the study, males utilised three of the four available microhabitats. RP3 parthenogens showed a more restricted microhabitat use than sexuals (males and females), only utilising two microhabitat types overall, and only one type within a season. In 2001 and 2002, the parthenogens were found under fence posts, and in 2003, the one lizard caught was under a rock.

Contingency Chi square test could not be used to compare microhabitat use by the three types within the ruins sites as even with years pooled many expected values were less than five, therefore a Fisher's exact test was used. With data for all three years pooled, the difference in microhabitat utilisation among the three types was not significant (Fisher's exact test = 6.074, p=0.626).

These results are reflected in the microhabitat niche breadths (Table 3.4). Males and RP3 parthenogens show a narrow niche breadth in all seasons, whereas sexual females had a narrow niche in 2001 and a fairly broad niche in 2002 & 2003. Overall, SAS females had the broadest niche breadth, and RP3 parthenogens the narrowest.

Table 3.4. Microhabitat niche breadth values for each year and overall (years pooled)

YEAR	SASf	SASm	RP3
2001	0.200	0.400	0.200
2002	0.571	0.345	0.200
2003	0.556	0.200	0.200
overall	**0.660**	**0.440**	**0.200**

Sharing microhabitats & niche overlap- The preferred microhabitat (that microhabitat in which they were found most frequently) was the same for all three types and was fence posts. As a result, sexual males and females and RP3 parthenogens exhibited very high microhabitat niche overlap (Table 3.5).

In each season there was one habitat that all three types utilised (fence posts in 2001 & 2002 & rocks in 2003), and this was the only habitat RP3s were found under. Due to their broader range of microhabitats sexual males and females were also able to utilise habitats not used by the parthenogen.

Table 3.5. Microhabitat niche overlap values for each year and overall (years pooled).

YEAR	SASf & SASm	SASf & RP3	SASm & RP3
2001	0.707	1.000	0.707
2002	0.941	0.879	0.919
2003	0.333	0.333	1.000
overall	**0.965**	**0.876**	**0.935**

Coexistence along the two fence lines

The frequent dead bushes along the two fence lines (BB&db sites) provided isolated habitat patches in which regular searches could be conducted. Captures under these dead bushes allowed assessment of coexistence of the different types within these habitat patches/bushes. The highest number of lizards caught under a bush during a single search session was nine. The majority of bushes contained zero, one or two lizards, while several bushes contained three or four lizards (Figure 3.10).

Figure 3.10. The number of dead bushes that contained zero to nine M. greyii.

Approximately 39% of searches resulted in no lizards being found. On the occasions where lizards were found 41% of bushes contained sexuals only, 36% of bushes contained parthenogens only and 23% contained sexuals and parthenogens together.

For the bushes in which two lizards were captured, nine bushes contained sexuals only, six bushes contained parthenogens only and the remaining six bushes contained a sexual and a parthenogen together. For bushes in which three lizards were found, one bush contained parthenogens only, while four bushes contained a mixture of parthenogens and sexuals. For bushes in which four lizards were found, one bush contained sexuals only, while three bushes contained a mixture of parthenogens and sexuals (Table 3.6). For the one bush that contained six *Menetia*, the assemblage consisted of two males, three sexual females and one RP3 parthenogen. And for the one bush that contained nine *Menetia*, there was one male, one sexual female, four WP parthenogens and three RP3 parthenogens.

Table 3.6.The number of bushes that contained sexuals only, parthenogens only and a mix of parthenogens and sexuals, for bushes containing from 1-9 lizards.

Number lizards under bush	**N**	**Number of bushes**		
		Sexuals only	**Parthenogens only**	**Sexuals + Parthenogens**
0	42	0	0	0
1	34	17	17	0
2	21	9	6	6
3	5	0	1	4
4	4	1	0	3
6	1	0	0	1
9	1	0	0	1
total	108	27	24	15

Contingency Chi square test was used to compare the proportion of occasions when sexuals and parthenogens were expected to occur under the same bush by chance and the actual observed proportion of occasions when sexuals and parthenogens were found occurring under the same bush. Co-occurrence did not happen more or less often than expected by chance (X^2= 0.005, *df*=1, p=0.945).

That is, there was no evidence for any non-random segregation of sexuals and parthenogens among the 108 sampled bushes.

Summary

Based on captures, one sexual and two parthenogenetic lineages occur at Bundey Bore, and the sexuals tend to be more abundant than the parthenogens. Although macro and microhabitat use is broader in the sexuals, habitat niche overlap is very high due to the preferred habitats of sexuals and parthenogens being the same. These results suggest that the different taxa are occurring in sympatry and there is minimal partitioning of habitat resources.

Morphology

Statistical results for morphological data are shown in Table 3.7 through to Table 3.10. The snout-vent length (SVL) of different lizard types was compared using a two-way ANOVA with type and year as fixed factors. To compare weight and tail length we used ANCOVA with type and year as the independent variables and SVL as covariate. For females that were caught gravid, post-laying weight was used. Only lizards with complete tails were used in the analysis of tail length. To compare differences in weight across months (Sept-Nov) among the four types ANCOVA with type and month as fixed factors and SVL as a covariate was used (Table 3.9).

Table 3.7. Two-way ANOVA or ANCOVA results for snout-vent.length (mm) (SVL), weight (g) and tail length (mm). Type (SASf, SASm, WP & RP3) and year (2001-2003) were fixed factors, and SVL was a covariate when comparing weights and tail lengths.

	SVL (mm)			**Weight (g)**			**Tail length (mm)**		
	F	**df**	**p**	**F**	**df**	**p**	**F**	**df**	**p**
Type	0.958	3	0.414	1.694	3	0.170	0.220	3	0.882
Year	3.185	2	0.044	8.100	2	<0.001	8.265	2	<0.001
Type*Year	1.186	6	0.316	1.411	6	0.212	0.920	6	0.980
Covariate SVL				375.644	1	<0.001	4.910	1	0.028

Table 3.8. Results of Bonferroni multiple comparisons tests comparing morphology among years.

	Year 1	Year 2	p
SVL (mm)	2001	2002	0.117
	2001	2003	1.000
	2002	2003	0.248
Weight (g)	2001	2002	1.000
	2001	2003	0.106
	2002	2003	0.051
Tail length (mm)	2001	2002	0.254
	2001	2003	<0.001
	2002	2003	0.020

Snout-vent Length (SVL)- Mean snout-vent lengths are shown in Figure 3.11.

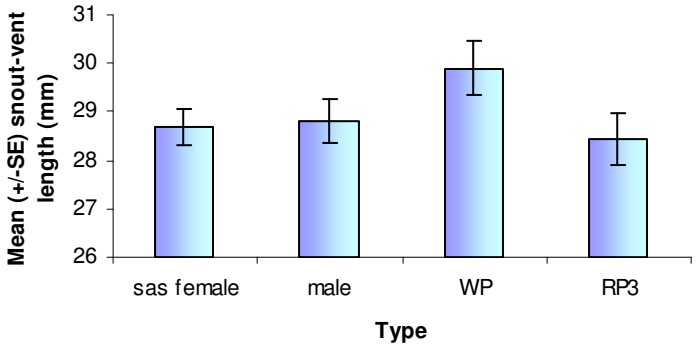


Figure 3.11. Mean (± SE) snout-vent length (mm) of each type.

Snout-vent lengths (SVL) ranged from 20-35mm (mean=28.9mm, SE=0.230), and did not differ significantly among the four types (Table 3.7). SVL differed significantly among years, however, Bonferroni multiple comparisons test was unable to determine where this difference occurred (Table 3.8).

Weight- Weight is plotted against SVL in Figure 3.12. Analysis showed that SVL had a significant effect on weight, but there was no significant difference in weight among the different types (Table 3.7). Average weight (g) differed significantly among years, however, Bonferroni multiple comparisons test was unable to determine where this difference occurred (Table 3.8). It appears that lizards in 2002 weighed less than those in 2003.

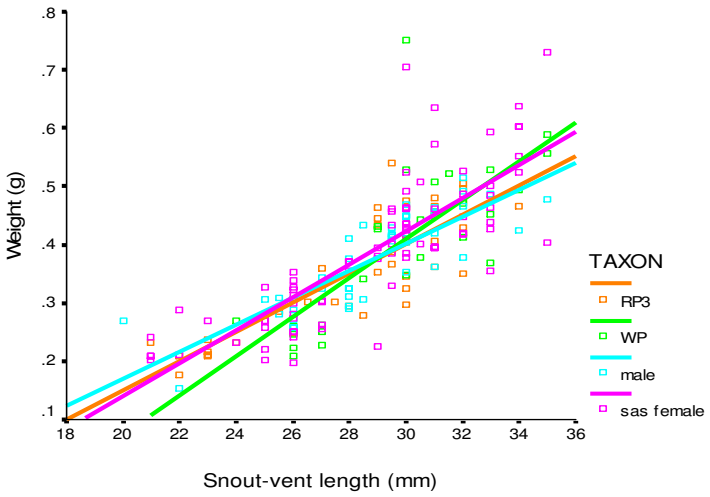


Figure 3.12. Weight (g) against snout-vent length (mm) for M. greyii.

When looking at differences in weight (reciprocal transformed) across the three months of the study (Figure 3.13), weight differed significantly among the three months with lizards weighing less in September than December (Table 3.10), but weight did not differ among the different types (Table 3.9). SVL again had a significant effect on weight.

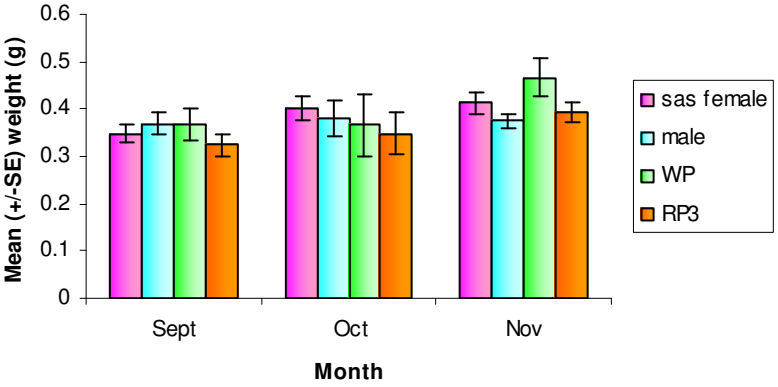


Figure 3.13. Mean weight (±SE)(g) of M. greyii *for each month of the field study.*

Table 3.9. Two-way ANCOVA results for weight (g)across months. Type (SASf, SASm, WP & RP3) and month (Sept – Nov) were fixed factors, and SVL was a covariate.

	Weight (g)		
	F	**df**	**p**
Type	0.481	3	0.696
Month	5.094	2	0.007
Type*Month	1.077	6	0.378
Covariate SVL	355.517	1	<0.001

Table 3.10. Results of Bonferroni multiple comparisons tests comparing weight(g) among months.

	Year 1	Year 2	p
Weight (g)	Sept	Oct	0.419
	Sept	Nov	0.007
	Oct	Nov	0.992

Tail length- Mean tail lengths are shown in Figure 3.14.

For those lizards with complete tails, SVL had a significant effect on tail length (Figure 3.15). Tail length did not differ significantly among the four types (Table 3.7), but lizards in 2003 had significantly longer tails than lizards caught in 2001 and 2002 (Table 3.8).

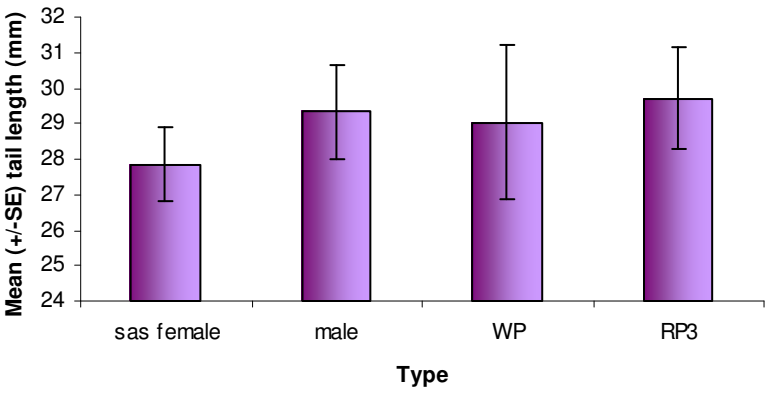


Figure 3.14. Mean (± SE) tail length (mm) of each type.

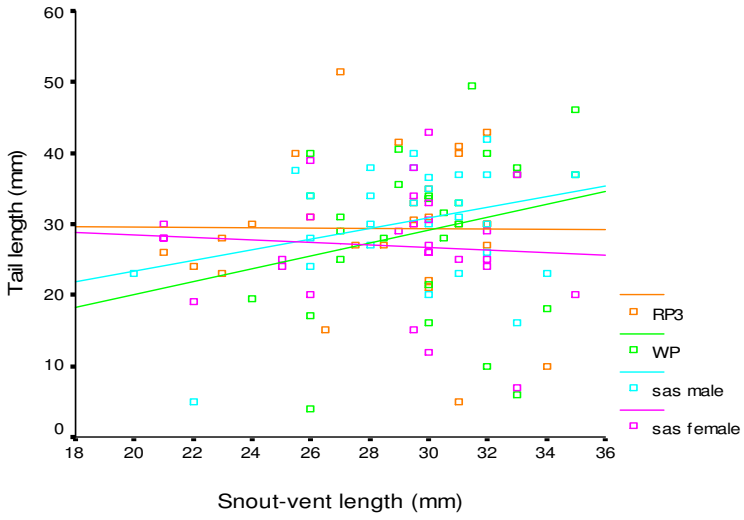


Figure 3.15. Tail length (mm) against snout-vent length (mm) for M. greyii.

Summary

Parthenogenetic and sexual *M. greyii* at Bundey Bore differ very little in their morphology.

Tail breakage

Tail loss occurred across both sexes and reproductive modes. The percentages of broken tails are shown in Figure 3.16. Adult sexual females had the highest percentage of broken tails (approx. 54%), while adult males had the lowest percentage (36%) followed closely by non-adult females (39%). The remaining types and status (adult or non-adult) suffered similar rates of tail loss (approx. 42-48%), with the exception that adults tended to have slightly lower frequency of broken tails than non-adults. The proportion of lizards with broken tails was compared by contingency chi-squared test, with the data pooled for all years. In both adult and non-adult *M. greyii* frequency of broken tails did not differ significantly among types (adults: X^2=2.367, *df*=3, p=0.500; non-adults: X^2=0.519, *df*=3, p=0.915).

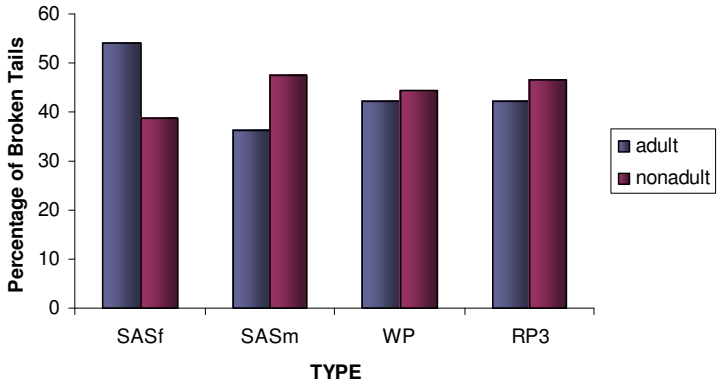


Figure 3.16. Percentage of sexual females (SASf) and males (SASm), and parthenogens (WP & RP3) with broken tails (includes recently broken and regenerated tails).

Summary

Parthenogenetic and sexual *M. greyii* at Bundey Bore had similar incidence of broken tails. If we assume these resulted from unsuccessful attacks by predators, the data suggest they are subject to similar predation pressures.

Discussion

Genetic Lineages Present

Within the study area three genetically distinct taxa were present , a sexual lineage consisting of males and females (SAS) and two parthenogenetic, all female lineages (WP and RP3).

Habitat Use

Comparison of the ecological requirements of the four types revealed very few differences.

Four macrohabitats were utilised by *Menetia greyii* in the study area, blue bush, bb&dfob, ruins and sheoak. Sexual males and females had a broader overall macrohabitat niche (females = 0.636; males = 0.698) than both of the parthenogens (WP = 0.250; RP3 = 0.409). Both sexuals were found in all four available habitats, whereas the two parthenogens were found in a limited subset of sites. RP3 parthenogens were found in three of the four habitats, while WP parthenogens posses the most restricted range only inhabiting the dead bushes in the bb&dfob habitat. Although these differences in macrohabitat use were apparent, niche overlap was very high and higher than average for coexisting lizard species (Pianka 1973). This high overlap in habitat use is due to the preferred habitat (that habitat with the highest numbers) being the same for all four types. This preferred habitat was the dead bushes in the bb&dfob. This high overlap suggests that there is in fact limited habitat segregation occurring on a broad scale.

Sexual males and females and RP3 parthenogens also occurred in ruins in high numbers. Within the ruins five distinct microhabitats were available for use by the lizards. As with macrohabitat use, sexual males and females possessed a wider microhabitat niche breadth (females = 0.660; males = 0.440) than the parthenogen (=0.200). Sexual females utilised all five available microhabitats, sexual males utilised three, and RP3 parthenogens only utilised two microhabitats. In all three years of the study the parthenogens only utilised a microhabitat type which was also utilised by both of the sexuals. Even though the sexuals were able to utilise

habitats not available to the parthenogen, the preferred habitat was the same for all three types (fence posts). Thus overall, overlap in microhabitat use was very high for all three types. Overlap was reduced in 2003 between both sexuals and the parthenogens (0.333) and was probably due to the fact that only one RP3 parthenogen was found in the ruins in that year. This suggests that there is also limited habitat segregation occurring on a fine (microhabitat) scale. It would be interesting to establish microhabitats and observe the colonizing ability among the different reproductive types.

The other finer scale habitat use examined was the use of the dead bushes along the fence line in the bb&dfob habitat. Sexuals and parthenogens were only found occurring under the same bush on 14% of the search occasions, this was not more often than expected by chance. Perhaps then, sexuals and parthenogens are partitioning this habitat resource by inhabiting different dead bushes. Further research could involve determining if the different dead bushes offer different levels of resource quality, and if so, determine if the sexuals or parthenogens are more likely to inhabit the higher quality bushes. In addition, sexuals and parthenogens may segregate within the bushes. For example they may occur at different levels within the piles. However, this was not measured as a component of the study.

These results suggest that, in general, the four types do not appear to partition local spatial resources based on macrohabitat and microhabitat preferences. While sexuals were more general in their use of available habitats, and the habitat available was partially unsuitable to the parthenogens, abundances were all highest in the bb&dfob macrohabitat and fence post microhabitat. However, partitioning of the dead bushes in bb&dfob habitat may be occurring.

We are aware that our sampling methods may not have included all habitats or microhabitats used by *M. greyii* at Bundey Bore. This species is very small and cryptic and on some of our searching days we only caught very few or sometimes even no lizards (see Table 3.1). Therefore, it is possible that the different types do have major niche differences involving habitats that were not searched with success during the current study.

Predation

Tail breakage occurred across all taxa at equal rates. The high incidence of tail loss suggests that predation attempts are frequent. Several reptiles including all the elapid snakes (e.g. *Pseudonaja nuchalis* (Western Brown) and *P. textiles* (Eastern Brown)) and some of the larger skinks (e.g. Bearded dragon, *Pogona vitticeps*) found in the study area, as well as avian (e.g. Wedge-tailed eagle, *Aquila audax*) and even invertebrate (e.g. Tanzanian blue ringleg centipede, *Sclolopendra* cf *morsitans*) predators potentially prey on *M greyii*. During staged pairwise interactions between the different types (Chapter 6), observed behaviour included a component of tail wagging that draws attention to the tail as opposed to the body. If a predator did attack it is more likely to attack a moving tail rather than a stationary body (Vitt and Cooper Jr., 1986, Cooper Jr., 1998). Since we were only able to compare the proportion of lizards that had a predation attack from which they escaped, and not the proportion of lizards of each type that were unsuccessful at avoiding predation (i.e. the proportion that were eaten), we can only imply that the lack of difference in tail length and no difference in the proportion of broken tails suggests that males, sexual females and parthenogens are subject to similar predation rates. Tail loss can also be attributed to intraspecific agonistic interactions (Ryhorchuk 2002), however aggressive interactions between pairs of *M. greyii* never resulted in a lost tail (Chapter 6). Therefore tail loss observed in the field is more likely due to predation.

Support for Hypotheses?

The three lineages (one sexual, two parthenogenetic) occurred in local sympatry. Based on capture rates, all three preferred the more modified and disturbed habitats (bb&db and ruins) as opposed to the more pristine natural habitats available (blue bush, mallee, sheaok). Thus the Weed Hypothesis doesn't appear to apply in this complex. However, it is possible that *M. greyii* also occurred in less disturbed habitats in high numbers but were easier to locate and catch in the disturbed areas.

More than one parthenogen existed within the area, and both possessed a habitat niche narrower than that of the sexuals. This suggests that the FNV model may be

supported here, although partitioning of resources was very limited between the parthenogens, and also between parthenogens and sexuals. Again, our measures of macro and microhabitat niche use were based on where we were able to locate and catch individuals, which is not necessarily the only places where they occurred. However, what we did find was no evidence to suggest habitat segregation at times when lizards were active.

Conclusions

To allow coexistence, resource partitioning would be expected. Spatial segregation at the micro and macro levels does not appear to be happening. In addition, the different types were also very similar in morphology, making resource partitioning via differences in body morphology (e.g. larger prey or larger retreats for larger lizards (Pianka and Pianka 1976)) unlikely. Therefore, there is a high likelihood of competition both between the two parthenogens, and between parthenogens and sexuals.

If they are existing in stable coexistence then other ecological differences must exist that were not examined in this current study, that allow the different types to partition niches, and thus reduce competition. Lizards tend to partition resources along three dimensions, space, time and food (Pianka 1973). It is unlikely that the four types would partition prey items. In addition to their similar morphology (mentioned above) *Menetia greyii* are insectivorous and are limited in what they can eat due to their very small size. General observation of food items in scats collected from individuals in the study population indicate that diet is very similar for the sexuals and parthenogens, with the predominant food source in all scats being termites, with the occasional cockroach, beetle and small spider (Gary Hallas, Pers. Comm.). The only study examining the diet of *M. greyii* showed that individuals within a population didn't differ in their stomach content (Smyth and Smith 1974). It is possible, however, that the different types partition along the time niche. This is investigated in Chapter 5.

Chapter 4

Reproduction in parthenogenetic and sexual female *Menetia greyii*

Introduction

It has been theorised that, all else being equal, parthenogens should have a two-fold reproductive advantage over sexuals as they do not produce males (Williams 1975, Maynard-Smith 1978). For instance, Cole (1984) used lab data on egg production in parthenogenetic *Cnemidophorus exsanguis* to estimate it would have a population twice the size of a sexual species within three years. This reproductive advantage should enable a parthenogenetic species to outnumber and eventually exclude a sexual species from an area (Bell 1982, Chaplin 1993). However, although there are examples of parthenogens outnumbering their sexual relatives on a local scale, in *Cnemidophorus* (the most widely studied group of coexisting sexual and parthenogenetic lizards), this fitness advantage does not translate into any consistent distributional or numerical superiority of the parthenogens (Case 1990). Hence, all else may not be equal.

Studies comparing reproduction between sexual and parthenogenetic lizards have had contrasting results. For instance, parthenogenetic *C.exsanguis* was found to have a clutch size half as great as that of its sexual parental taxon *C. tigris* (Echternacht 1967), eliminating the 'two fold reproductive advantage' of the parthenogens. And parthenogenetic individuals have been found to suffer from a higher frequency of developmental problems, such as poor hatching success of eggs (Roth 1974, Lamb and Willey 1979, Lynch 1984), or lower egg production (Enghoff 1976, Taylor 1981). Conflicting results have been found for the Australian gecko, *Heteronotia binoei. W*hile Kearney and Shine (2005) found that some parthenogenetic races of *H. binoei* suffered a lower fecundity through fewer clutches over a shorter period than their coexisting sexual progenitors, Ryhorchuk (2002) found parthenogenetic *H. binoei* to have up to a four-fold reproductive advantage over sexual females. She found that sexual *H. binoei* laid at most two

clutches, while parthenogens were capable of laying up to four clutches per season. Other studies have found no differences in reproductive characteristics between parthenogens and related sexual forms of lizards (Schall 1978, Jokela et al. 1997b).

In the previous chapter, no ecological advantage to the sexual taxa at Bundey Bore was detected. This means that under the two-fold cost of sex theory, the parthenogens should rapidly outnumber the sexuals and even eventually displace them. However, the abundance of the different taxa at Bundey Bore does not support this. Therefore, perhaps parthenogen *M. greyii* at Bundey Bore do not possess a two-fold reproductive advantage over the sexual females.

By comparing the reproductive characteristics of sexual and parthenogenetic *M. greyii* we can investigate the theorised 2-fold reproductive advantage of parthenogens, and test the hypothesis that parthenogenetic females have greater representation in the following generation through higher production of female offspring. Where the two reproductive modes coexist an equal average lifetime production of one female offspring per female for both modes is expected, otherwise the population would not be at equilibrium. If the parthenogens do possess this reproductive advantage then we would predict that the sex ratio in the sexuals would be 1:1 and the reproductive parameters in both modes of reproduction will be the same. Some factors that might offset this reproductive advantage could include, reduced reproductive output, (for example through fewer eggs in a clutch, lower average egg weight, lower relative clutch mass, or lower proportion of reproductive females in the parthenogens), and reduced viability of eggs or hatchlings in the parthenogens (Stewart 1996).

The most direct test for the intrinsic cost of sex involves comparing reproductive capacities of the offspring when cultured under ideal (intrinsic) conditions, and measuring reproductive rate, generation length and gender of sexual offspring. All of these measurements were not possible during the current study, but the data collected was considered against this template.

These parameters were measured in sympatric parthenogen and sexual forms of *M. greyii*, to determine the extent of any reproductive advantage for the parthenogens.

Methods

Data on reproduction were collected over the three breeding seasons of the study (2001-2003). Upon capture, possibly gravid female *M. greyii* were identified by the obvious presence of eggs or by unusually high weight (>4.0g) indicating that the female was potentially gravid.

All potentially gravid females were housed individually in small plastic containers (12cm X 12cm) with a sand substrate, and a piece of bark for shelter. These containers were housed in a temperature controlled room (20^{o}C) under a 12hr light : 12hr dark photoperiod. The containers were heated at one end using a heat mat placed underneath the containers creating a temperature range of 22-30^{o}C within the container. This temperature gradient was maintained for the entire period (i.e. 24hrs a day). The sand was moistened four times a day with distilled water to prevent any eggs laid between inspections from drying out. Females were fed crickets twice a week and drinking water was added *ad lib*. Females were weighed every two days. Containers were checked for eggs six times per day (from 0600hrs to 2300hrs) at regular intervals. Once an egg was laid it was removed from the mother's container, and the date, time of day, mother's number, number of eggs in the clutch, and weight of the egg(s) to the nearest 0.00001g using a Mettler scale were recorded. The egg was then placed in an incubator set at 29 ^{o}C.

Plastic containers with unfertilised vermiculite were used to incubate the eggs. The vermiculite was first dried and sterilised by placing it in an oven at 105^{o}C for 24 hours. A vermiculite to water ratio of -150kPa was created by combining 100g of vermiculite with 138g of distilled water in the container. A plastic lid was then placed on the container. The method of incubation was the same as that used by Thompson and Russel (1998) for *M. greyii*. The mother was then weighed to obtain post-laying weight.

Eggs were incubated for 25 days, undisturbed, then checked twice daily for hatching. Upon hatching juveniles were weighed (nearest 0.00001g) and measured (SVL and tail length to nearest 0.5mm). They were then housed in individual containers under UV and heat lamps, in a temperature controlled room (20^{o}C) set at a 12hr light : 12hr dark photoperiod. All lizards were fed wingless *Drosophila* and baby crickets twice a week, and supplied with water *ad lib*.

To determine if *M. greyii* may lay more than one clutch per season, female lizards were collected from the field site in August, December, January and February of each of the three years (2001-2003), and the proportion of gravid females was determined each month.

The day of laying was defined as the day each female laid her clutch, relative to the first clutch laid in the season. For example if the first clutch was laid on November 1st, this clutch had a derived day of laying of 1. If another clutch was laid on the November 15th, this clutch had a day of laying of 15.

If there was more than one egg in a clutch the weight of the eggs were combined to give the relative clutch mass (RCM) for each clutch/female. The measure of RCM I used was weight of the clutch / post-laying female weight.

In analysis using egg weight, for clutches with more than one egg, the average weight of the eggs in the clutch was used.

Data collected from the three years were pooled for analysis.

Hatchling Growth rates

Upon hatching, juveniles were measured (Snout-vent length; SVL to nearest 0.5mm). The juveniles were then subsequently measured every 7 days for a month, and then every 30 days for 12 months or until they died. Date of death was recorded. For analysis, SVL at hatching was considered SVL at day zero.

Growth rate (GR) in mm/day was estimated for each juvenile. Growth rate over each time interval was calculated as the difference between size (SVL (mm)) at the previous measurement (SVL_1) and size at the subsequent measurement (SVL_2), divided by the time interval between the two measurements (in days). For example, if at the age of 7days a juvenile had a SVL of 14mm (SVL_1), and at age 14 days that same juvenile had a SVL of 14.5mm (SVL_2), the growth rate would be;

GR = 14.5 – 14.0 / 7 = 0.071mm/day

These raw growth rates were then transformed into Specific Growth Rates (SGR) by dividing GR by the average of SVL_1 and SVL_2 following Kaufmann (1981). Linear regression was then used to fit three sigmoid growth curves; Logistic, Gompertz and Von Bertalanffy to the data by using appropriately transformed values of SGR as the dependent variable and the mean of SVL_1 and SVL_2 as the independent variable.

Table 4.1. Equations for the three growth curves used to describe growth in juvenile M. greyii.

Growth Model	Differential equation	Integrated equation	Asymptotic size
Logistic	SGR = b-aS	$S = S_\infty[1+\exp\text{-}b(t+t_o)]^{-1}$	$S_\infty = b/a$
Gompertz	SGR = b-$a$lnS	$S = S_\infty \exp[\text{-}\exp\text{-}a(t+t_o)]$	$S_\infty = \exp b/a$
Von Bertalanffy	SGR = b-a(1/S)	$S = S_\infty[1\text{-}\exp\text{-}b(t+t_o)]$	$S_\infty = - a/b$

Table 4.1 shows the equations for the three growth curves. The second column gives the differential form of the equations showing the relationship between Specific Growth Rate (SGR) and size (S). The relationship between SGR and S should be linear if these variables are appropriately transformed. The third column gives the more commonly used integrated form of the equations, which gives size as a function of time (t). The fourth column gives the equation for calculating the asymptote (S_∞) of each growth equation. The parameters *a* and *b* are the slope and y-intercept, respectively, of the linear estimate of the differential forms of the equations, and t_o is the constant of integration (Kauffman 1981). The slope of the linear estimate of the differential form of each equation describes the rate at which

the growth curve approaches the asymptote (S_∞) and is called the characteristic growth rate.

Of the three models, the one which produced the highest value of R^2 from a linear regression of the original data was taken as the model that best fitted the data (Ricklefs 1968).

Initially curves for sexual males, sexual females, WP parthenogens and RP3 parthenogens were fitted separately to data pooled from all lizards of that type. This was to determine which growth curve best fitted the data. Then the curves were calculated separately for each lizard of type sexual, WP parthenogen and RP3 parthenogen to test for significant differences in *a* (characteristic growth rate) and Asymptotic SVL (S_∞). The variables were analysed for the effect of type using One-way ANOVA.

Results

Sex Ratio in sexual Menetia greyii.

Contingency chi square tests were used to test whether the sex ratio of sexuals caught in the field population differed from a ratio of 1:1. The sex ratio of sexual *M. greyii* was biased towards females in all three years, significantly so in 2001, 2002 and for all years combined (Table 4.2).

Due to the small sample size of sexual juveniles born in the lab over the three years of the study (a total of seven hatchlings survived past their first year) we were unable to compare the sex ratio of hatchling *Menetia greyii*.

Table 4.2. The number of sexual males and females caught within each year of the field study, and the results of contingency Chi–square tests comparing the ratio of sexual males and females against an expected ratio of 1:1.

Year	females	males	ratio	X^2	df	p
2001	33	18	1.8 : 1	4.412	1	0.036
2002	41	18	2.3 : 1	8.996	1	0.003
2003	12	7	1.7 : 1	1.316	1	0.251
Years pooled	86	43	2 :1	14.333	1	<0.001

Breeding Season

I defined the breeding season as the months when females laid eggs.

Sexual and parthenogenetic females began reproducing in the same month (November) and both forms laid their last clutch in the next month (December) (Figure 4.1a); a span of two months. This corresponded to an identical span of hatching for the eggs; beginning in December and ending in January (Figure 4.1b). A majority of the clutches for all three taxa were laid in November and hatched in December.

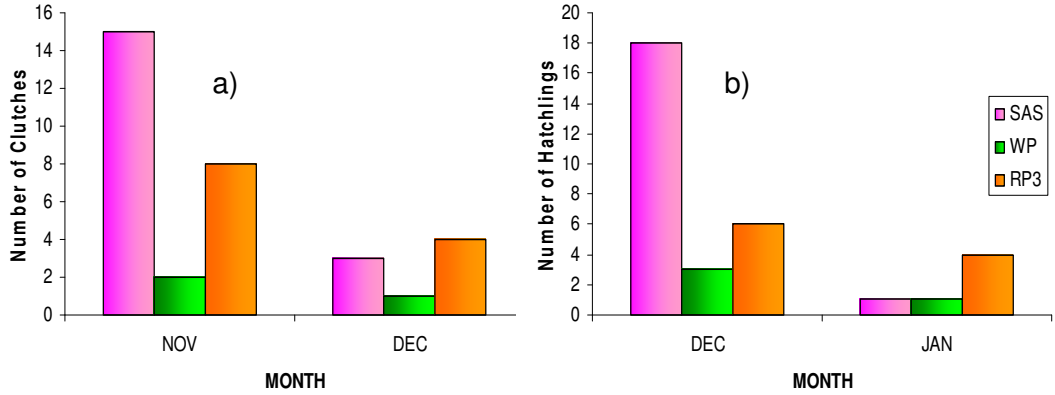


Figure 4.1. Summary of the reproductive seasons for M. greyii*: a) laying season; b) period of hatching for sexual females (SAS), WP parthenogens (WP), and RP3 parthenogens (RP3).*

Sexual females lay their clutches on average on day 12.1 (S.E.= 2.51) of the season, WP females lay on average on day 21.3 (S.E= 7.27) of the season and RP3 females lay on average on day 18.1 (S.E= 3.42) of the season. There was no difference among taxa in mean time of laying (day lay) of clutches (One-way ANOVA, *df*=2, F=1.521, p=0.235).

Proportion and size of Breeding Females

For this analysis, a limit of 29mm SVL was chosen to distinguish between juveniles (i.e. <29mm) and adults (>/= 29mm), for both sexual and parthenogenetic *M. greyii*. This decision was based on the smallest SVL of females that produced a clutch. Contingency chi square tests were used to compare the proportion of adult females breeding among taxa.

Of the sexual females captured during the three breeding seasons (Sept-Nov, 2001-2003) of the study, 50 were considered to be mature, and 18 (36%) of these produced a clutch. A total of 19 adult WP parthenogens were captured, 3 (15.8%) of which produced a clutch. Of the RP3 parthenogens captured, 26 were considered to be mature, and 12 (46.2%) of these produced a clutch. There was no significant difference overall in the proportion of females reproducing among the taxa (X^2=4.539, *df*=2, p=0.103). However, a pairwise contingency chi square test showed that a significantly higher proportion of RP3 parthenogens than WP parthenogens were breeding in the population of captured individuals (X^2=4.555, *df*=1, p=0.033).

Table 4.3. Mean size (mm) and weight (g) of sexual (SAS) and parthenogenetic (WP & RP3) adult females.

Maternal Taxon	Attribute	N	Range	Mean	SE
SAS	**SVL (mm)**	18	29.0 – 34.0	31.22	1.904
	Weight (g)	18	0.330 – 0.502	0.417	0.060
WP	**SVL (mm)**	3	30.0 - 31.5	30.50	0.866
	Weight (g)	3	0.338 – 0.583	0.449	0.124
RP3	**SVL (mm)**	12	29.0 – 32.0	30.54	1.117
	Weight (g)	12	0.334 – 0.464	0.385	0.040

Table 4.4. One-way ANOVA and ANCOVA results for snout-vent.length (mm) (SVL), and weight (g) of breeding females among the three taxa, SVL was a covariate.

				Covariate	
	F	**df**	**p**	**F**	**p**
SVL (mm)	0.759	2	0.477		
Weight (g)	0.725	2	0.493	20.02	<0.001

Maternal size can affect reproductive output, since in reptiles increased body size has often been correlated with increased fecundity (Ballinger et al. 1979, Thompson and Pianka 2001, Wapstra and Swain 2001). There was no significant difference in the average SVL (mm) or weight (g) of breeding females among the three taxa (Tables 4.3 and 4.4).

The effect of maternal SVL on the timing of laying clutches (day lay) was investigated. Pearson's correlation showed that there was no correlation between maternal SVL and day lay (Table 4.5).

Table 4.5. Pearson Correlations between maternal SVL and season (day lay).

Maternal Taxon	n	r	p
SAS	18	0.173	0.479
WP	3	-0.899	0.111
RP3	12	0.160	0.659

r= pearsons correlation coefficient
SAS= sexual; WP= **WP** parthenogen; **RP3=** RP3 parthenogen

Reproductive output and Reproductive effort of parthenogen and sexual females

Gravid females were only detected in the months September to November. Additional searches in the study area in August, December, January, February, and March recovered no gravid females (Table 4.6). This result suggests that this population of sexual and parthenogenetic *M. greyii* only produce one clutch per season.

Table 4.6. Number of females caught, and the percentage of caught females that were gravid during the identified breeding season (Sept – Oct) and at other times of the year (Aug, Dec-March).

Period	# mature females caught	% gravid
Sept – Oct	95	34.7
Aug, Dec - March	41	0

Table 4.7 summarises clutch-size for both parthenogenetic and sexual *M. greyii*. Clutch size ranged from 1 – 3 eggs for sexual females and RP3 parthenogens. The three reproductive WP parthenogens laid 1 or 2 eggs per clutch.

Table 4.7. Number of one, two, and three-egg clutches laid by individual sexual (SAS) and parthenogenetic (WP & RP3) females.

Maternal Taxon	n	# one egg clutches	# two egg clutches	# three egg clutches	# clutches laid
SAS	18	8	9	1	18
WP	3	1	2	0	3
RP3	12	8	3	1	12
Total	33	17	14	2	33

The average number of eggs laid per female, average egg weight, and average relative clutch mass (RCM) for sexual and parthenogenetic females are summarised in Table 4.8. None of these parameters differed significantly among taxa nor did maternal SVL affect any of these parameters (Table 4.9).

Table 4.8. Mean egg weight (g), clutch size and relative clutch mass (RCM (g) from sexual females (SAS) and parthenogens (WP & RP3).

Maternal Taxon	Variable	N	Range	Mean	SE
SAS	**Clutch size**	18	1 - 3	1.72	0.14
	Egg Weight (g)		0.06820 – 12224	0.08965	0.011
	RCM (g)		0.18365 – 0.57858	0.35158	0.104
WP	**Clutch size**	3	1 - 2	1.67	0.33
	Egg Weight (g)		0.08357 – 0.10210	0.09130	0.008
	RCM (g)		0.23967 – 0.54763	0.35923	0.165
RP3	**Clutch size**	12	1 - 3	1.58	0.19
	Egg Weight (g)		0.05664 – 0.12224	0.08486	0.014
	RCM (g)		0.21000 – 0.54299	0.35327	0.121

Table 4.9. ANCOVA results comparing clutch attributes among SAS, WP and RP3 M. greyii. Covariate was maternal SVL.

Attribute	ANOVA			Covariate	
	df	**F**	**P**	**F**	**P**
Clutch size	2	0.176	0.677	0.176	0.677
Egg weight (g)	2	0.176	0.677	0.176	0.677
RCM (g)	2	0.011	0.918	0.011	0.918

The possible relationship between maternal SVL and clutch size, egg weight and RCM was investigated for each taxon using Pearson's correlation. There were no significant correlations (Table 4.10).

The effect of season on clutch size, egg weight, and RCM was also tested for each taxon by comparing day of laying with each of these parameters using Pearson's correlation (Table 4.10). For sexual females there was a significant negative correlation between clutch size and day of laying (Figure 4.2). Sexual females tended to lay smaller clutches as the season progressed. No other significant correlations were apparent.

Table 4.10. Pearson Correlations between maternal SVL, season (day lay) and clutch attributes.

Maternal Taxon	Attribute 1	Attribute 2	n	r	P
SAS	Maternal SVL	Clutch size	18	-0.21	0.934
		Egg weight	18	0.282	0.124
		RCM	18	-0.560	0.827
	Season (day lay)	Clutch size	18	-0.485	0.041*
		Egg weight	18	0.240	0.322
		RCM	18	-0.362	0.140
WP	Maternal SVL	Clutch size	3	0.500	0.667
		Egg weight	3	0.146	0.815
		RCM	3	0.988	0.098
	Season (day lay)	Clutch size	3	-0.803	0.407
		Egg weight	3	0.153	0.847
		RCM	3	-0.968	0.162
RP3	Maternal SVL	Clutch size	12	0.086	0.790
		Egg weight	12	-0.395	0.094
		RCM	12	0.008	0.980
	Season (day lay)	Clutch size	12	0.142	0.695
		Egg weight	12	0.411	0.237
		RCM	12	-0.036	0.912

r= pearsons correlation coefficient

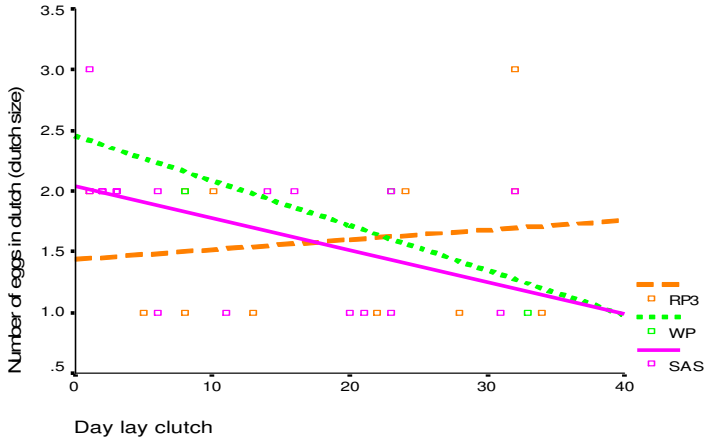


Figure 4.2. The effect of season (day lay) on clutch size for sexual females (SAS) and parthenogens (WP & RP3).

Incubation Length

Mean (+/- SE) incubation times for clutches laid by sexual and parthenogenetic females are shown in Figure 4.3. For clutches that contained more than one egg, the average incubation time for all eggs in the clutch was used. Incubation time was significantly shorter for sexual females than for both of the parthenogens (30 Vs 32-33 days), (One-way ANOVA; *df*=2, F=9.989, p<0.001).

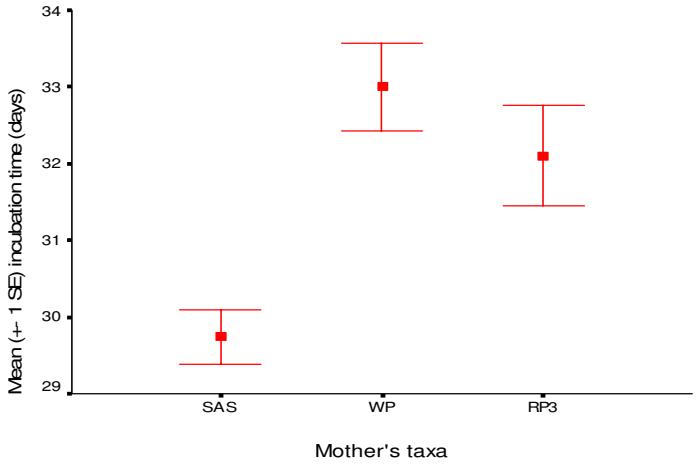


Figure 4.3. Mean incubation time (days) for eggs laid by sexuals (SAS) and parthenogenetic (WP and RP3) M. greyii.

The effect of two life history variables (egg weight and maternal SVL), and season (day of laying) on incubation length was investigated using Pearson's correlation. None of these variables showed a significant correlation (Table 4.11).

Table 4.11. Pearson Correlations between maternal SVL, egg weight, season (day lay) and incubation length.

Maternal Taxon	Attribute 1	Attribute 2	n	r	P
SAS	Maternal SVL	Incubation length	18	0.315	0.188
	Egg weight	Incubation length	18	0.118	0.631
	Season (day lay)	Incubation length	18	0.430	0.066
WP	Maternal SVL	Incubation length	3	0.577	0.423
	Egg weight	Incubation length	3	0.894	0.106
	Season (day lay)	Incubation length	3	-0.140	0.860
RP3	Maternal SVL	Incubation length	12	-0.328	0.356
	Egg weight	Incubation length	12	-0.314	0.377
	Season (day lay)	Incubation length	12	-0.481	0.159

Reproductive Success

Egg viability / Hatching Success

Over the three years, sexual females laid 29 eggs, 19 of which hatched, giving a 65.5% hatching success. WP parthenogens laid 5 eggs, 4 of which hatched, giving an 80% hatching success. RP3 parthenogens laid 17 eggs, 10 of which hatched, giving a 58.8% hatching success. Contingency chi square tests were used to compare egg viability among taxa. There was no significant difference among the three taxa in the proportion of eggs that hatched (X^2= 0.754, *df*=2, p=0.686). These figures did not include one or two eggs that were broken due to handling errors.

Hatchling Survival

Hatchling survival rates are shown in Figure 4.4. Approximately 50% of sexual and RP3 parthenogen hatchlings survived past their first year, whilst 75% of WP parthenogen hatchlings survived past their first year. Survival rates of hatchlings past their first year did not differ significantly (Fisher's exact Test: value=1.018, p=0.699).

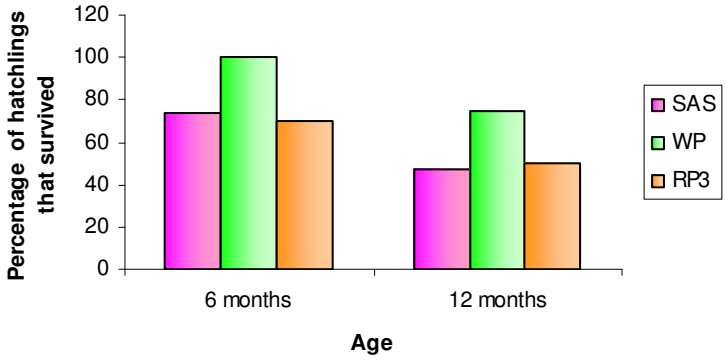


Figure 4.4. Percentage (of total number) of sexual (SAS) and parthenogenetic (WP & RP3) hatchlings that survived to the ages of 6months and 12months.

Hatchling Attributes

A possible deformity was observed in two hatchlings, one a sexual hatchling the other an RP3 parthenogen. Both hatchlings had bent spines. Although the bent spine persisted throughout growth both lizards gained as much weight as the other hatchlings, and this deformity did not seem to affect survival with both lizards living past 6 months. However, their measurements were excluded from the analyses.

Table 4.12. Mean SVL (mm), weight (g) and tail length (mm) of sexual (SAS), WP parthenogen, and RP3 parthenogen hatchlings.

Maternal taxon	Hatchling Attribute	*n*	Range	Mean	SE
SAS	**SVL (mm)**	19	12.50 – 14.50	13.56	0.151
	Weight (g)	19	0.03710 – 0.08810	0.05825	0.002
	Tail Length (mm)	19	14.00 – 19.00	16.55	0.324
WP	**SVL (mm)**	4	13.50 – 15.50	14.50	0.457
	Weight (g)	4	0.05610 – 0.06330	0.05867	0.002
	Tail Length (mm)	4	13.00 – 21.50	17.63	1.930
RP3	**SVL (mm)**	10	9.0 – 14.5	13.45	0.508
	Weight (g)	10	0.03201 – 0.06593	0.05681	0.003
	Tail Length (mm)	10	14.00 – 18.00	16.55	0.391

Body size attributes for sexual, WP parthenogen, and RP3 parthenogen hatchlings on day of hatching are shown in Table 4.12. There was no significant difference in

SVL, weight or tail length of hatchlings among the three types (Table 4.13). The Kruskal Wallis test was used to compare tail length as the data were not homogeneous.

Table 4.13. One-way ANOVA, ANCOVA and Kruskal Wallis results comparing hatchling attributes among SAS, WP and RP3* M. greyii. *Covariate= hatchling SVL.*

Attribute	**F or H***			**Covariate**	
	df	**F or *H**	**P**	**F**	**P**
SVL (mm)	2	1.593	0.22		
Weight (g)	2	0.725	0.493	20.02	<0.001
*Tail length (mm)	2	0.488	0.784		

Effect of Maternal SVL on hatchling attributes

In both sexual and parthenogenetic (both WP and RP3) hatchlings, there was no correlation between maternal SVL and hatchling SVL or maternal SVL and hatchling weight (Table 4.14).

Table 4.14. Pearson's correlation results between maternal SVL (mm) and hatchling attributes.

Maternal Taxon	**Attribute 1**	**Attribute 2**	**r**	**P**
SAS	Maternal SVL	Hatchling SVL (mm)	0.180	0.462
		Hatchling weight (g)	0.370	0.119
WP	Maternal SVL	Hatchling SVL (mm)	-0.365	0.635
		Hatchling weight (g)	0.912	0.088
RP3	Maternal SVL	Hatchling SVL (mm)	0.503	0.138
		Hatchling weight (g)	0.563	0.090

Effect of Egg Weight on hatchling attributes

In sexuals, egg weight was important in determining hatchling SVL, with hatchling SVL, being significantly correlated with egg weight (Table 4.15). Heavier eggs produced longer hatchlings (Figure 4.5). Egg weight did not have an effect on the attributes of RP3 and WP hatchlings (Table 4.15).

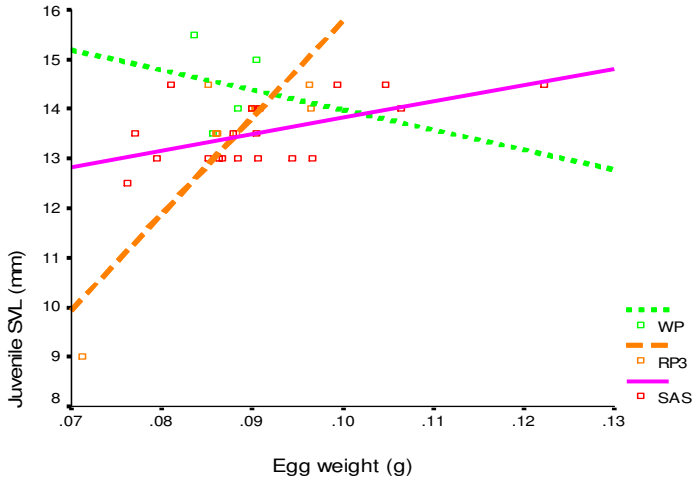


Figure 4.5. The effect of egg weight (g) on hatchling SVL (mm) for sexual (SAS) and parthenogenetic (WP & RP3) M. greyii.

Table 4.15. Pearson's correlations between Egg weight and hatchling attributes.

Maternal Taxon	Attribute 1	Attribute 2	r	P
SAS	Egg weight	Hatchling SVL (mm)	0.508	0.026*
		Hatchling weight (g)	0.384	0.104
WP	Egg weight	Hatchling SVL (mm)	-0.200	0.800
		Hatchling weight (g)	<0.001	1.000
RP3	Egg weight	Hatchling SVL (mm)	0.515	0.128
		Hatchling weight (g)	0.406	0.244

r= Pearson's correlation coefficient
*significant correlation at the 0.05 level

ANCOVA showed that egg weight did have a significant effect on both juvenile SVL and juvenile weight, but juvenile SVL and weight did not differ significantly among taxa (Table 4.16).

Table 4.16. ANCOVA results comparing SVL(mm) and weight (g) among SAS, WP and RP3 juveniles. Covariate was egg weight (g).

Attribute		df	F	p
SVL (mm)	Egg Weight (g)	1	11.829	0.002
	Mother's Taxon	2	3.009	0.065
Weight (g)	Egg Weight (g)	1	9.606	0.004
	Mother's Taxon	2	0.169	0.846

Effect of Incubation time

For all three taxa there was no correlation between hatchling SVL or hatchling weight and incubation time (Table 4.17).

Table 4.17. Pearson's correlations between incubation time and hatchling attributes.

Maternal Taxon	Attribute 1	Attribute 2	r	P
SAS	Incubation time	Hatchling SVL (mm)	0.219	0.369
		Hatchling weight (g)	0.384	0.104
WP	Incubation time	Hatchling SVL (mm)	<0.001	1.000
		Hatchling weight (g)	0.447	0.553
RP3	Incubation time	Hatchling SVL (mm)	0.161	0.656
		Hatchling weight (g)	-0.094	0.796

r= Pearson's correlation coefficient
*significant correlation at the 0.05 level

Growth Rates of Hatchlings

Snout-vent measurements were recorded for a total of 17 juveniles, including 9 sexual, 3 WP parthenogen and 5 RP3 parthenogen juveniles. Only measurements for those juveniles that survived past 12 months of age were used to investigate growth rates.

The Von Bertalanffy model fitted the data best across the three taxa, explaining 37% of the variance in sexuals, 41% of the variance in WP parthenogens and 40% of the variance in RP3 parthenogens (Table 4.18). The von Bertalanffy growth model (Bertalannfy 1951, Fabens 1965) has been used for lizards in a number of other studies (Trivers 1976, Schoener and Schoener 1978, Van Devender 1978).

Table 4.18. Comparison of the differential forms of the Logistic, Gompertz and Von Bertalanffy growth models calculated for male, sexual female, WP parthenogen and RP3 parthenogen M. greyii. **P<0.0001*

Model	SAS		WP		RP3	
	Equation	**R^2**	**Equation**	**R^2**	**Equation**	**R^2**
Logistic	SGR= -0.0119-0.0004SVL	0.269 *	SGR= –0.0066-0.0002SVL	0.380 *	SGR= -0.0080-0.0003SVL	0.373 *
Gompertz	SGR= -0.0298-0.0089lnSVL	0.279 *	SGR= -0.0156–.0044lnSVL	0.384 *	SGR= -0.0188-0.0055lnSVL	0.363 *
Von Bertalanffy	SGR= 0.0595+0.1762(1/SVL)	0.365 *	SGR= 0.0027+0.0906(1/SVL)	0.410 *	SGR= 0.0037+0.1050(1/SVL)	0.396 *

The growth curves of sexual, WP parthenogen and RP3 parthenogen juveniles are shown in Figure 4.6.

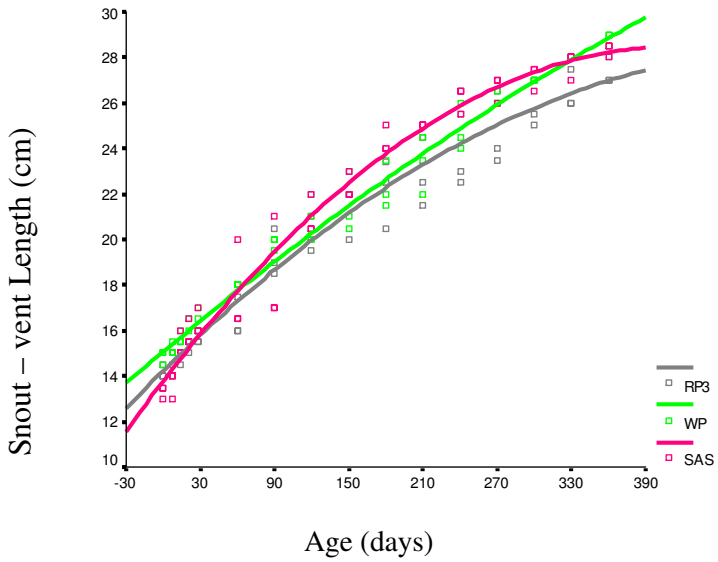


Figure 4.6. Growth rates of sexual, WP parthenogen and RP3 parthenogen lab reared juvenile M. greyii.

Sexual juveniles grew faster than all parthenogen juveniles for approximately the first 180 days since hatching. However, the difference in growth rate over this time span was not significant (Table 4.19). Between days 180 and 270, growth rates were similar for all three taxa. After this time the growth rates of sexual and RP3 juveniles dampened off, while WP juveniles continued to grow. This resulted in sexual and RP3 individuals reaching their asymptotic snout-vent length (svl) at approximately the same time and sexual individuals having a slightly larger asymptotic size then RP3 individuals. WP individuals achieved a larger asymptotic size than both sexual and RP3 individuals, but took longer to reach it. Averaged over the 360 days, sexual, WP and RP3 individuals grew at a similar rate (Figure 4.7). There was no significant difference among the three taxa in either raw growth rate or characteristic growth rate (Table 4.19), indicating that individuals of all three taxa approached their respective asymptotic sizes at the same rate. There was a significant difference among the taxa in asymptotic SVL (mm) (Table 4.19), however the results were inconclusive. Although WP

individuals achieved a larger asymptotic size than RP3 individuals (Bonferroni multiple comparisons test, p=0.037), there was no significant difference in asymptotic SVL between sexual individuals and either RP3 or WP individuals (Bonferroni multiple comparisons test, p= 0.110 and p=1.000 respectively), (Figure 4.7).

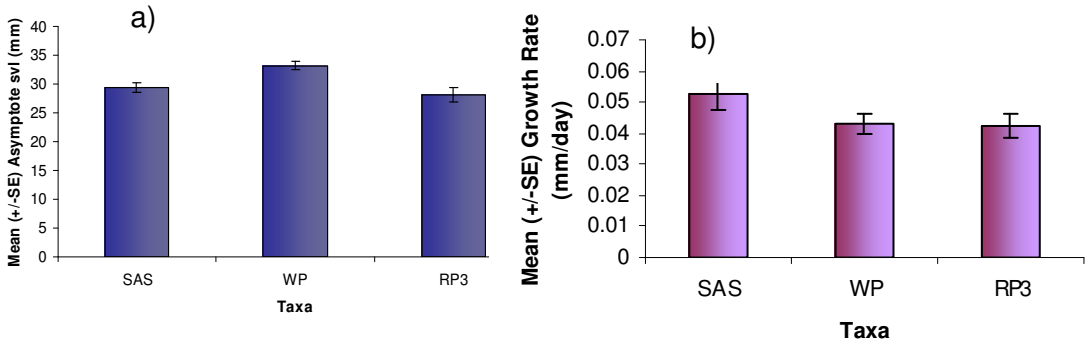


Figure 4.7. Mean (+/-SE) a) asymptote snout-vent length (svl)(mm), and b)raw growth rates of sexual, WP parthenogen and RP3 parthenogen juvenile M. greyii.

Table 4.19. ANOVA results comparing Asymptote SVL (mm)(S_∞), and raw growth rate (mm/day) and characteristic growth rate among SAS, WP and RP3 individuals.

Variable	**ANOVA**		
	df	**F**	**P**
S_∞	2	4.336	0.036
Growth Rate (mm/day) (360 days)	2	1.476	0.231
Characteristic Growth Rate (360 days)	2	2.214	0.149
Growth Rate (mm/day) (0-180 days)	2	1.804	0.168
Characteristic Growth Rate (0-180 days)	2	2.987	0.086

Discussion

Parthenogenetic females are expected to have a two-fold reproductive advantage over related females, all else being equal (Williams 1975).

One of the assumptions of the 2-fold reproductive advantage is that the sex ratio of sexuals is 1:1. In the current study, hatchling sex ratio could not be determined due to the low survival rate of eggs and hatchlings (to an age where sex can be determined). However, in the sexual field population, the sex ratio differed

significantly from a ratio of 1:1, with twice as many sexual females being collected than males. This bias was consistent across years although not significant in the third year, possibly due to the reduced numbers of sexuals found in this year (see chapter 3). There are several reasons why the sex ratio in the field may be biased towards females. One is that the sex ratio in hatchlings is skewed towards females. An alternative reason is that males are the dispersing sex in *M. greyii*, and that even with an offspring ratio of 1:1, adult males are in lower proportions because they have moved out of the natal area prior to the following breeding season (The equilibrium expectation would be Immigration equals emigration unless the site is a source to surrounding skinks). However, due to their very small size, and the large area searched for the study it is unlikely that the males would have moved completely out of the search area. In addition, Adams (2003) found a sex ratio of 1:1 in his populations sampled. Another alternative is that sexual females and males may segregate by habitat, and the habitat in which the females occur was searched more rigorously than the habitat containing males. However, when comparing the ecology of the different taxa of *M. greyii* (see Chapter 3) all apparently suitable habitats within the area of Bundey Bore were searched equally well and males and females did not appear to segregate by macro or microhabitat. Alternatively, females may be more active than males, spending more time on the surface during the day. This would make them more prone to capture than males. However, in the laboratory, results indicate that males actually emerge early than females in the morning and spend the same amount of time on the surface as females at Bundey Bore (Chapter 5). Another possible reason is that males are faster than females rendering them better able to escape capture. Again, this is disputed in Chapter 5, with males and females not differing in their sprinting ability. Finally, mortality rates in male juveniles may be higher than mortality in female juveniles. This is a possibility worth future consideration, with no research to date having been done comparing mortality rates in *M. greyii* populations. In light of the above observations and results of experiments, it would appear that the sex ratio in sexual *M. greyii* at Bundey Bore is potentially skewed towards females and therefore the theorised two-fold reproductive advantage of parthenogens may be reduced.

Two factors that might offset the reproductive advantage of parthenogens are reduced reproductive output and reduced viability of eggs or hatchlings in the parthenogens (Stewart 1996). Results showed very little difference in reproductive effort and output among sexual females, WP and RP3 parthenogen *M. greyii*. Breeding season did not differ and although a greater proportion of RP3 parthenogens in the population were breeding than WP parthenogens, the proportion of breeding sexual females in the population did not differ from that of breeding parthenogens. Adult females did not differ in size, thus one type did not have the potential to increase its reproductive output. A larger body size could allow recruitment of more follicles and hence allow production of more than one clutch a season, or could allow the production of larger eggs or a larger clutch size (Fitch 1958, Schall 1978). In turn, larger eggs could produce larger offspring that could have a competitive advantage due to their larger size. However, results suggested that all three types only lay one clutch per season and average clutch size, average egg weight (g) and RCM (g) were the same for all three types. These results suggest that reproductive effort and output were similar for sexual females and the two parthenogenetic lineages.

In reptiles, egg size and clutch size are often correlated with maternal SVL (Fitch 1958, Schall 1978). This was not the case in *M. greyii*. The lack of effect of maternal SVL on egg size would suggest that egg size is optimised in sexual and parthenogenetic *M. greyii* (Vitt 1986).

Reproductive success was also similar for sexual females, WP parthenogens, and RP3 parthenogens. A higher rate of lack of development in parthenogen eggs than sexual eggs can be an expression of genetic incapabilities among the maternal genes, and viewed as a consequence of Muller's ratchet whereby parthenogen taxa accumulate deleterious mutations until the viability of the clone is seriously compromised (Muller 1964). This was not seen in the current study as egg survival did not differ. The failure of both sexual and parthenogen *M. greyii* eggs to develop may be attributable to handling errors or unsuitable incubation conditions, or else it may be a reflection of low survival rates in nature. Hatchling viability was also compared. Survival rate did not differ among sexual, WP and RP3 juveniles suggesting that hatchlings of one type are not inherently

disadvantaged in comparison to the others. Similarly, although abnormalities have been shown to be more prevalent in some parthenogenetic lizards, reducing the reproductive success of the parthenogens (e.g. in *Lacerta*, reviewed by Darevsky et al., 1985), this was not seen in the population of *M. greyii* at Bundey Bore. Rate of deformities were low in sexuals and parthenogens, with only one sexual hatchling and one RP3 hatchling showing any obvious deformity.

Two differences in reproduction between sexual and parthenogen *M. greyii* were observed. Firstly, eggs from sexual females incubated for three days shorter than eggs from both parthenogens. As there was no significant difference in timing of laying eggs (day lay) and size at hatching among the three types, this would suggest that sexual hatchlings have on average a three day head start on parthenogen hatchlings. Whether this delay would be long enough to translate into an advantage to the sexual hatchling is uncertain, but it may mean that they get first access to available resources or that the eggs have fewer days in a potentially damaging environment. Because eggs are immobile, they are vulnerable to predation, fungal attacks (if too moist), and desiccation (if too dry). So hatching early may be a major advantage as it reduces the time spent in this vulnerable period.

Differences in growth rate have been identified as having major implications for important components of fitness and the life history of lizards, including time to reach sexual maturity, size at maturity, brood size, predator avoidance, social dominance, survival, resistance to stress and capacity to move to more favourable habitats (Schultz and Fielding 1989, Weeks and Gaggiotti 1993, Downes and Bauwens 2002). The results of the current study would suggest that the different taxa invest the same energy into growth, with growth rates being similar. Although this indicates that no particular taxa gains an advantage through a higher growth rate, since sexual juveniles hatched earlier, but growth rates of juveniles among the taxa do not differ, the sexual juveniles are potentially slightly larger than the parthenogen hatchlings for some time perhaps giving them a competitive advantage for limited resources (Weeks and Gaggiotti 1993).

Secondly, although parthenogen and sexual *M. greyii* juveniles approached their respective asymptotic sizes at the same rate, WP parthenogens grew for a longer period to achieve a greater size. A larger size as an adult could incur advantages such as a competitive edge and the ability to eat larger food items and therefore partition resources. This result, however, was inconclusive since there was only a significant difference in asymptotic SVL between WP and sexual juveniles, while there was no significant difference between RP3 and both sexual and WP juveniles. The higher asymptotic size observed in WP hatchlings also does not coincide with data collected on field caught *M. greyii*. For lizards caught in the field (chapter), there was no significant difference in the mean SVL or in the range of SVL observed among the different taxa and all taxa achieve SVLs larger than the asymptote SVL calculated in the growth rate experiment, (sexual females, (range, 21-35mm, mean 28.7, SE=0.38), WP (range, 24-35mm, mean 29.9, SE=0.56), RP3 (range, 21-34mm, mean 28.4, SE=0.53)). These inconsistencies may be due to the sample size of RP3 and WP hatchlings being low, or due to laboratory conditions.

Two other factors, that were not measured in the current study, but that may reduce the reproductive advantage of parthenogens, are if parthenogens take longer to attain reproductive maturity, or have a shorter lifespan (Darevsky et al. 1985, Case and Taper 1986, Stewart 1996). It is unlikely that lifespan is an important factor in the *M. greyii* complex. This species is thought to have a short lifespan of approximately two years (Smyth and Smith 1974), and furthermore, in the lab colony, one type did not appear to die at an earlier or later age than another type. Even so, a comparison of the lifespan and thus lifetime reproductive success, of females from the two reproductive modes could provide valuable data.

More detailed data on size at maturity needs to be collected on the different forms of *M. greyii* in order to investigate more thoroughly the relationship between maturity and asymptotic size among the taxa. For instance, if WP parthenogens do in fact possess a larger asymptotic size this could be countered by the RP3 and sexual juveniles if they are able to reproduce at a smaller percent of their asymptotic size. Alternatively, data on size at maturity may show one reproductive mode to have an inherent advantage either due to a larger size at

maturity (although this was not reflected in data on field caught females in this study) or one form reaching sexual maturity at an earlier age. The data collected in this study suggest that at the time of the following breeding season (after hatching) (Sept-Oct), both sexual and parthenogen juveniles will be approximately nine months of age. The average SVLs of lab reared juveniles at this age were, WP= 26-27mm, SAS=26.3-27.4mm, and RP3=25.5-25.8mm. A comparison of size at maturity among these taxa may show that one form does not reach sexual maturity until the following year, putting it at a disadvantage.

Summary

The findings of this study agree with those of other authors (e.g. Maynard Smith, 1978, Darevsky et al. 1985, Moritz 1993) in suggesting that parthenogen females have a reproductive advantage over sexual females. However, in the case of *Menetia greyii*, the advantage may be less than two-fold due to the skew in sex ratio in the sexuals.

A more complete picture would emerge with the collection of additional information on lifespan and age-specific reproduction. Furthermore, the small number of WP eggs and hatchlings in this study may be masking differences. And, finally, the results obtained in this study may not reflect reproduction in nature since it is not known how these measures of viability, egg and juvenile survival, in a captive population correspond to those in the field.

Chapter 5

Activity patterns and physiological characteristics of parthenogenetic and sexual *Menetia greyii*

Introduction

With broad similarities in both habitat and diet, the question remains how the parthenogen and sexual taxa of *M. greyii* at Bundey Bore coexist, and why the faster reproductive rate of parthenogens has not lead to the elimination of the sexuals.

Partitioning of resources in lizards has led to three categories: they may differ in where they forage, what they eat, and when they are active (Pianka 1973). Pianka (1973) determined that all three dimensions (time, space and food) were important in separating lizards in Australian deserts. Since *M. greyii* at this study site do not appear to segregate by space or food, perhaps they are partitioning via time.

Nearly all behavioural and ecological characteristics of lizards, including activity patterns are influenced by body temperature (Porter and James 1979, Huey 1982, Grant and Dunham 1988). During daylight hours, active lizards are presented with a thermally diverse environment created through shading effects and the differential heating of the various microhabitats available for use (Pianka and Pianka 1976). During activity in this thermally diverse environment, lizards usually maintain body temperatures within a relatively narrow range, through behavioural shifts in basking, shuttling between sunny and shade locations, microhabitat selection, postural changes that enhance heat gain or loss, and time of activity (Huey et al. 1977, Crowley 1985, Stevenson 1985, Bauwens et al. 1996, Grover 1996). Therefore, the body temperatures a lizard will accept while it engages in surface activities will dictate when, where and for how long the lizard may be active. For example, initiation, peak and cessation of activity in

Sceleporus merriai is dependent on temperature (Grant and Dunham 1988). Additionally, differences in temperature preferences might be associated with differing times of activity or different levels of activity on days of different ambient temperature. For example, three species of *Ptyodactylus* geckos differ significantly from each other in mean selected body temperature and these selected body temperatures are closely associated with their different daily activity patterns (Arad et al. 1989). Similarly, other studies have found a correlation between thermal preference or tolerance and activity time (Porter and James 1979, Waldschmidt and Tracy 1983, Huey and Bennett 1987, Arad et al. 1989). These thermal constraints on activity times and behaviours are especially important for small lizards such as *M. greyii* (SVL~ 30mm), because a failure to select an appropriate thermal microclimate for even a few minutes can result in temperature impairment or death (Grant and Dunham 1988).

Several previous studies have compared activity patterns and body temperature preferences between sympatric sexual and parthenogenetic lizards, to determine factors allowing them to coexist. Again most of this work has been done on the *Cnemidophorus* group. Mean temperature preferences (Casas-Andreu and Gurrola-Hidalgo 1993, Sievert and Paulissen 1996) and preferred temperature ranges (Schall 1977) were compared among sympatric sexual and parthenogenetic *Cnemidophorus* lizards, and in general no differences were found. Similarly, most studies have found no difference between sexual and parthenogenetic *Cnemidophorus* in the duration and time period when they are active (Medica 1967, Schall 1977, Mitchell 1978, Mitchell 1979, Paulissen et al. 1988b, Schall 1993, Paulissen 2001). However, two studies found a difference in emergence time with sexual *C. inornatus* emerging earlier in the day than the parthenogens *C. uniparens* (Mitchell 1978), and *C. exsanguis* (Medica 1967). Differences in behaviour have also been identified. Mitchell (1978) found that *C.uniparens* (parthenogen) spent activity time both foraging and basking, while *C. tigris* (sexual) foraged continuously over the same activity time. Similarly, the two parthenogens LAR-A, LAR-B and sexual *C. gularis* selected the same body temperatures (Casas-Andreu and Gurrola-Hidalgo 1993, Sievert and Paulissen 1996), activity time, and amount of time in different microhabitats, but *C. gularis* males spent more time engaged in social interactions, and moved further and

faster than parthenogenetic females (Paulissen 2001). Other studies have found no difference in behaviour between coexisting sexual and parthenogenetic *Cnemidophorus* lizards (Karasov and Anderson 1984, Paulissen 1987, Anderson and Karasov 1988, Vitt et al. 1993, Vitt et al. 1997), although behavioural differences between sympatric parthenogens have been reported (Bowker 1993, Bolger and Case 1994, Paulissen 2001).

Thus differences in behaviour among sexual and parthenogenetic *Cnemidophorus* are generally minor and resource partitioning via time in these lizards is thought to be minimal.

Often linked with activity patterns in lizards, and also dependant on body temperature is physiological performance (Huey 1982, Wei-Guo et al. 2000). Since physiology influences fitness (Arnold 1983) the narrow range of body temperatures selected by active lizards usually encompasses the temperature range that is optimal for physiological performance (Avery 1982). For example, in the Insular Lizard *Podarcis hispanica*, body temperatures recorded in the field closely matched selected body temperatures in a laboratory gradient and most fell within the temperature range at which they ran at least 80% of their maximum sprint speed (Castilla and Bauwens 1991). Several studies have shown that when lizards are active at body temperatures above or below their optimum they perform less well in physiologically dependent behaviours. Avery *et al*. (1982) demonstrated that low body temperatures in the lizard *Lacerta vivipara* reduced foraging speed and ability to capture and consume prey. Greenwald (1974) showed prey capture success and strike velocity of the gopher snake (*Pituophis melanoleucus*) increased with body temperature. And, Christian and Tracy (1981) found that low body temperatures in the land iguana (*Conolophis pallidus*) reduced their ability to avoid predation, as hawks were more successful in preying upon the iguanas when their sprinting ability was reduced by low body temperatures.

Physiological traits that have previously been measured in lizards and found to be correlated with body temperature and/or to influence activity include oxygen consumption (Paulissen et al. 1988a), endurance (Garland 1993), water loss rates (Bowker 1993), and sprint speed (Bauwens et al. 1995).

Sprinting ability is an important trait in *M. greyii*. They move quickly to avoid capture, to avoid aggressive encounters during paired interaction trials, and they also chase each other at high speed (see Chapter 6). All four types (sexual males and females, WP and RP3 parthenogens) are under high predation pressure, suffering high levels of tail loss (see Chapter 3). Thus differences in sprint speed ability may affect both social dominance and evasion of predators in *Menetia greyii*. Sprint speed has been shown to influence predator avoidance and survivorship, and social dominance in other lizard species, as well as foraging success (Greenwald 1974, Huey 1979, Bennett 1980, Christian and Tracy 1981, Avery 1982, Huey 1982, Huey and Hertz 1984, Van Berkum et al. 1986, Huey and Bennett 1987, Bauwens et al. 1995, Cejudo and Marquez 2001).

This chapter reports data collected on temperature preferences, physiological performance and activity patterns in *M. greyii* to explore differences among the taxa. These data can be used to test several of the contrasting theories to explain co-existence of sexual and parthenogenetic forms.

To test the FNV and GPG hypotheses in *M. greyii*, two measurements of niche breadth additional to those related to food and habitat can be compared among the types. These are the activity niche (breadth and overlap), and the breadth of temperature ranges tolerated. If consistent with the FNV model we would expect the parthenogens individually to exhibit distinct and narrow activity time and temperature ranges, relative to the sexuals, and their range of activity time and temperatures to be contained within those of the sexual taxa. If consistent with the GPG model we would expect the parthenogens to exhibit wider activity time and temperature niches than the sexuals.

In addition to the GPG hypothesis, another form of the generalist view, the Spontaneous Heterosis hypothesis can be tested (Wetherington et al. 1987). Due to their hybrid origin, WP and RP3 parthenogens have a higher level of heterozygosity than the sexually reproducing *M. greyii* at Bundey Bore (Adams et al. 2003). It has been proposed that increased heterozygosity may be functionally correlated with superior performance in a variety of fitness related traits. For example, several studies have found heterozygosity associated with improved

physiological performance (Bulger and Schultz 1979, Mitton et al. 1986). Alternate to the Spontaneous Heterosis Hypothesis, Price et al. (1993) suggested that the hybrid origin, reproductive mode and accumulation of deleterious mutations by parthenogens should cause them to perform poorly relative to their sexual relatives. Several studies on parthenogenetic and sexual lizards support this idea. For example, parthenogenetic *C. tessalatus* are more approachable, less cautious and presumably more vulnerable to predators than are sexual *C. tigris (Price 1992)*, parthenogenetic *Cnemidophorus* generally have lower endurance than their sexual congeners (Cullum 1997), LAR-A parthenogens are slower and more easy to catch during flight than are sexual *C. gularis* females (Paulissen et al. 1988a), and *C. gularis* is a more efficient forager than LAR-A (Paulissen 2001).

Further to examining physiological performance breadth between sexual and parthenogenetic *M. greyii*, to test the spontaneous heterosis hypothesis sprinting ability can be compared. If heterozygosity and superior performance are associated, parthenogenetic *M. greyii* should be better performers than their sexual congeners.

Hypotheses, Aims and Predictions

The aims of this chapter were several fold;

1.Activity Patterns

The primary aim was to determine the diurnal activity pattern of males, sexual females, WP parthenogens, and RP3 parthenogens, and determine if any differences occur among the types in activity pattern that might allow the observed ecological coexistence.

For this, activity will be defined as any behaviour while emerged from refuges. Activity time is the period during which lizards are out of their refuges.

There are three ways the different types could segregate by time;

a) They are active at different times of the day.

To test this we compared the mode of activity, emergence time, cessation time, peak activity time, and amount of time spent on the surface.

b) They are active at the same time of the day but spend the majority of their day performing different activities (i.e. exhibit different activity behaviour).

To test this we compared the percentage of active time spent performing each observed activity.

c) They are active during the same time periods of the day, and spend similar amounts of time performing the different activities, but perform these activities at different time periods of the day (morning, afternoon, evening).

To test this we compared the percentage of time spent performing the different activities within each period of the day (morning, afternoon, evening), and compare how activity behaviour patterns change across the day.

2. Temperature Preferences

The aim was to determine the body temperature preference characteristics (mean, minimum, maximum, range) for males, sexual females, WP parthenogens and RP3 parthenogens, and to compare these characteristics among types.

3. Sprint Speed Ability

Sprinting abilities in nature depend on both maximum capacities and relative performance levels (i.e. percent of maximum) that can be attained (Bauwens et al. 1995). Thus the aims here were to;

a) determine the maximum sprinting velocity of each type over a range of temperatures and overall,
b) to calculate the performance breadth of each type, that is the range of temperature over which each type runs well, and then,
c) to compare these abilities among types.

4. Correlations between body temperature, sprinting performance, and activity patterns

The aim was to examine to what extent the observed activity patterns in the four types are explained by the thermal and physiological constraints observed. That is, are thermal preferences and sprinting performance correlated for each type? and

are the lizards active only during their preferred temperature range and range of temperatures over which they perform well physiologically?

If differences were found among types in their preferred body temperatures and this is correlated with their physiological performance, this may correspond to a difference in activity. For example;

Lower preferred minimum body temperature = emerge earlier, when temperatures are cooler.

Higher preferred maximum body temperature = stay on surface at higher temperatures while others must retreat.

Wider range of tolerated body temperatures or broader physiological performance range = active for longer periods

Differ in their body temperature range and physiological range overall = active at different periods of the day.

5. Test the models described above

The aim was to discuss the results in relation to the FNV, GPG, and spontaneous heterosis hypotheses as discussed above.

To test the FNV and GPG Hypothesis, the aim was to calculate and compare activity (time) niche breadth, and breadth of selected body temperature range for each type.

The spontaneous heterosis hypothesis was tested by determining if the parthenogens possess superior physiological performance in comparison to the sexual form, by comparing maximum sprint speed velocity and sprint performance breadth.

Methods

Lizards used in all of the experiments described below did not differ significantly in either SVL (mm) or weight (g).

Daily Activity Patterns

The daily activity pattern of lizards is often determined in the field by calculating the number of lizards either caught or observed per observer hour (Echternacht 1967, Vitt and Ohmart 1977, Paulissen et al. 1988a, Grover 1996, Vitt et al. 2000). Differentiating the daily activity of the different taxa (sexual and parthenogenetic) of *Menetia greyii* in the field is difficult because lizards must be captured for genetic identification (tail tissue is required – see chapter 2). Although *Menetia* were observed to be active at all hours of the day during field seasons (Sept-Nov), captures were not usually successful during the hotter parts of the day because they are very fast. Therefore daily activity patterns were determined in the laboratory.

Figure 5.1. Experimental tank setup for observing activity patterns in Menetia greyii.

Forty experimental tanks (60cm L X 45cm W X 50cm H) were set up in a controlled temperature room (20^{o}C). The tanks consisted of a 5cm deep sand substrate. In the centre of the tank there was a pile of leaf litter (30cm L X 40cm W X 2cm D) and at either end of the pile of leaf litter there was open sand substrate (Figure 5.1). A heat lamp (210-W) was placed at one end of the tank. This provided additional heat to one half of the tank. This setup resulted in the tank having four different habitats available for use by the lizards; 1) open sand in heat, 2) leaf litter in heat, 3) leaf litter, no heat, and 4) open sand, no heat. Those habitats under the heat source simulated habitats in the sun in the field, while the

non heated sections simulated shade. Environmental conditions in the room were set to mimic as closely as possible conditions in the natural habitat of the lizards. The room had a12:12 light dark cycle with overhead fluorescent lights coming on at 7am and turning off at 7pm. The heat lamps turned on at 8.30am and off at 4pm. Ibutton thermocouples were placed in six of the experimental tanks for a week prior to experiments commencing to determine temperature ranges within the test arena over the course of the day (Figure 5.2). Eight ibuttons were placed within each tank, two in each of the four available habitats.

Shading effects (heat or no heat) and the presence of different habitats produced a thermally diverse environment within the test arena (Figure 5.2). All habitats had a surface temperature of 20°C from sunrise to when the heat lamps turned on. Surface temperature in the two habitats in the sun (heated sections of tank) rose dramatically after heat lamps turned on and reached a plateau around midday, and then decreased after heat lamps turned off (4pm). While the heat lamps were on, surface temperatures where higher in the open sand (26.7-41.3°C) than the leaf litter (26.5-33.9°C). Surface temperatures in the two habitats in the shade (those in the unheated sections of the tank), also increased during the course of the day due to room temperatures increasing with the heat lamps on, but surface temperature in these habitats never exceeded 27°C.

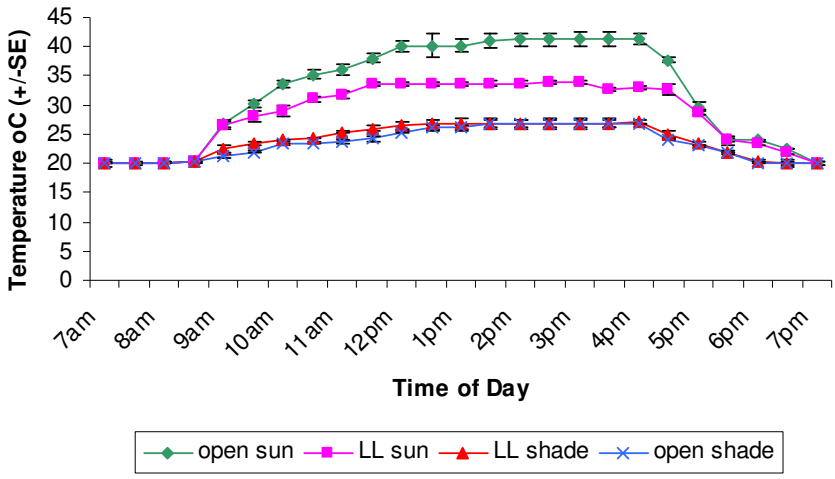


Figure 5.2. Surface temperature °C (+/-SE) in the four available habitats (open sand in sun (open sun), leaf litter in sun (LL sun), leaf litter in shade (LL shade), and open sand in shade (open shade)) during diurnal hours.

All lizards were fed crickets twice weekly, and water was added as required. No lizards were fed for the 24hrs prior to being tested.

Pilot studies revealed no nocturnal activity of any lizards in these arenas so only diurnal activity was investigated.

Trials were conducted in the months Sept-Nov in 2001 and 2002. Forty adult lizards were used in this experiment; 10 males, 10 sexual females, 10 WP parthenogens, and 10 RP3 parthenogens. All lizards were collected from the field, placed in individual experimental tanks at Flinders University, and tested within seven days of capture. The lizards were left for 3-7 days to habituate to the test conditions. Then a video recorder (SONY) mounted above the tank recorded lizard behaviour on eight days for the 12 light hours (7am-7pm). Five lizards were recorded each day and the order of testing the four types was random. Each lizard was recorded on just one day.

A lizard was defined as active when it was on the surface in any location and inactive when it was under the leaf litter.

From the video tapes we recorded the location of the lizard each 10minutes and whether it was active or inactive. For active lizards we recorded the behaviour (e.g. basking, moving) the lizard was engaged in.

From these data we calculated for each individual the percentage of time spent;

a) on the surface (i.e. active) or under leaf litter (i.e. inactive)

b) in the heated section or non heated section of the tank

c) in the open sand or in leaf litter

d) performing each of the observed behaviours while on the surface

for each hour of the day and also overall (all daylight hours combined).

Emergence time was determined as the time (in minutes) since the overhead lights turned on (sunrise) that the lizard first emerged. Retreat time was determined as the time (minutes) prior to the overhead lights turning off (sunset) that the lizards finally retreated under the leaf litter and did not emerge again for that day.

Time niche breadth and overlap was determined for each of the four types using the same formulae as those used for measuring habitat breadth and overlap in Chapter 3 (see pg.48). Hourly intervals were used as resource categories and number of lizards on the surface per hour as the raw data.

Temperature Selection

Preferred body temp was measured in a laboratory thermal gradient located in a control temperature room (20^{o}C). The gradient had wooden sides and flooring and measured 60cm length X 10cm width X 8cm height. Four internal wooden barriers (60cm X 0.4cm X 8cm) were also constructed and were placed 2cm apart thus producing five separate lanes each 60cm long. Lizards were unable to move between the lanes and were visually isolated from other lanes. The bottom and sides of the gradient were encased in 5cm thick styrofoam to reduce radiant heat loss (Figure 5.3). The gradient was filled to a depth of 1cm with clean sand. The heat source was provided by two 210-W (total=420-W) infrared globes placed at one end of the gradient. This arrangement provided a range of surface temperatures, grading gradually from >50^{o}C directly beneath the heat source to 20^{o}C at the end furthest from the heat source (Figure 5.4). Ibutton thermocrons numbered 1 – 30 were placed at 2cm intervals, flush with the sand surface along each of the five lanes. Position of the thermocouples was marked on the top of the lane barrier wall.

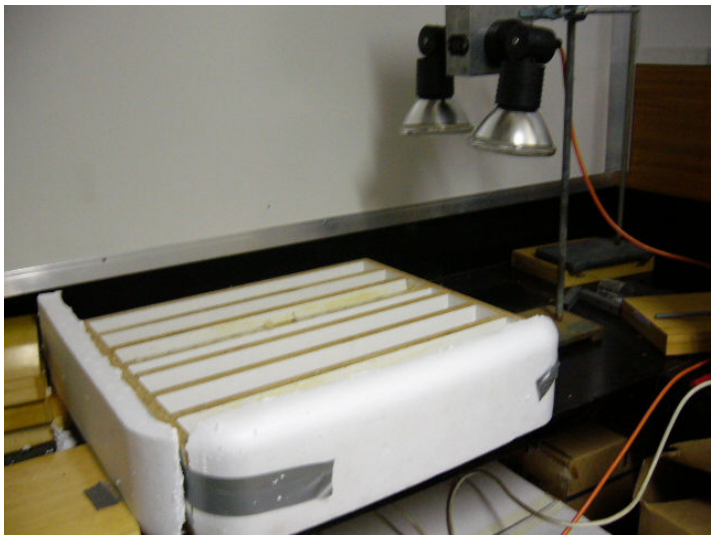


Figure 5.3. Thermal gradient used to test temperature preferences in Menetia greyii.

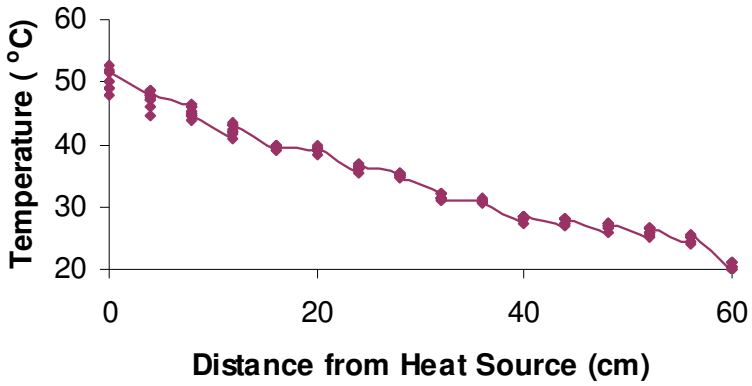


Figure 5.4. Temperature (^{o}C) on the sand surface along the length of the gradient.

Tests were conducted over Oct-Dec 2002 and 2003. A total of 73 lizards were tested (five at a time), comprising 19 sexual males, 22 sexual females, 15 WP parthenogens, and 17 RP3 parthenogens. All animals were tested within 4-7 days after being collected. Prior to being tested the lizards were kept in individual and identical plastic containers in a 25^{o}C room, so all were acclimated to the same conditions. The lizards had no access to food two days prior to measurements as some reptiles may regulate higher body temps after feeding (Huey 1982). All lizards tested were healthy adults, with either intact or fully regenerated tails. All females tested were non-gravid. Each animal was tested only once.

Five lizards were tested per day. Heat lamps were turned on and lizards were placed into the gradient at 0600hr, two hours prior to the start of the experiment. This allowed the gradient to reach maximum and steady temperatures, and for the lizards to explore the gradient, and become habituated to the test arena. Only one lizard occupied each lane. The trial was videotaped so that the animals were not disturbed by human presence during the course of the experiment. From the playback at each 30 minute interval the thermocouple corresponding to the position of each lizard was identified and the temperature reading subsequently determined from that thermocouple at that time was used to infer the body temperature selected by the animal. Thus, the temperature measured was the temperature of the sand substrate at the point below the centre of the lizards' body. The low weight of this species (<1g) suggests that they would rapidly achieve thermal equilibrium with the substrate (Crisp et al. 1979, Bartholomew 1982) and thus substrate temperature below their position should be representative

of body temperature. During the experiment all lizards placed themselves at intermediate positions in the gradient and did not retreat to walls or corners. Body temperature readings began at 0800h, and were taken every 30mins until 1700h when the heat lamps were still on, giving a total of 19 readings per lizard.

Lizards of all four types were selected in random order for the trials. At the end of each day the sand substrate was removed, the gradient was cleaned and fresh sand was added in order to eliminate any chemical cues.
From the 19 temperature readings for each lizard we determined four variables for each lizard;

1) minimum body temperature selected
2) maximum body temperature selected
3) mean selected body temperature (±SE)
4) body temperature range

Sprint Speed

We determined sprint speed in 52 adult *Menetia greyii* (14 males, 15 sexual females, 12 WP parthenogens, 11 RP3 parthenogens) at a sequence of body temperatures (15, 20, 25, 30, 35, 40^{o}C). Forty degrees centigrade was chosen as the maximum temperature to race at as this is close to the critical thermal maximum previously reported for this species (Greer 1980). The lizards selected for this experiment had intact or completely regenerated tails. Each lizard was weighed on each day of trials.

Body temperature of the lizards was controlled by placing them in an incubator at the appropriate test temperature for at least one hour prior to being raced. Each lizard was run every two days at one body temperature per day. On each test day each lizard was run twice at the selected temperature, and was given a minimum of two hours rest between runs. The order of body temperature tested was randomised for each lizard. Following the trials at these temperatures, each lizard was rerun at the temperature of its first race to determine any changes in sprint ability during the experiment. Hertz et al. (1983) recommended that any lizard that changed speed by more than 15% between the two trials, or that lost more

than 15% of body mass by the end of the trials, or that lost its tail should be eliminated from analysis. No lizards exceeded these elimination values in the current trials.

Sprint speed was measured on a 75cm long race track with 10cm high walls to prevent the lizards from escaping and a funnel trap at the far end. One side of the track was transparent, which allowed lateral filming with a video camera (SONY). The racetrack had a cork tile surface that afforded good traction and the first 15cm of the track provided distance for acceleration (Figure 5.5). In each videotaped trial each lizard was chased by hand down the racetrack. From the videotapes sprint speed (cm/sec) over each of three 20cm sections of the track (15-35; 35-55; 55-75cm) was calculated for each lizard for all trials. Because each lizard was run twice at each temperature, this led to six readings of speed over 20cm for each lizard at each temperature. From these trials we selected the fastest 20cm track interval for each lizard at each temperature and used this value as an estimate of a lizards' maximum sprinting ability at that temperature. It was always the same person that chased the lizards therefore standardizing the stimulus.

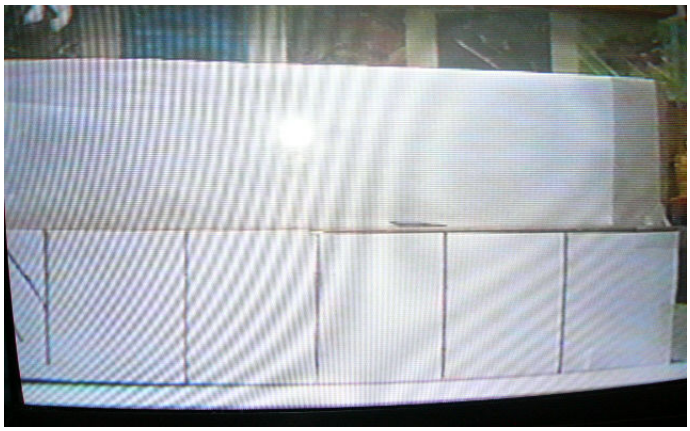


Figure 5.5. Racetrack used to determine sprint speed in Menetia greyii.

In addition to maximum sprint speed at each temperature, two other sprint speed parameters were determined for each lizard;

1) Vmax = maximum sprint speed achieved over all temperatures
2) Tmax = body temperature associated with Vmax

Sprint performance breadths were also examined for each lizard using methods similar to those of Van Berkum *et al.* (1986), Bennett (1980) and Hertz *et al.*

(1983). To quantify the thermal sensitivity of sprint speed, and subsequently determine performance breadths we standardised performances among lizards by dividing an individual's speed at each temperature by its maximum sprinting speed (% Vmax). We plotted a performance curve (relative speed against body temperature) and used the procedure described by (Van Berkum et al. 1986) to connect data points and to construct a minimum convex polygon for each individual (Figure 5.6). These polygons were then used to estimate the following measurements for each individual lizard;

1) **L_{80}**= lower body temperature at which the lizard can run at 80% of its maximum (Vmax)
2) **U_{80}**= upper body temperature at which the lizard can run at 80% of its maximum
3) **L_{95}**= lower body temperature at which the lizard can run at 95% of its maximum
4) **U_{95}**= upper body temperature at which the lizard can run at 95% of its maximum
5) **B_{80}** = body temperature range over which speed is at least 80% of its maximum
6) **B_{95}**= body temperature range over which speed is at least 95% of its maximum
7) **M_{95}**= optimal temperature for sprinting. Estimated by calculating the midpoint of B_{95}.

The two measurements of performance breadth represent the temperature range that is optimal for sprinting (B_{95}), and good for sprinting (B_{80}).

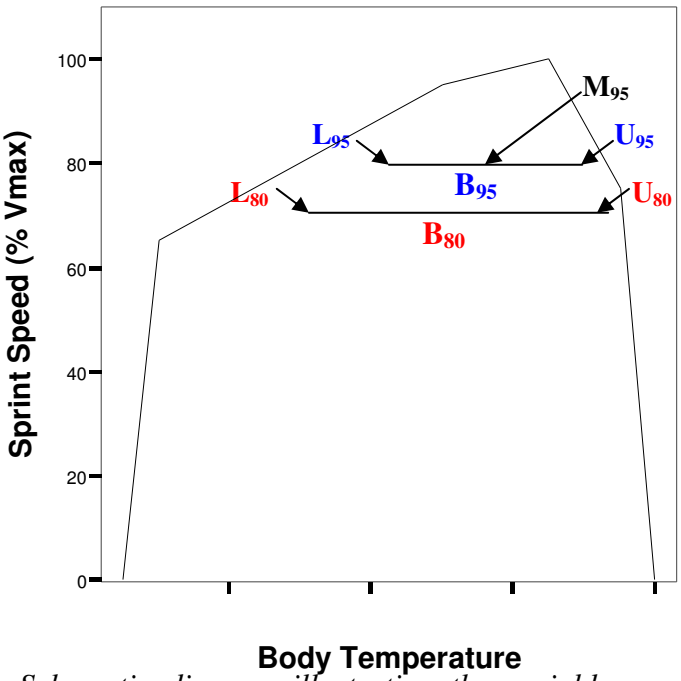


Figure 5.6. Schematic diagram illustrating the variables used to analyse the thermal sensitivity of sprint speed.

Statistical Analyses

In statistical analyses using percentage data, we performed arcsin transformations.

Specific tests used are explained in more detail throughout the results section.

Results

Activity

Are males, sexual females, WP parthenogens and RP3 parthenogens active at different times of the day?

Start (emergence) and Finish (retreat) of Daily Activity

Kruskal Wallis non parametric test was used to compare emergence and retreat times among types. Where a significant difference was found, Mann-Whitney *U*-tests were used to compare between each pair of type (e.g. males Vs WP parthenogens).

Emergence and retreat times are summarised in Figure 5.7 below.

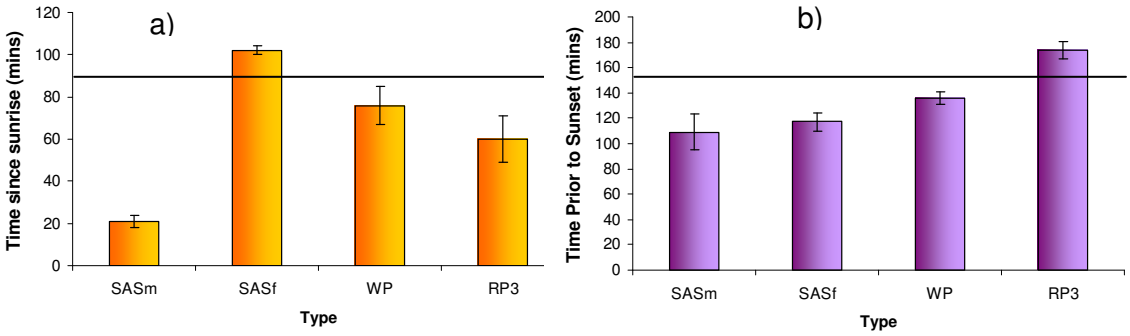


Figure.5.7 a) the number of minutes (mean +/-SE) after lights on that each type emerged. Line represents the time the heat lamps turned on. Times above the line are after the heat lamps turned on, times below the line are prior to the heat lamps turning on. b)the number of minutes (mean +/-SE) prior to lights off each type retreated. Line represents the time the heat lamps turned off. Times above the line are when the heat lamps were on, times below the line when heat lamps were off.

Males were the first to emerge (~21 mins after lights on), followed by RP3 parthenogens (~60 mins after lights on), WP parthenogens (~76mins after lights on), and lastly sexual females (~102mins after lights on). Males and both

parthenogens emerged before the heat lamps came on corresponding to a surface temperature of 20°C throughout the test arena. Sexual females did not emerge until after heat lamps had been on for approximately 10 minutes and the surface temperature had risen to approximately 23.5°C. Emergence time differed significantly among types (Table 5.1), with males emerging significantly earlier than all female, and sexual females emerging significantly later than both parthenogens (Table 5.2).

All lizards were in the heated section of the tank just prior to retreating for the day. Retreat time differed significantly among types (Table 5.1), with RP3 parthenogens ceasing activity significantly earlier than all other types, retreating under the leaf litter just prior to the heat lamps turning off (Table 5.2). The surface temperature in the heated section of the test arena at this time was between 33-41°C. The other three types continued surface activity after the heat lamps turned off and surface temperature of the tanks cooled down. WP parthenogens retreated approximately 2hrs15mins prior to lights off (temp= >30°C), sexual females retreated approx. 2hrs prior to lights off (temp= 28-29°C), and males were the last to cease daily activity, approx. 1hr50mins prior to lights turning off (temp=26-27°C).

There was a significant difference in duration of daily activity period (Table 5.1), with activity period being significantly longer for males (~9hrs50min) than sexual (~8hr20min) and parthenogenetic (WP ~8hr25min; RP3 ~ 8hr5min) females. Sexual and parthenogen females did not differ in their length of daily activity (Table 5.2).

Table 5.1. Kruskal Wallis (*) and One Way ANOVA results comparing emergence time, retreat time and duration of daily activity (hrs) among males, sexual females, WP parthenogens and RP3 parthenogens.

Variable	df	H* or F	p
*Emergence time	3	24.426	<0.001
*Retreat time	3	19.928	<0.001
Duration of Activity (hrs)	3	16.221	<0.001

Table 5.2. Mann-Whitney U-test (*) and Tukey multiple comparisons test comparing emergence time, retreat time and duration of daily activity (hrs) between each type.

Variable	Type 1	Type 2	p
*Emergence time	SASm	SASf	<0.001
	SASm	WP	<0.001
	SASm	RP3	<0.001
	SASf	WP	0.001
	SASf	RP3	0.009
	RP3	WP	0.646
*Retreat time	SASm	SASf	<0.001
	SASm	WP	0.114
	SASm	RP3	0.002
	SASf	WP	0.125
	SASf	RP3	<0.001
	RP3	WP	0.001
Duration of Activity (hrs)	SASm	SASf	<0.001
	SASm	WP	<0.001
	SASm	RP3	<0.001
	SASf	WP	0.979
	SASf	RP3	0.798
	RP3	WP	0.544

Mode of Activity & Peak Activity Times

Sexual males and females, WP parthenogens and RP3 parthenogens all showed a unimodal pattern of diurnal activity (Figure 5.8).

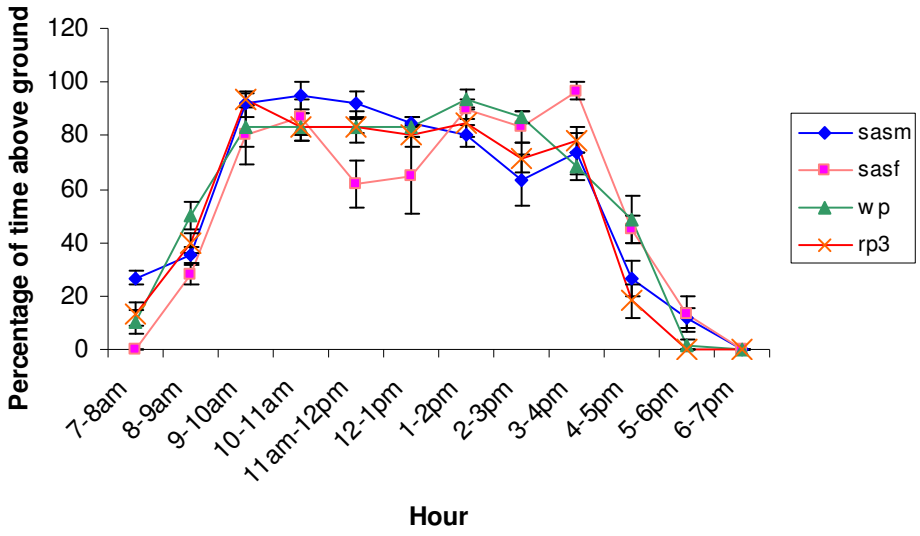


Figure 5.8. Percentage of observations (at 10min intervals) when lizards were on the surface for males (SASm), sexual females (SASf), WP parthenogens (WP) and RP3 parthenogens (RP3) during each daylight hour. N=10 in each case. Values are mean (±SE).

In all four types, surface activity (percentage of observations on the surface) increased between 8 and 10am corresponding to an increase in surface temperature after the heat lamp turned on at 0830hrs (Figure 5.2). Lizards then spent the majority of each hour on the surface before reducing surface activity after 4pm, when heat lamps turned off. RP3 parthenogens spent no time on the surface after 5pm, sexual males and females and WP parthenogens spent no time on the surface after 6pm. There was a slight lull in activity for sexual females between 11am-1pm, but they still spent >60% of time on the surface during these hours.

Peak Activity Time was defined as the hour with the highest percentage of observations on the surface. For RP3 parthenogens peak activity occurred between 9 and10am; for sexual males between 10 and11am, for WP parthenogens between 1 and 2pm, and for sexual females between 3 and 4pm.

The total amount of time spent on the surface during daylight hours did not differ significantly among types (One-way ANOVA, F=0.530; *df*=3; p=0.664).

Conclusions

Males emerged earlier than all females and hence had a longer daily activity period. However this did not result in males spending more time on the surface during the day than sexual and parthenogenetic females. Sexual females emerged last and at a warmer surface temperature. RP3 parthenogens retreated earlier. Again these did not result in overall differences in total time active.

All four types are very similar in their daily activity patterns. Although hours of peak activity differed, the majority of surface activity occurs over the same hours.

Are males, sexual females, WP parthenogens and RP3 parthenogens investing their surface activity time into different activities or using different microhabitats?

One-way ANOVA was used to compare the percentage of time spent performing each activity and the percentage of time spent in each habitat type among males, females, WP and RP3 parthenogens. Where differences were identified, the Tukey

multiple comparisons test was used to determine differences between each pair of types.

Activities

Lizards were observed performing three main activities while on the surface; basking, moving, and sitting. These activities are defined below;

Basking – the body is flattened onto the substrate. This was usually observed when the lizard was under the heat source

Moving – a lizard moves from one place to another

Sitting – lizard is motionless, but the body is not flattened to the surface. This was usually observed when the lizard was away from the heat source

All four types spent the majority of their time on the surface basking and the least amount of time sitting (Figure 5.9).

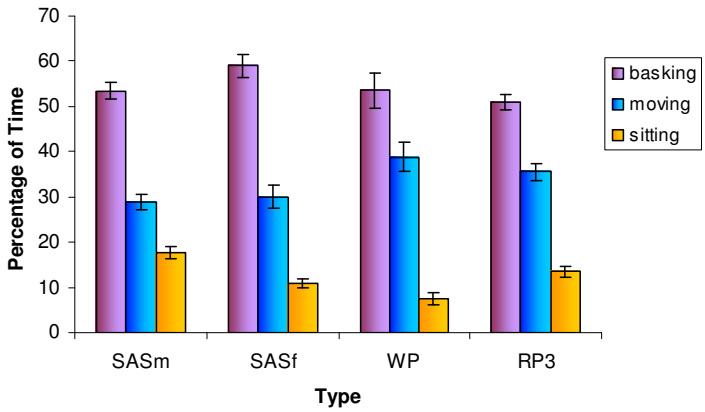


Figure 5.9. Percentage of time while on the surface spent performing each activity (basking, moving, sitting) for males (SASm), sexual females (SASf), WP parthenogens (WP) and RP3 parthenogens.

There were significant differences among types in the amount of surface time spent moving and sitting motionless (Table 5.3). WP parthenogens spent significantly more time moving through the habitat than both sexual males and sexual females, and males spent significantly more time sitting motionless than sexual females and WP parthenogens (Table 5.4). All four types basked for the same amount of time (Table 5.3).

Table 5.3. One Way ANOVA results comparing the amount of surface time spent in each of the observed behaviours among males, sexual females, WP parthenogens and RP3 parthenogens.

Variable	df	F	p
Sitting motionless	3	8.290	<0.001
Moving	3	3.754	0.019
Basking	3	1.952	0.139

Table 5.4. Tukey multiple comparisons test comparing time spent sitting motionless (mins) and time spent moving (mins) between each type.

Variable	Type 1	Type 2	p
Sitting motionless	SASm	SASf	0.008
	SASm	WP	<0.001
	SASm	RP3	0.102
	SASf	WP	0.519
	SASf	RP3	0.708
	RP3	WP	0.085
Moving	SASm	SASf	1.000
	SASm	WP	0.033
	SASm	RP3	0.571
	SASf	WP	0.031
	SASf	RP3	0.553
	RP3	WP	0.408

Habitat use

Within the experimental tanks the lizards had four different habitats available for use: leaf litter or open sand in the heated or non heated sections of the tank.

There was no significant difference among males, sexual females, WP and RP3 parthenogens in the amount of time spent in the heated section, with all four types preferring the heated sections of the tank (Figure 5.10a, Table 5.5).

All four types preferred leaf litter habitat as opposed to open sand (Figure 5.10b). However the parthenogens spent significantly more time in the open sand and less time in the leaf litter than sexual females (Table 5.6).

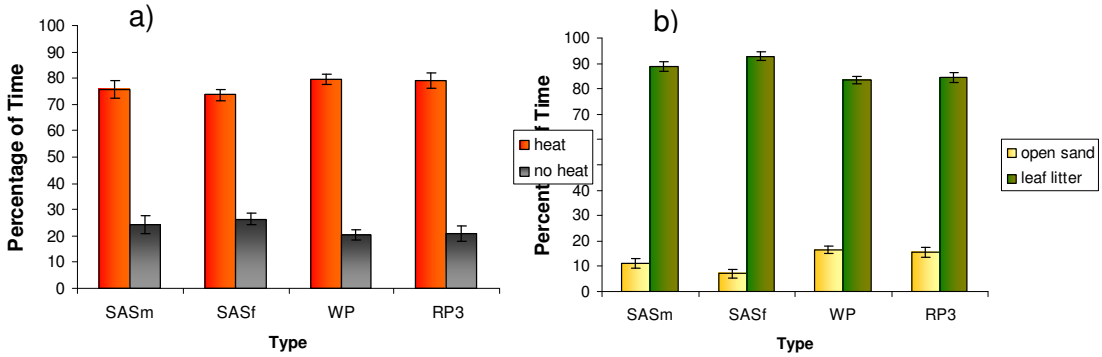


Figure 5.10. a) percentage of time (+/-SE) spent in the heated and non-heated areas of the test arena by each type. b) percentage of time (+/-SE) spent in the open sand and leaf litter areas of the test arena by each type.

Table 5.5. One Way ANOVA results comparing the amount of surface time spent in the available habitats among males, sexual females, WP parthenogens and RP3 parthenogens.

Time in habitat (mins)	**df**	**F**	**p**
Heated section of tank	3	0.748	0.531
Open sand	3	4.721	0.007

Table 5.6. Tukey multiple comparisons test comparing time spent sitting motionless (mins) and time spent moving (mins) between each type.

Variable	**Type 1**	**Type 2**	**p**
Time (mins) spent in open sand	SASm	SASf	0.441
	SASm	WP	0.233
	SASm	RP3	0.531
	SASf	WP	0.008
	SASf	RP3	0.033
	RP3	WP	0.940

Conclusions

Parthenogenetic females utilised open areas more than sexual females, but the preferred habitat for all types was leaf litter in the heated sections of the tank.

In addition to the different types being active on the surface primarily in the same time period, there was minimal difference in the amount of time spent performing the different activities. The majority of time was spent basking and the least amount of time to sitting. Parthenogens tended to move a little more than sexuals.

It is possible that the four types were still partitioning time by performing these activities at different times of the day.

Are males, sexual females, WP parthenogens and RP3 parthenogens performing activities at different times of the day?

Diurnal hours were split into three periods;

- **morning**; included the hours 7am-12pm which were the hours when surface temperatures were gradually rising (Figure 5.2).
- **afternoon**; included the hours 12:01-4pm which were the hours when surface temperatures were at their highest and steady.
- **evening**; included the hours 4:01-7pm which were the hours when heat lamps were turned off and surface temperatures were gradually decreasing.

The percentage of time spent under the leaf litter, basking, moving and sitting were calculated for each time period for each type (Figure 5.11). The general pattern of time spent performing each of the observed behaviours from morning through to the evening was similar for all four types.

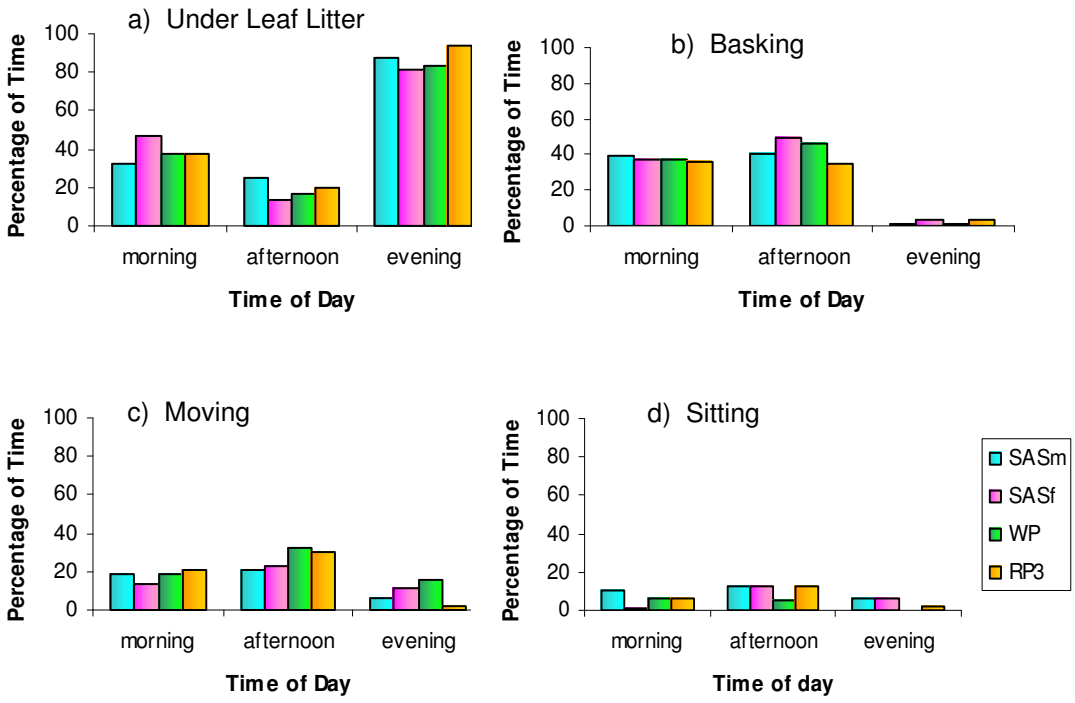


Figure 5.11. Percentage of time each type spent a) under the leaf litter (under), b) basking, c) moving and d) sitting in each time period (morning, afternoon, evening).

Repeated measures ANOVA, with time period (morning, afternoon or evening) as the within subjects factor and type (male, sexual female, WP parthenogen, or RP3 parthenogen) as the between subjects factor, was performed for each activity to determine if there were any differences in activity pattern among types. In determining if there were differences in activity pattern across the day, I was interested in the interaction between time period and type (time period*type). Results indicated that for each activity there were highly significant effects of time, but also for the interaction time*type, indicating that the different types of lizard did not change behaviour patterns consistently over different times of the day (Table 5.7).

Table 5.7. Repeated Measures ANOVA results comparing activity pattern among type.

	Basking			Moving			Sitting			Under Leaf Litter		
	df	F	p	df	F	p	df	F	p	df	F	p
Time	2	333.89	0.000	2	64.516	0.000	2	34.593	0.000	2	619.149	0.000
Type	3	1.495	0.232	3	3.296	0.031	3	3.896	0.016	3	1.964	0.137
Time *Type	6	2.694	0.020	6	4.789	0.000	6	5.189	0.000	6	8.476	0.000

The main differences observed among type in activity behaviour pattern were;

Under Leaf litter

- Males spent less time than all females (sexual & parthenogen) under the leaf litter in the morning but more time than the other types under the leaf litter in the afternoon
- Sexual females spent more time than parthenogens and males under the leaf litter in the morning but less time than the other types under the leaf litter in the afternoon

Basking

- WP parthenogens and sexual females basked less than males in the morning but basked more than males in the afternoon

- Sexual males and females basked more than RP3 parthenogens in the afternoon but basked less in the evening

Moving

- RP3 parthenogens moved more than sexual males and females in the afternoon but less than sexuals in the evening
- WP parthenogens moved less than RP3 parthenogens in the morning but moved more in the afternoon and evening.
- Males moved more than sexual females in the morning but moved less than sexual females in the afternoon and evening

Sitting

- WP parthenogens sat motionless for longer than sexual females in the morning but less than sexual females in the afternoon and evening

However, despite these differences, the patterns also showed similarity with the majority of time in the morning and afternoon being spent basking, and majority of time in the evening spent under leaf litter. All four types moved through the habitat predominantly in the afternoon.

Conclusion

Males, sexual females, WP parthenogens and RP3 parthenogens appear to have slightly different activity behaviour patterns across the day, thus, they could be partially partitioning their activity periods in this manner.

Time Niche Breadth and overlap

Time niche breadth and overlap values are shown in Table 5.8. Sexual males and females, and both parthenogens possessed a broad activity breadth (Table 5.8. above diagonal line). All four types spent a proportion of time on the surface during most daylight hours. Overlap in the time niche is very high between all pairs of type (Table 5.8. below diagonal line).

Table 5.8. Time Niche Breadth values (above diagonal line) and Time Niche Overlap values (below diagonal line).

	SASm	SASf	WP	RP3
SASm	0.906			
SASf	0.944	0.801		
WP	0.967	0.980	0.825	
RP3	0.972	0.954	0.988	0.801

Temperature Selection

The minimum, maximum, and mean body temperatures selected by each lizard type are summarised in Figure 5.12. The Kruskal Wallis non-parametric test was used to test for a difference in minimum and maximum selected body temperatures. Where a difference was found the Mann-Whitney *U*-test was used to test between each pair of types. One-way ANOVA was used to test for differences among types in mean selected body temperature and selected temperature range. Results of these tests are shown in Table 5.9.

There were no significant differences in the mean selected body temperature or the maximum body temperature chosen among the four types. There was a significant difference in the minimum body temperature chosen with WP parthenogens choosing a significantly higher minimum body temperature than males and RP3 parthenogens (Table 5.10).

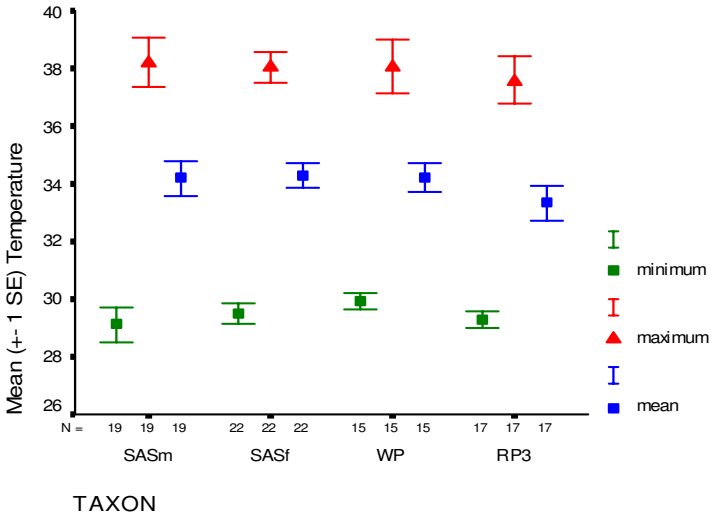


Figure 5.12. The minimum, maximum and mean selected body temperatures of males (SASm), sexual females (SASf), WP parthenogens (WP) and RP3 parthenogens (RP3) in a temperature gradient.

All four types maintained their body temperature in the gradient within a relatively narrow range; males 9.11°C (±0.918); sexual females 8.55°C (±0.546); WP parthenogens 8.17 °C (±0.895); RP3 parthenogens 8.31 °C (0.851). The body temperature range selected did not differ significantly among types (Table 5.9).

Table 5.9. Kruskal Wallis (*) and One Way ANOVA results comparing temperature preferences among males, sexual females, WP parthenogens and RP3 parthenogens.

Temperature Variable (°C)	**df**	**H* or F**	**p**
*Minimum	3	8.926	0.030
*Maximum	3	1.356	0.716
Mean	3	3.546	0.555
Range	3	0.263	0.852

Table 5.10. Mann-Whitney U-test comparing minimum body temperature selected (°C) between each type.

Temperature Variable	**Type 1**	**Type 2**	**p**
Minimum	SASm	SASf	0.105
	SASm	WP	0.018
	SASm	RP3	0.092
	SASf	WP	0.167
	SASf	RP3	0.694
	RP3	WP	0.009

Conclusions

Males, sexual females, WP and RP3 parthenogens differed very little in their temperature preferences. Over all types the mean selected body temperature was 34°C (±0.262), and the mean range of selected temperatures was 8.6 °C (±0.39).

Sprint Speed

Are Males, Sexual Females, WP parthenogens, or RP3 parthenogens faster?

Vmax & T max

The maximum speed achieved by each type (Vmax) and the mean temperature associated with this fastest speed (Tmax) are shown in Figure 5.13. One-way ANOVA was used to test for differences among type in Vmax, Tmax, L_{80}, U_{80}, B_{80}, B_{95}. Kruskal Wallis non-parametric test was used to test for differences among type in L_{95}, U_{95}, and M_{95}. See methods for definitions of variables.

Repeated Measures ANOVA with test temperature (15-40°C) as the within factor and type as the between factor was used to test for differences among type in sprint speed at each of the test temperatures. Bonferroni multiple comparisons test was used to test for differences between each pair of type.

There was a significant difference among types in maximum sprint speed (Table 5.13). WP parthenogens had a significantly faster maximum speed (Vmax) than males and sexual females (Figure 5.13a, Table 5.14).

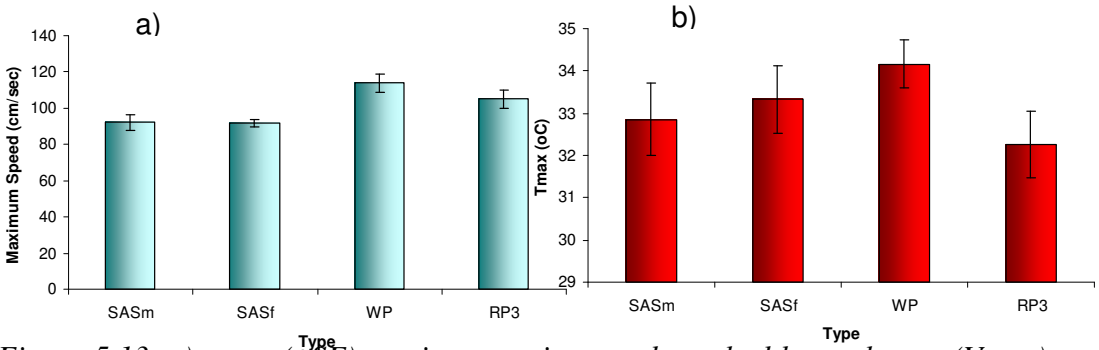


Figure 5.13. a) mean (±SE) maximum sprint speed reached by each type (Vmax). b) mean (±SE) body temperature of each type when they ran at maximum velocity (Tmax)

All lizards reached their maximum speed while at a test body temperature of 30°C or 35°C, and there was no significant difference among types in the mean body temperature at which maximum speed was achieved (Tmax) (Figure 5.13b, Table 5.11).

Table 5.11. Results of one–way ANOVA tests comparing maximum sprint speed (Vmax) and the mean body temperature at which maximum speed was achieved (Tmax)..

Variable	F	df	P
Vmax	6.483	3	0.001
Tmax	0.952	3	0.425

Table 5.12 Results of Tukey Post-hoc Test comparing maximum sprint speed (Vmax) between each type.

Variable	Type 1	Type 2	p
Vmax	SASm	SASf	1.000
	SASm	WP	0.003
	SASm	RP3	0.166
	SASf	WP	0.002
	SASf	RP3	0.140
	RP3	WP	0.500

Speed at Each Temperature

Besides the slight decrease in sprint speed between 25-30°C for sexual females and WP parthenogens, sprint speeds of all four types increased with body temperature,
peaked at 35°C, and then dropped at 40°C (Figure 5.14).

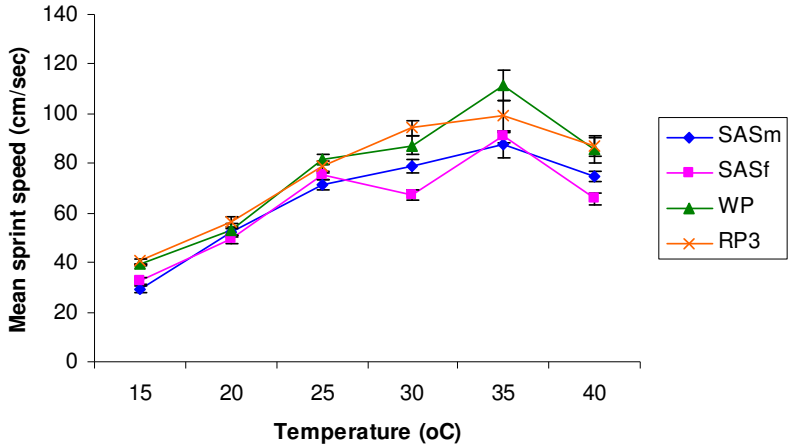


Figure 5.14. Mean sprint speed (cm/sec ±SE) at each of test body temperatures for males (SASm), sexual females (SASf), WP parthenogens (WP) and RP3 parthenogens.

Repeated Measures ANOVA showed a significant interaction affect between temperature and type (Table 5.13) indicating that these two variables are not independent of each other and therefore cannot be examined separately. The interaction effect probably results from alternatively WP and RP3 parthenogens being faster than each other at temperatures 30, 35 and 40 °C. In addition, over these same temperatures males and sexual females alternate as to which is faster. However, WP and RP3 parthenogens are consistently faster than sexual males and females at warmer temperatures.

Table 5.13. Repeated Measures ANOVA results for sprint speed.

	df	F	p
Temperature	5	234.85	<0.001
Type	3	20.335	<0.001
Temperature*Type	15	3.086	0.004

Conclusions

The temperature at which the four types ran the fastest is the same, but the parthenogens have superior sprinting abilities than the sexuals over the warmer range of tested temperatures.

Can males, sexual females, WP parthenogens, or RP3 parthenogens produce maximum sprint speeds over a wider range of temperatures?

Results of the measurements taken to compare sprint speed performance breadth in the four types are shown in Table 5.14. None of the measures of physiological performance (M_{95}, B_{95}, B_{80}), differed significantly among types using ANOVA (or Kruskal Wallis where appropriate) analysis. The performance curves did not differ in breadth (B_{80}, B_{95}), or in position along the temperature axis (M_{95} L_{80}, U_{80}, L_{95}, U_{95}). See Table 5.15 for results of statistical analyses.

Table 5.14. Mean (±SE) optimal sprint speed temperature (M95); lower (L80), upper (U80), and range (B80) of temperatures at which lizards ran at 80% of their maximum; lower (L95), upper (U95), and range (B95) of temperatures at which lizards ran at 95% of their maximum.

Type	M_{95} mean (SE)	L_{95} mean (SE)	U_{95} mean (SE)	B_{95} mean (SE)	L_{80} mean (SE)	U_{80} mean (SE)	B_{80} mean (SE)
SASm	33.05 (0.730)	30.80 (0.770)	35.30 (0.775)	4.50 (0.508)	25.63 (0.679)	38.96 (0.361)	13.33 (0.792)
SASf	34.44 (0.157)	32.59 (0.319)	36.29 (0.145)	3.69 (0.382)	25.53 (0.498)	37.92 (0.766)	12.39 (0.812)
WP	34.02 (0.574)	31.97 (0.683)	36.07 (0.570)	4.10 (0.512)	26.93 (0.683)	38.80 (0.468)	11.88 (0.890)
RP3	32.23 (0.616)	29.77 (0.800)	34.68 (0.592)	4.91 (0.68)	26.21 (0.84)	38.92 (0.388)	12.71 (1.029)

Table 5.15. Results of one–way ANOVA and Kruskal-Wallis (*) non-parametric tests comparing sprint speed performance among type. All results were not significant.

Variable	F or *H	df	P value
$*M_{95}$	*6.512	3	0.089
$*L_{95}$	*6.509	3	0.089
$*U_{95}$	*3.606	3	0.307
B_{95}	1.036	3	0.385
L_{80}	0.926	3	0.435
U_{80}	0.857	3	0.470
B_{80}	0.491	3	0.690

Conclusions

The temperature ranges over which they run well (80%) and best (95%) are the same for males, sexual females, WP parthenogens and RP3 parthenogens.

Relationship between Selected Body Temperatures and Sprint Speed

For all four types;

The mean selected body temperature was very close to optimal sprinting temperature.

The selected temperature range incorporates the optimal temperature range for sprinting (B_{95}), and the higher temperatures in the 80% performance breadth range.

Is Activity pattern correlated with Selected Body Temperature, & Physiological Performance?

Activity pattern in all four types generally appears to correspond with preferred temperatures and hence temperatures that optimise sprint performance.

Emergence & Cessation - All four types emerged at temperatures below those good for sprinting (B_{80}) and at a temperature below the minimum selected in the gradient. SAS females that emerged last, had a body temperature closer to the selected minimum and L_{80} than the other types.

Males, sexual females and WP parthenogens however, ceased activity while surface temperatures where in the B_{80} range; and RP3s while temperatures were still in the B_{95} range.

Habitat Use - Surface temp in the preferred habitat (LL sun) was between 26.65-33.92^{o}C in the hours when most surface activity occurred (9am-4pm). This encompasses the mean preferred temperature selected in the lab gradient and the temperature range over which sprinting is optimized (B_{95}).

The Maximum chosen temperature in the gradient was approximately 38^{o}C for all four types, hence this high temperature tolerance may have allowed for the occasional shuttling into the open sand in the sun which was observed.

All four types spent very little time in the habitats in the shade. Surface temperatures in these habitats ranged from 20.08-27^{o}C. Thus these areas were always cooler than the minimum selected temperature gradient and the majority of the time the temperatures were outside the B_{80} range.

The open sand habitat under the heat lamp reached temperatures up to 41^{o}C, during the hours when surface activity was at its highest (12-4pm). Thus body temperatures while in this habitat would have been hotter than that for good sprinting performance (B_{80} and B_{95} range), and hotter than maximum temp chosen in the gradient.

SAS females reduced their time on the surface during 11am-1pm. Temperatures during this time (31-33.7^{o}C) were in the preferred range and the range optimal for sprinting (B_{95}).

Conclusions

Males, sexual females, WP parthenogens and RP3 parthenogens selected temperatures at which physiological performance is maximised.

Activity pattern generally follows that of thermal dependence. Apart form emerging at body temperatures below optimal, activity throughout the day occurs

in habitats that allow for body temperatures within the range of preferred temperatures and that allow physiological performance to be at 80% or higher of it's maximum.

Discussion

Males, sexual females, WP parthenogens and RP3 parthenogens differed very little in their body temperature preferences selected in the laboratory gradient, and in the thermal relations of physiological performance. They all ran best (95%) and well (80%) over the same range of temperatures. Furthermore all four types selected body temperatures in a gradient that maximise sprint ability.

Activity pattern and behaviour also generally followed that of thermal dependence. Apart from emerging at temperatures below that of 80% performance range and lower than selected minimum temperature, sexual and parthenogenetic *M. greyii* were active at body temperatures within their preferred range (selected in the gradient) and at which their sprint capacity was at least 80% of its maximum. In addition they ceased activity while capacity was still 80% or greater.

Not surprisingly then, the daily activity periods of sexual males and females, WP parthenogens and RP3 parthenogens were very similar. They did not differ in mode of activity, time period in which surface activity was high, preferred microhabitat, and proportion of time spent in different exposures. The only real difference was in emergence times. Males emerged earlier than all females and retreated at cooler surface temperatures. This suggests that males tolerate being active at cooler temperatures even though they did not select cooler minimum body temperatures in the temperature gradient, and did not run better at cooler temperatures. This behaviour may be the result of a tradeoff between physiological performance and either mating or competitive success. Although active at temperatures which may make them more vulnerable to predation, emerging earlier and retreating last may give males an advantage by giving them first and last access to resources. Alternatively males may be spending this time searching for females. Differences in activity pattern between the sexes have been

observed in other lizard species. Similar to *M. greyii*, male sleepy lizards (*Tiliqua rugosa*) become active at cooler temperatures than females. Males were also active for a longer period than females during the breeding season, moving faster and further (Kerr and Bull in review). Adult male *C. tigris* spend less time foraging and move farther per hour than females (Anderson 1993). These authors suggest that these differences may be due to males searching for mates. Sexual females emerged last and at temperatures closer to the selected minimum in the gradient, thus minimising the risk of predation and other behavioural costs due to reduced physiological performance. Despite these differences, time niche width was broad for all four types and overlap between each pair of type was higher than average (Pianka 1973). Thus the general pattern is for sexuals, and WP and RP3 parthenogens to be active at the same time.

There were some small but significant differences between sexual and parthenogen individuals in the proportion of time dedicated to the different activities in each of the time periods. These differences in behaviour may provide some relief from the overlap in time use. However, there were also many similarities in general behaviour pattern across the day. Therefore, segregation via activity period was concluded to be minimal, and the relief from possible competition experienced from differences in activity behaviour pattern was determined to be slight.

The superior sprinting ability of the parthenogens at all warm temperatures (above 20^{o}C), and the fact that WP parthenogens ran fastest overall lends some support to the Spontaneous Heterosis Hypothesis. However, the parthenogens did not exhibit wider performance breadths than the sexuals, a second prediction of the hypothesis. Superior sprinting ability has been linked with social dominance and increased foraging success in lizards in previous studies (Huey 1979, Bennett 1980, Avery 1982, Huey 1982, Huey and Hertz 1984, Van Berkum et al. 1986, Huey and Bennett 1987, Bauwens et al. 1995) and may offer an advantage to the parthenogens over the sexual taxa. Social dominance and competition for food between sexual and parthenogen *M. greyii* is investigated in the next chapter.

This study offers support to neither the FNV model nor the GPG model for explaining how sexual and parthenogenetic forms coexist. Both sexual and parthenogenetic *M. greyii* possessed broad time niches and tolerated the same range of temperatures.

There are some issues associated with determining physiological and activity characteristics of lizards in the laboratory. A potential problem of thermal gradient studies is that animals in the laboratory face different thermal conditions than in nature. In the wild lizards receive heat from a variety of different sources and face a heterogeneous environment. And the activity patterns observed in a laboratory environment may not reflect those seen in nature. Movement patterns have been shown to differ between filed and lab conditions because of behavioural impacts of caging, differences in ambient conditions and differences in habitat (Jayne and Ellis 1998, Irschick and Jayne 1999). However, due to their cryptic nature and the difficulty with catching *Menetia greyii* during the hottest part of the day (due to their speed) direct observation of their activity and measurements of their thermal preferences in the field would have been challenging. In addition, while it would be beneficial to observe and compare differences among the taxa in seasonal activity patterns, these same reasons would make such an exercise difficult.

Summary

There is very little difference in the activity patterns, and temperature preferences of males, sexual females, WP parthenogens and RP3 parthenogens. However, parthenogen *M. greyii* do possess superior physiological performance (to some extent) over sexual *M. greyii* which may translate into a competitive advantage for the parthenogens.

Chapter 6

Aggression, dominance and competitive abilities of parthenogenetic and sexual *Menetia greyii*

Introduction

Individuals in a species will compete for ownership of a territory, for mates, for a food source, or for a combination of these. Social behaviour and the acquisition and defense of territories, mates and resources has been the subject of many studies (Case and Gilpin 1974, Jaeger 1974, Carothers 1981, Stamps 1983, Tokarz 1985, Moore 1986, Wise and Jaeger 1998). Competition can occur between individuals of the same species (intraspecific competition) and between individuals of different species although in this case competition is usually just for resources (interspecific competition). Competition can be either through exploitation whereby individuals compete directly for resources, and where these are in short supply, the more efficient species is successful, or via behavioural interference whereby individuals of one species will prevent another from occupying or utilising a certain portion of the resource (Begon et al. 1990). In interference competition, the importance of aggression as a mechanism of competitive exclusion has been shown in several vertebrates systems (Tilman 1987, Dickman 1991, Bolger and Case 1992, Niemela 1993, Downes and Bauwens 2002) and dominance of the more aggressive individual is often the result of these agonistic interactions (Coulon 1875, Carpenter 1960, Siegel and Siegel 1961, Carpenter 1962, Adams and Finn 1972, Brackin 1978). Exploitation and interference competition are not alternate forms of competition. Resource limited populations experience either exploitation competition alone or exploitation and interference competition together.

While social dominance is not always correlated with ownership of a resource (O'Connor et al. 2000), most studies on agonistic interactions have found the dominant individuals to be in control of limiting resources (Stamps 1977, Tokarz 1985). Socially dominant individuals have been shown to be more successful than

subordinates in acquiring and defending resources such as food, habitat, feeding areas and mates (Brown 1971, Price 1978, Andersson 1984, Dickman 1984, Fausch 1984, Dickman 1988, Dolmen 1988, Caraco et al. 1989, Higgs and Fox 1993, Johnsson and Bjornsson 1994, Nakano 1994, Maitz and Dickman 2001), and subordinate animals have been shown to have lowered survival and reproductive success (Packard et al. 1985, Abbot 1987, Eckman 1987) or slower growth rate (Hojesjo et al. 2002).

Although lizards are thought to be less socially complex than higher vertebrates such as birds and mammals, several studies have shown that dominance hierarchies occur in lizard groups and studies have also provided evidence for the importance of interspecific competition in lizards (Carpenter 1960, 1962, Schoener 1975, Brackin 1978, Oritz and Jenssen 1982, Pacala and Roughgarden 1982, Jensenn et al. 1984, Tokarz and Beck 1987, Fleishman 1988, Downes and Bauwens 2002). Dominance has been found to influence habitat use (Oritz and Jenssen 1982, Jensenn et al. 1984, Hertz et al. 1994, Downes and Bauwens 2002), reproductive state (Brackin 1978), activity patterns (Carpenter 1960, 1962), growth (Downes and Bauwens 2002) and food acquisition (Dunham 1980).

In lizards, larger individuals can usually obtain and defend a resource, that is, have better resource holding potential (RHP) than smaller individuals (Stamps 1977, Carothers 1981, Stamps 1983, Andersson 1994). The capacity to obtain resources can be modified by uncorrelated asymmetries, such as prior ownership (Maynard Smith and Parker 1976), which may give the owner some advantage due to, for instance a greater motivation to defend the resource (Kemp 2000, Olsson and Shine 2000). Prior ownership of a resource has been shown to be an important factor in the outcome of competition (Stamps 1983, Verrell 1986).

Superior competitive ability has been suggested as a short-term advantage for sexual reproducers that may allow sexually reproducing individuals to overcome the theorised two-fold cost of sex (Williams 1975, Maynard Smith 1978). An advantage in competitive ability would allow the sexuals either better access to, or better utilisation of resources compared with asexual individuals. The competitive inferiority of the asexuals may render them incapable of competitively excluding

the sexuals, even with the reproductive advantage (Price et al. 1993). Although studies examining competition in sexual and asexual animals are limited, several ecological and genetic models have been developed predicting the superior competitive ability of sexuals compared to asexuals.

Theories explaining the geographical distribution of asexuals and sexuals include the weed hypothesis (Wright and Lowe 1968), and theories established by Maslin (1968, 1971) and Cueller (1977). These models suggest that parthenogens are competitively inferior and thus can only persist in novel and/or highly disturbed habitats where sexual forms do not occur. As a result, these models suggest parthenogens occur predominantly at higher altitudes, on islands, or in island-like habitats and in more disturbed habitats (Glesner and Tilman 1978, Bell 1982). The distribution of sexual and parthenogenetic strains of the brine shrimp *Artemia* (Clark and Bowen 1976), of sexual and parthenogenetic *Cnemidophorus* lizards, (Gongdon et al. 1978, Walker et al. 1989) and of sexual and parthenogenetic lineages of the gecko *Heteronotia binoei* in Australia (Kearney 2003) support these theories. All of these theories predict that coexistence between sexuals and asexuals is unlikely.

Theories based on the advantage of genetic variability in sexually reproducing species also predict the superior competitive abilities of sexuals. Genetic variation has two distinctly different ecological consequences: reducing intra-specific competition and reducing inter-specific competition (Pound et al. 2002). Many of the proposed theories, including the 'elbow-room' sib-competition models (Ghiselin 1974, Maynard Smith 1978, Young 1981, Bell 1982) focus on the differences in the levels of intraspecific competition between sexual and asexual animals, in that the intensity of competition is thought to increase with the genetic similarity of the competitors. This is because asexual clones have equal capabilities and will be competing for identical resources (Maynard Smith and Price 1973, Maynard Smith 1978, Young 1981, Bell 1982). Therefore, genetically heterogeneous populations (sexuals) with a wider range of phenotypes and resource requirements will have a competitive advantage over genetically homogeneous populations (asexuals).

Similar in concept to the elbow-room 'sib-competition' models are two theories explaining coexistence between sexual and asexual animals. These are the frozen niche variation (FNV) hypothesis (Vrijenhoek 1979, 1984a, Case and Taper 1986, Weeks and Gaggiotti 1993) and the Tangled Bank hypothesis (Ghiselin 1974, Maynard Smith 1976, Maynard Smith and Parker 1976, Bulmer 1980, Bell 1982, 1985, Koella 1988). These models suggest that genetically variable populations have higher relative fitness when compared to genetically homogeneous populations because they can utilise a broader range of resources, thus avoiding competitive exclusion. Several studies have shown that mixed groups of asexual strains perform better than homogeneous groups, supporting the Elbow-room, FNV and Tangled Bank hypotheses. These include studies comparing the performance of asexual and sexual strains of *Poeciliopsis* fish (Vrijenhoek 1979, 1984a, Schenck and Vrijenhoek 1986b, Wetherington et al. 1987, Schenck and Vrijenhoek 1989, Weeks et al. 1992, Weeks 1995), parthenogenetic and sexual species of *Cnemidophorus* lizards (Gustafsson 1953) and sexual and hemiclonal species of *Rana* frogs (Semlitsch et al. 1997). Weeks and Sassaman (1990) tested the predictions of the Tangled Bank Hypothesis by comparing competition within genetically homogeneous and heterogeneous populations of the tadpole shrimp *Triops longicaudatus* at differing competition levels. They found little support for the hypothesis of sib-competition as all treatments performed equally well.

Another model that assesses competition between sexual and asexual organisms and explains coexistence between multiple asexual clones and a sexual species is a model developed by Doncaster et al. (2000) and further developed by Pound *et al* (2002 and 2004). Their model is based on classic Lotka Volterra dynamics. It suggests that the advantage to the sexuals arises from reduced inter-specific competition (rather than intraspecific as predicted by the sib-competition models) for the sexual form with asexuals since the asexuals are also competing among themselves for shared resources. Through their computer simulation experiments Pound et al. (2002) determined that only a small advantage in competitive ability can be enough to fully compensate a sexual population for its two-fold reproductive disadvantage in growth capacity and prevent the simultaneous invasion by multiple asexual clones. This will allow coexistence between the sexual and asexual forms over an ecological time scale. Sex then has time to

express its longer-term advantages of genetic variation in meeting environmental change, resulting in the eventual displacement of asexuals (e.g. Kondrashov 1993, Pound et al. 2004).

In support of the interspecific competition theory, several studies have found asexual species have high aggression levels, strong dominance hierarchies and large fitness advantages for dominant individuals. For example, Brown and Sakai (1988) and Brown et al. (1991) found that in the parthenogenetic gecko, *Lepidodactylus lugubris,* dominant animals produce a greater number of eggs than subordinate geckos. Similarly dominance behaviour was positively related to egg production in parthenogenetic *Cnemidophorus uniparens* (Gustafson and Crews 1981, Grassman and Crews 1987). And Leuck (1985) found that dominant individuals of the parthenogenetic *C. tesselatus* and *C. neomexicanus* groups obtained significantly more crickets than subordinates. Ryhorchuk (2002) investigated dominance in the parthenogenetic gecko *Heteronotia binoei* and the effect that prior ownership (residency) had on the outcome of contests. She found that the resident lizards were always the dominant lizards, and possessed the highest quality shelter. In addition subordinates spent less time in general maintenance and feeding behaviours.

In contrast, other parthenogenetic lineages such as the gecko *Hemidactylus garnotti* demonstrate very little aggression towards conspecifics (Frankenberg 1982). Also, sexual species have similar high levels of aggression. For example, Hardy (1962) and Brackin (1978) found that the sexual species *C. sexlineatus* forms dominance hierarchies. Hardy (1962) found that dominants obtained food more readily than subordinates, although Brackin (1978) found no such correlation. Other studies examining whether sexual animals are more or less aggressive towards conspecifics than asexual animals, have found that asexual animals in general tend to be less aggressive than closely related sexual species. These include several studies on the behaviour of *Cnemidophorous* species in the field (Milstead 1957, Echternacht 1967, Schall 1976). Also, Bolger and Case (1992) found that in staged laboratory contests, sexual *Hemidactylus frenatus* individuals were more aggressive towards each other than were parthenogenetic *H. garnotti* females, and in experiments in outdoor enclosures, Leuck (1985) found that aggressive interactions and competition over food items, were less

common in parthenogen than sexual *Cnemidophorus* groups. Sexual groups were also more likely to be organised into dominance hierarchies than were parthenogen groups. This observed 'reduced' aggression between asexual individuals could be due to the absence of males because males are often more aggressive than females (Williams 1966), or due to the close genetic relatedness of asexual species (or taxa). Animals that are closely related may be less aggressive towards each other because they have a high percentage of genes in common (Hamilton 1964a, 1964b, Maynard Smith and Price 1973).

Direct examination of aggression, dominance and / or competition between syntopic asexual and sexual lineages has received far less attention. In those experiments that have been performed, results vary. Some studies detected a lack of aggression. For instance, it was expected that the asexual gecko *Lepidodactylus lugubris* would be behaviourally dominant over the syntopic sexual *L. sp.* (Takapoto) since *L.sp* (Takapoto) is confined to one habitat in areas where both species occur. However, laboratory based contests found no asymmetry in levels of aggression (Hanley et al. 1994). Similarly, in long-term field based studies of competition between syntopic parthenogenetic and sexual *Cnemidophorus* species, using population manipulation experiments, the population responses of one species to removal of the other varied from weak to absent. For example, the parthenogen *C. tesselatus* failed to respond to the removal of its sexual congener, *C. marmoratus* (Price 1986). And while removal of the parthenogen *C. uniparens* resulted in an increase in the sexual species *C. tigris*, the habitat of the sexual is normally partly avoided by the parthenogen (Cueller 1993). Similarly, Price et al. (1993) investigated interspecific competition between the sexual *C. tigris* and syntopic unisexual species *C. tesselatus* and found that neither species responded strongly to the removal of the other.

Other studies have found a superior competitive ability in asexuals. For example, Cueller (1979) found that the sexual *C. marmoratus* ultimately invaded the habitat of the parthenogenetic *C. uniparens*, only after the local population of *C. uniparens* had been partially removed over a four year period, suggesting competitive superiority of the parthenogen. Laboratory based studies have also shown cases of a higher competitive ability in asexuals. Aggression by asexuals

was found to be associated with the reduction of microhabitat overlap of clonal and sexual forms of *Poeciliopsis* (Schenck and Vrijenhoek 1986b), and in *Artemia* brine shrimp asexuals outcompete their closely related sexual counterparts (Browne and Halanych 1989).

Alternatively, other studies have found the sexuals to have greater competitive success. Results from salamanders, *Ambystoma* (Wilbur 1971), brine shrimp, *Artemia* (Brown 1980), the perennial herb *Antennaria* (Michaels and Bazzaz 1986) and from the grass *Anthoxanthum* (Ellstrand and Antonovics 1984, Ellstrand and Antonovics 1985) demonstrate that sexual populations outcompete their asexual counterparts. The sexual gecko, *Hemidactylus frenatus* was found to outcompete the parthenogenetic gecko *Lepidodactylus lugubris* through better exploitation of insect resources. This translated into significant reductions in the body condition, fecundity and survivorship in *L. lugubris* (Petren and Case 1996).

It has also been suggested that the accumulation of deleterious mutations by parthenogens is a factor that should cause them to perform poorly compared to sexually reproducing individuals (Price et al. 1993). Competition is known to amplify the negative effects of mutation accumulation (Kondrashov and Houle 1994), and therefore it is proposed that mutations might have a more negative effect on fitness as the level of competition is increased (Lively et al. 1998). Lively et al. (1998) tested the prediction that, under conditions of food stress, parthenogenetic individuals should show a lower survivorship than sexual individuals, using a freshwater snail (*Potamopyrgus antipodarum*) from New Zealand. However, they did not find support for the theory with survival being the same in both asexuals and sexuals. Similarly, at high density food levels sexual strains significantly outcompeted parthenogenetic strains of *Artemia alsina* (Browne 1980), but when food availability is low (thus competition introduced), neither type of reproductive strain was superior.

In summary, there appears to be no consistent pattern among the species studied, for sexuals or asexuals to be more fit, nor any consistent pattern to explain the persistence of co-existence of the two reproductive modes.

Hypothesis, Aims and Predictions

In previous chapters, sexual and parthenogenetic *M. greyii* at Bundey Bore were found to differ very little in their ecology. Therefore, the potential for intense competition between sexuals and parthenogens is high. The question of how alternative forms can persist together remains unanswered. In this chapter I used laboratory experiments to investigate aggression levels, dominance and its relation to food acquisition, between sexual and parthenogenetic *Menetia greyii* collected from Bundey Bore. Although resource limited populations experience exploitation and interference competition together, in this chapter I only test the interference impact.

I hypothesise that, sexual Menetia greyii *are behaviourally dominant to parthenogenetic Menetia greyii, and this dominance translates into an increase in the acquisition of a resource for the sexuals (or reduction in acquisition of a resource for the parthenogens).*

In order to test this hypothesis I developed several aims;
The initial aim was to determine whether there is aggression between sexual and parthenogen *Menetia greyii* captured at Bundey Bore.

If aggression does occur, then the aim was to describe aggressive behaviours exhibited by male, sexual female, WP parthenogen and RP3 parthenogen *Menetia greyii* and to discuss any behavioural differences observed between sexuals and parthenogens. This was to provide a comprehensive knowledge of the basic behaviour exhibited by each type and was used to assess aggression levels and dominance.

Subsequent aims were;

1) to determine aggression levels of sexuals towards parthenogens and parthenogens towards sexuals,
2) to determine if clear dominant – subordinate relationships are formed between parthenogenetic and sexual *M. greyii*,
3) to determine if dominant animals obtain more food items than subordinates,

4) to determine whether a reduction in food acquisition in the subordinates translates into a fitness reduction by comparing weight loss between dominants and subordinates.

Competition was investigated under two different conditions using interactions between pairs of individuals. The first was a novel environment in which both lizards were introduced into an unfamiliar area at the same time. This simulated parthenogens and sexuals moving into a new, previously uninhabited area or previously unexploited area, and eliminates any 'prior ownership' advantage of one form over the other. The second condition was under a resident / intruder environment. This simulated a situation in which lizards invade areas already inhabited by another lizard of a differing reproductive mode. This condition also assessed the influence of prior ownership on the outcome of a competitive contest.

In the novel environment, it is predicted that the male and female sexuals will display higher aggression levels towards parthenogens, than WP and RP3 parthenogens will towards sexuals. This higher aggression will allow the sexuals to dominate the parthenogens and lead to greater food acquisition in the sexuals.

Under the condition of residency it is predicted that due to a 'prior ownership' advantage, aggression levels displayed by residents will be higher than those seen in the novel environment. In order for the sexuals to still maintain a competitive advantage it is predicted that the sexual residents will be more aggressive towards the parthenogen intruders than the parthenogen residents will be towards the sexual intruders. In addition I predict that parthenogen intruders will exhibit low aggression levels, whereas the sexual intruders will either exhibit aggression levels equal to, or higher than those shown by parthenogen residents. This will allow the sexual residents to dominate the parthenogen intruders, and lead to the higher acquisition of food items by the residents. In the parthenogen resident / sexual intruder dyads, it is predicted that, either clear dominant-subordinate relationships will not be developed or the sexual intruders will dominate the parthenogen residents. This will lead to resident parthenogens and sexual intruders consuming similar numbers of food items or sexual intruders consuming more food items than the parthenogen residents.

Methods

Prior to conducting the trials

Prior to conducting the trials, all lizards were housed in individual plastic holding containers (40 x 30 x 30cm) with a 5cm deep sand substrate, leaf litter for shelter and a basking surface. The lizards were housed in a temperature controlled room (20^{o}C), with a 12:12 light:dark photoperiod. A heat lamp (210-W) placed at one end of the tank provided additional heat from 0830hr to 1630hr. Lizards were fed wingless *Drosophila* and baby crickets twice a week (up to two months before the experiment), and water was provided.

For two months prior to the start of each experiment, lizards were trained to feed on small meal worms (approximately 7mm in length) presented to them in a Petri dish in the centre of their holding tank. The Petri dish prevented the meal worms from burrowing into the sand. Lizards were fed twice a week between 1100hr and 1400hr, and in each feeding session, they were offered two meal worms introduced one at a time 20 minutes apart. Meal worms were placed into the Petri dish using forceps. By the end of the 2 month training session, all lizards regularly consumed both food items presented to them in this manner (within 10 minutes).
In all experiments lizards were starved for five days prior to the commencement of trials in order to intensify competition over food items.

All females used in the trials were non-gravid, and all lizards used had intact tails.

1) Competition between sexual and parthenogenetic M. greyii in a Novel Environment

All trials for study 1 and study 2 for the novel condition were performed between 1000hr and 1500hr in January 2002.

Study 1 – Aggression and Dominance

Study 1 was designed to document aggression behaviours, and aggression levels for each type (male, sexual female, WP parthenogen, RP3 parthenogen) and to determine if there was a clear dominant / subordinate relationship between sexuals and parthenogens.

We assessed aggression in staged laboratory contests between pairs of sexual and parthenogenetic lizards. Animals used for the experiment were collected in the 2001 and 2002 seasons. Fourty-eight lizards were tested in total consisting of 12 males, 12 sexual females, 12 WP parthenogens and 12 RP3 parthenogens. Four types of pairings were made, male and WP parthenogen, male and RP3 parthenogen, sexual female and WP parthenogen, sexual female and RP3 parthenogen, and there were six replicates of each pairing type. Thus in the 24 pair-wise trials, each lizard was used only once. Contests were conducted in experimental tanks equivalent to the holding tanks. Twenty-four experimental tanks were used, one for each pair. In lizards, body size and dominance are often correlated (Battsrom 1974), therefore, lizards comprising a pair were matched for body mass and year of capture. Individuals were randomly paired within the weight and year matching constraint. Order of contests was randomised. Before initiating observations, one individual of each pair was marked with a small dot of white non-toxic enamel paint on the dorsal surface to allow them to be differentiated.

Just prior to commencing a trial, both lizards of the pair were weighed (to the nearest 0.0001g using a Mettler scale) and this weight was referred to as the lizards' initial weight. Both of the animals were introduced in the centre of the test arena at the same time, at the start of the experiment. Consequently there was no difference in resource holding potential based on familiarity of the arena. Directly following introduction to the test arena, the behaviour of both lizards within the pair was recorded for the next hour by video camera suspended over the aquarium. There was no food provided in study 1.

Videotapes were analysed for the aggressive behaviours exhibited by each lizard in the pair and the frequency with which each individual performed these aggressive behaviours. To quantify the level of aggression displayed by each lizard, each aggressive behaviour observed was given a points value (Table 6.1). The more aggressive the behaviour was judged to be, the greater the points. An overall aggression score (AS) was then determined for each lizard by summing the number of times a lizard performed each aggressive behaviour multiplied by the corresponding aggression score for that behaviour. The number of aggressive

encounters (E) initiated by each lizard in a pair was also determined. To obtain an aggression score per interaction for each lizard, we divided AS by E (AS/E). An aggression score for each trial (AS_t) and the number of aggressive encounters for the trial (E_t) were calculated by summing the AS for each lizard in the pair, and E for each lizard in the pair respectively. To obtain an aggression score per interaction for each trial, we divided AS_t by E_t (AS_t/E_t). In addition, the amount of time spent engaged in aggressive interactions was determined for interactions initiated by each lizard as well as summed for each trial.

Each lizard was also categorised as dominant, subordinate or unclear. A clear dominant / subordinate relationship was defined as a relationship in which one lizard in the pair directed more aggressive acts towards the other lizard, while the other lizard in the pair fled more often. Dominant lizards were those directing the aggressive acts, while the subordinate lizard was the lizard that fled. 'Unclear' pairings were defined as those pairings in which either a) both lizards directed aggressive acts towards the other and both lizards fled from the other at similar frequencies, or b) pairings in which little aggression was recorded.

Table 6.1. Aggression Score given to each aggressive behaviour observed.

Aggressive Behaviour	**Aggression Score**
Approach	1
Supplant	3
Tail twitch	3
Tail wag	3
Back arch	3
Move over	4
Straddle	4
Caused Fleeing	5
Lunge	6
Nip	7
Bite	8
Wrestle	9
Lock jaw	10
chase	10

At the completion of the 60 minutes of study 1, all pairs were left undisturbed in their test cages; this was the initiation of study 2. Each pair of lizards remained in

their test arena for a total of eight days.

Study 2 – Food Competition

The second study began immediately after the cessation of study 1 and examined competition for food and its relationship to dominance. This involved staging feeding interactions over seven days and periodically measuring food acquisition. All feeding interactions were performed between 1000 and 1500 hrs in January 2004.

For study 2, during each of three separate feeding periods (feed1, feed2 and feed3) two small meal worms were offered to the pair to create a potential food competition situation between the two lizards in the replicate. The two food items were presented to the lizards 20 minutes apart in the same manner as in the prior training sessions. The first feeding session (feed 1) was one day after the pair was established, the second (feed 2) three days later, and the third (feed 3) after another three days. All feeding sessions were videotaped as before.

From the playback, for each feeding period, we recorded which lizard captured each of the food items offered during the period.

After 8 days, each lizard was weighed (to the nearest 0.0001g using a Mettler Scale). Change in weight was calculated for each lizard by subtracting their initial weight from their final weight.

2) Competition between sexual and parthenogenetic M. greyii in a Resident Vs Intruder Environment

All trials for study 1 and study 2 for the resident vs intruder condition were performed between 1000hr and 1500hr in May 2003.

Study 1 – Aggression and Dominance

The method of study 1 for the resident/intruder condition was similar to that of the novel environment with the following differences;

A total of 96 lizards were tested in the resident/intruder trials including, 24 males, 24 sexual females, 24 WP parthenogens and 24 RP3 parthenogens. Twelve of

each type were randomly assigned as residents and twelve of each type were randomly assigned as intruders. Eight types of pairings were made (Table 6.2) and there were six replicates of each. Animals used for the experiment were collected in the 2001, 2002 and 2003 seasons. Each resident and intruder in a pair were matched for body mass and year of capture. Individuals were randomly paired in the weight and year of capture constraint.

Table 6.2. Treatments for resident intruder trials

Resident type	**Intruder type**
Male	WP parthenogen
Male	RP3 parthenogen
Sexual female	WP parthenogen
Sexual female	RP3 parthenogen
WP parthenogen	Male
WP parthenogen	Sexual female
RP3 parthenogen	Male
RP3 parthenogen	Sexual female

Due to the limited size of the laboratory population, nine WP parthenogens and two RP3 parthenogens used in the novel environment trials were also used in the resident/intruder trials. To decrease the chance of prior experience affecting the outcome of the subsequent aggressive disputes, we allowed at least three months between completion of the novel trials and initiation of the resident / intruder trials. All sexual lizards used in the resident / intruder trials were different, therefore, there was no chance that the reused parthenogens had met their sexual contesters on a previous occasion.

One month prior to testing the 48 assigned residents were transferred into individual test arenas (equivalent to those used in the novel experiment). A single resident was placed within each arena and fed two meal worms, twice a week as before. Following the acclimation period and just prior to commencing the trial, both the resident and the intruder lizard were weighed to obtain an initial weight for each lizard. Each lizard had equivalent handling stress. Then the residents were returned to their home tank. Five minutes later a single intruder was placed into the arena and behavioural interactions were recorded for one hour using a video camera suspended over the cage.

The data collected from the video playback were the same as those collected for the novel environment. Data were collected separately for the resident and intruder in the trial.

Study 2 – Food Competition

The method of study 2 was the same as that for trials in a novel environment.

Statistical Analyses

Statistical tests used are highlighted throughout the results section.

Results

Ethogram

Table 6.3. Ethogram of aggressive behaviours observed between sexual and parthenogenetic M. greyii*, with a description of each act.*

Level	Behaviour	Description
Non-contact	Approach	One lizard (approaching lizard) moves towards the second lizard.
	Supplant	One lizard is stationary while the second lizard approaches it. The first lizard moves away and the second lizard occupies the position of the first lizard.
	Tail twitch	Side to side undulation of the entire tail.
	Tail wag	Rapid vibration of the distal third of the tail.
	Back arch	One lizard orientates itself so that its back is towards the other lizard and tucks its head in.
	Flee	Similar to supplant, but one lizard darts away from another lizard rapidly. This may occur as the first lizard approaches, or after an aggressive encounter.
Low Level Contact	Move over	One lizard moves over the top of the other lizard.
	Straddle	One lizard climbs on to the tail or back of another lizard. This position is held for a few seconds to a couple of minutes. The lizard being straddled usually remains stationary, but in two cases the straddled lizard moved forward approximately 5cm dragging the straddling lizard on its tail.
Attack	Lunge	Rapid jumping movement by one lizard towards another.
	Nip	One lizard grasps another with its jaws and then releases immediately (less than one second later).
	Bite	Lizard grasps another with its jaws. Usually directed towards the tail, but occasionally to the jaw or neck. Last from one up to several seconds. Often occurred directly after lunging.
	Wrestle	While biting, the aggressor lizard wraps around the subordinate lizard and they rapidly roll around. Lasts one to several seconds.
Elevated Aggression	Lock jaw	One lizard bites the other for an extended period of time (lasting for up to several minutes). During, the lizard being bitten may slowly roll the aggressor lizard over several times to try to pry off the aggressor. Bite is usually to the neck or jaw region.
	chase	One lizard rapidly follows another fleeing lizard.

Description of Aggressive Behaviours

Aggressive behaviour was observed in all pairings studied (both in novel and resident v intruder trials). Table 6.3 includes a description of these aggressive behaviours and the context of the behaviours is described below.

Context / function of Behaviours

In those pairs in which a clear dominant / subordinate relationship was established, rank was usually determined within the first or second interaction between the lizards, and once established was not contested by the subordinate lizard. Social status is discussed in more detail on page 171.

Dominant lizards exhibited all 14 of the described behaviours (although fleeing was rare in dominants) while subordinate lizards displayed only eight of the described behaviours (Table 6.4). Subordinate lizards never moved over or straddled a dominant lizard, and once rank was established, they were never seen to engage in the more aggressive acts seen including biting, wrestling, jaw locking and chasing.

Table 6.4. The social status of the lizard exhibiting each observed behaviour. ✓ indicates behaviour was performed

Aggressive Behaviour	**Dominant**	**Subordinate**
Approach	✓	✓
Move over	✓	
Supplant	✓	✓
Tail twitch	✓	✓
Tail wag	✓	✓
Back arch	✓	✓
Straddle	✓	
Flee	✓	✓
Lunge	✓	
Nip	✓	✓
Bite	✓	✓
Wrestle	✓	
Lock jaw	✓	
chase	✓	

Approach - Approaches were observed both in non agonistic and agonistic encounters. They were performed predominantly by the dominant lizard, but also occasionally by the subordinate lizard. However, if the subordinate approached it

always occurred within the first or second interaction for the trial and the subordinate usually fled shortly after approaching. If the aggressor/dominant lizard initiated an approach, the subordinate lizard would either flee immediately or the interaction ended in an agonistic event involving contact between the lizards.

Move over or Straddle - These behaviours were not observed often, and were only performed by the dominant lizard. They usually occurred after a dominant approached a subordinate and the subordinate froze and did not respond to any behaviour initiated by the dominant.

Supplant - This action was performed by both subordinate and dominant lizards. It was however, predominantly a response by subordinate lizards to avoid an interaction with a dominant lizard.

Tail twitch and Tail wag - These actions were performed by both subordinate and dominant lizards and were used interchangeably. Tail twitching was the more widely used tail movement and was seen more often in subordinate lizards and usually occurred upon receiving a threat (an agonistic action such as approach or straddle) from the dominant lizard. A tail twitch by the subordinate nearly always preceded fleeing. The dominant lizard often performed a slow tail wag or fast tail twitch upon sighting a subordinate but before initiating an agonistic interaction.

Tail twitch and tail wag are thought to be an anti-predator display (Torr and Shine 1994). These actions may draw a predator's attention away from the lizard's body and towards the more 'expendable' tail. The second likely function is social, possibly functioning to indicate submission, aggression or simply agitation (Torr and Shine 1994).

Back arch - In *M. greyii*, back arching involved a lizard lying on one side and orientating itself so that its back is towards the other lizard. The head is tucked in. This action was usually observed during the establishment of a rank. It was mostly conducted only by one of the lizards, but sometimes by both lizards in the dyad (either separately or simultaneously). If conducted by only one of the lizards in

the dyad it induced either an aggressive behaviour (lunge or straddle) or a subordinate behaviour (flee) in the other lizard. Once dominance was asserted by one lizard, back arching was rarely observed. This behaviour was often accompanied by tail wagging or tail twitching.

Cause to Flee - This act appeared to be instigated through an action by the dominant lizard towards the subordinate. This action occurred at several stages within an aggressive interaction – either immediately upon being approached, after some initial non-contact behaviour by the dominant lizard but prior to attack behaviour, or after being attacked. Fleeing often induced a chase by the dominant lizard.

Lunge - Usually performed by the dominant lizard and generally preceded an attack (bite, wrestle, lock jaw or chase) by the dominant on the subordinate.

Nip - This action was performed by both dominant and subordinate lizards, but was not seen often. A subordinate would use this behaviour if it was being bitten (for at least a few seconds) or lock jaw by a dominant, to attempt to get the dominant to release its grip. A dominant would occasionally nip before biting a subordinate, or would nip the tail of a subordinate while chasing.

Bite - A bite was instigated either after an approach or chase. Although this behaviour was performed by both dominant and subordinate lizards, it was only performed by the subordinate while rank was being established. Once rank was established this behaviour was only displayed by the dominant lizard. Occasionally biting was accompanied by wrestling.

Lock jaw – This was the most aggressive behaviour seen and occurred rarely. On occasion, the subordinate would begin to roll over and over on the sand attempting to force the release of the grip. When released the subordinate would flee, and may or may not be chased.

Chase - Most chases involved only a quick pursuit lasting a few seconds. At other times, the chase was performed in several stages, where the fleeing lizard ran,

then stopped, and ran again. The aggressor followed the same pattern – run, stop, run. In pursuits where contact was made, the pursuer caught up with the retreating individual and nipped or bit it along the base of the tail. The grip was usually broken quickly, and the chase continued or was terminated due to the 'fleeing' lizard remaining immobile.

All the behaviours described here for *M. greyii* have been documented for other skink species, with the exception of the method of back arching. Back arching in other lizard species involves the arching of the back dorsally, whereby the lizard lifts its belly off the ground and arches its back so that its nose is pointed down (e.g. Paulissen 1997, Jennings and Thompson 1999, Ryhorchuk 2002). In *M. greyii*, back arching involved a lizard orientating itself so that one side rests on the ground surface and its back is towards the other lizard. The head is tucked in.

Are the aggressive behaviours observed consistent across type?

Table 5 documents which aggressive behaviours were performed by each lizard type (males, sexual females, WP and RP3 parthenogens) under each condition (novel and resident vs. intruder). In a novel environment male and sexual female *M. greyii* did not engage in the more aggressive attack behaviours and did not display any elevated aggression. They did not bite, wrestle, lock jaw or chase parthenogens (Table 6.1). The most aggressive behaviour displayed by sexuals in a novel environment was nipping. Male and sexual females increased their aggression as residents, with sexual females displaying all the aggressive behaviours described, and sexual males displaying all of the behaviours identified except for lock jaw.

WP parthenogens were equally aggressive towards sexuals in a novel environment and as residents, performing all of the aggressive behaviours described, under both conditions.

Resident RP3 parthenogens displayed all aggressive behaviours described, while in a novel environment they were not seen jaw locking.

Therefore, all four types were seen to exhibit the same range of aggressive behaviours over the course of the study. As residents, sexual and parthenogenetic *M. greyii* displayed the same aggressive behaviours towards intruders, however, in a novel environment, parthenogens engaged in more attack and elevated aggressive behaviours towards sexuals than sexuals did towards parthenogens.

Table 6.5. Aggressive behaviours performed by each lizard type (male, sexual female, WP, RP3) under novel and resident vs intruder (R vs I) conditions. ✓ indicates behaviour was performed.

Behaviour	**male**		**SAS female**		**WP**		**RP3**	
	novel	**R vs I**	**novel**	**R vs I**	**novel**	**R vs I**	**novel**	**R vs I**
Approach	✓	✓	✓	✓	✓	✓	✓	✓
Supplant	✓	✓	✓	✓	✓	✓	✓	✓
Tail twitch	✓	✓	✓	✓	✓	✓		✓
Tail wag	✓	✓	✓	✓	✓	✓	✓	✓
Back arch		✓	✓	✓	✓	✓	✓	✓
Move over	✓	✓		✓	✓	✓	✓	✓
Straddle	✓	✓	✓	✓	✓	✓	✓	✓
Flee	✓	✓	✓	✓	✓	✓	✓	✓
Lunge		✓		✓	✓	✓	✓	✓
Nip	✓	✓	✓	✓	✓	✓	✓	✓
Bite		✓		✓	✓	✓	✓	✓
Wrestle		✓		✓	✓	✓	✓	✓
Lock jaw				✓	✓	✓		✓
chase		✓		✓	✓	✓	✓	✓

Competition in a Novel Environment.

Aggression Levels

Are sexuals more aggressive than parthenogens?

a) Comparing aggression levels among the four types.

Aggression scores (AS), aggression level per encounter (AS/E), duration of aggressive encounters (mins) and the number of encounters (E) initiated by males, sexual females, WP parthenogens and RP3 parthenogens are shown in Figure 6.1.

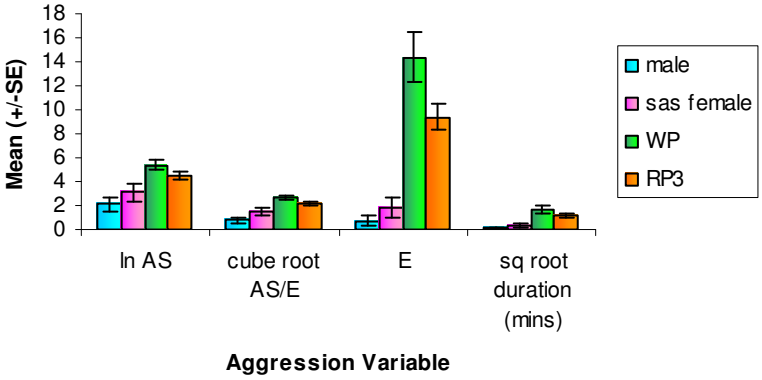


Figure. 6.1. Mean (+/-SE) aggression levels displayed by males, sexual females, WP parthenogens and RP3 parthenogens.

For all of the variables measured, except the number of encounters (E), the data required transformation in order to comply with the assumptions of one-way ANOVA. The transformation used, was the one that produced the best normality and homogeneity in the data, as described in the general methods (Chapter 2).

One-way ANOVAs (Table 6.6) showed that there was a significant difference among the four types in all of the aggression variables. A Tukey multiple comparisons test (Table 6.7) revealed that WP parthenogens exhibited significantly higher aggression than males and sexual females. RP3 parthenogens had significantly higher aggression levels than males and initiated a higher number and longer aggressive encounters than both males and sexual females.

Table 6.6. Results of One-way ANOVAs comparing aggression levels among males, sexual females, WP parthenogens and RP3 parthenogens.

Aggression Variable	**df**	**F**	**p**
Ln AS	3	7.681	<0.001
Cb root AS/E	3	11.345	<0.001
Sq root duration (mins)	3	15.434	<0.001
E	3	23.89	<0.001

Table 6.7. Results of Tukey Post Hoc test comparing aggression levels between each lizard type.

Aggression Variable		**p**
Ln AS	WP v male	<0.001
	WP v sas female	0.027
	RP3 v male	0.013
	RP3 v sas female	0.439
Cb root AS/E	WP v male	<0.001
	WP v sas female	0.006
	RP3 v male	0.002
	RP3 v sas female	0.290
Sq root duration (mins)	WP v male	<0.001
	WP v sas female	<0.001
	RP3 v male	0.002
	RP3 v sas female	0.013
E	WP v male	<0.001
	WP v sas female	<0.001
	RP3 v male	0.001
	RP3 v sas female	<0.001

b) Comparing aggression levels between sexuals (males and females pooled) and parthenogens (WP and RP3 pooled)

Aggression levels of sexuals and parthenogens are summarised in Figure 6.2. Paired t-tests (Table 6.8) showed that parthenogens were significantly more aggressive towards sexuals than sexuals were towards parthenogens, in all variables measured.

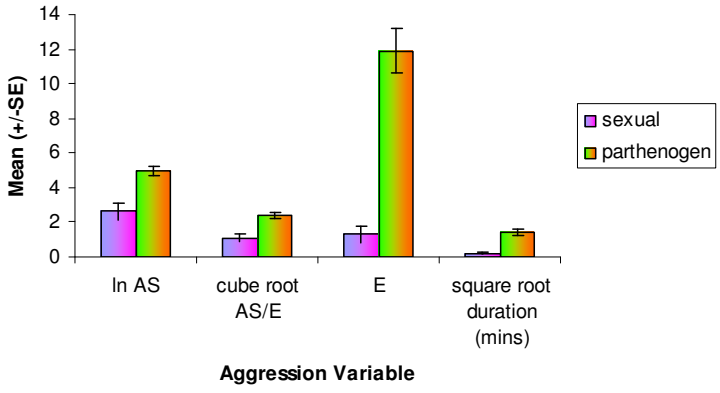


Figure. 6.2 Mean (+/-) aggression levels displayed by sexuals towards parthenogens and parthenogens towards sexuals.

Table 6.8. Results of paired t-tests comparing aggression levels between sexuals and parthenogens.

Aggression Variable	N	t	df	p
Ln AS	24	-7.001	23	<0.001
Ln AS/E	24	-8.747	23	<0.001
E	24	-6.711	23	<0.001
Duration (mins)	24	-7.591	23	<0.001

c) Comparing aggression levels of sexuals towards WP parthenogens and sexual towards RP3 parthenogens.

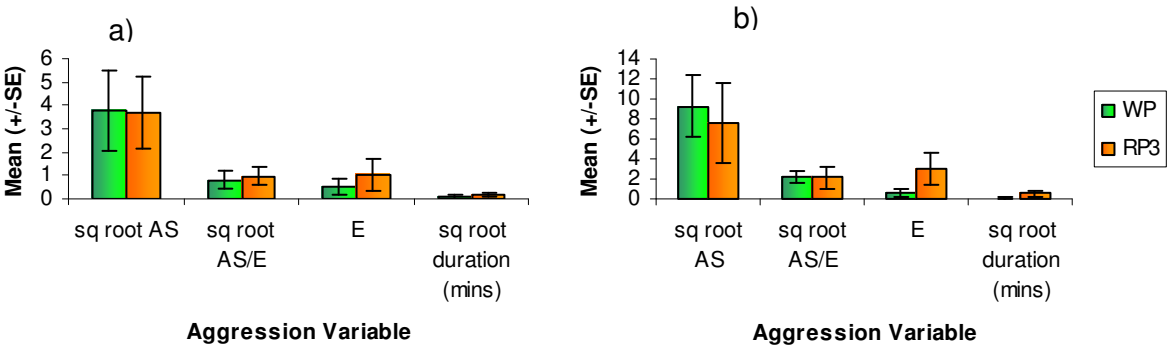


Figure 6.3. Mean (+/-) aggression levels displayed by a) males towards WP and RP3 parthenogens and b) sexual females towards WP and RP3 parthenogens.

Males and sexual females showed the same level of aggression towards each parthenogen (Table 6.9).

Table 6.9. Results of independent t-tests comparing aggression of sexual males and females towards WP and RP3 parthenogens;

Lizard type	Aggression Variable	t	df	P
Male	Sq root AS	0.039	10	0.970
	Sq root AS/E	-0.324	10	0.752
	E	0.867	10	0.406
	Sq root duration (mins)	-0.288	10	0.779
Sas female	Sq root AS	0.352	10	0.732
	Sq root AS/E	0.017	10	0.987
	E	1.171	10	0.269
	Sq root duration (mins)	-1.621	10	0.136

d) Comparing *aggression levels of parthenogens towards males and parthenogens towards sexual females*

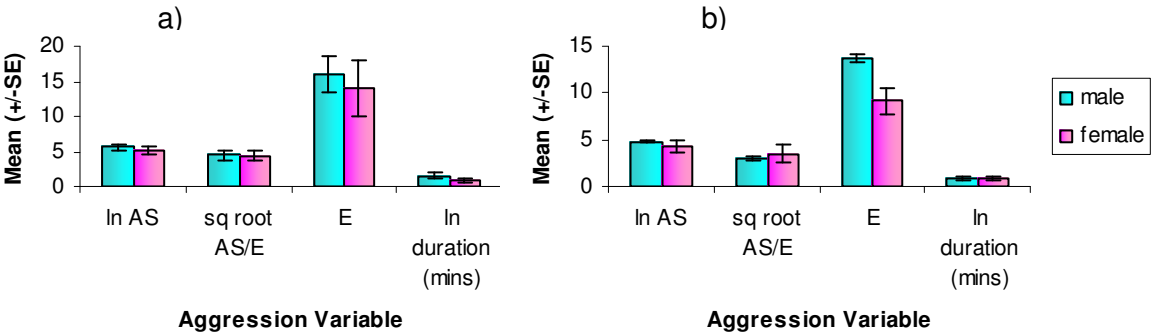


Figure 6.4. Mean (+/-) aggression levels displayed by a) WP parthenogens towards males and sexual females and b) RP3 parthenogens towards males and sexual females.

WP parthenogens showed the same level of aggression towards sexual males and females. RP3 parthenogens had significantly more aggressive encounters with sexual females than males, however, they did not differ in their level of aggression towards males and sexual females (Figure 6.4,Table 6.10).

Table 6.10. Results of paired t-tests comparing aggression of WP ad RP3 parthenogens towards males and sexual females;

Lizard type	Aggression Variable	t	df	P
WP	Ln AS	0.555	10	0.591
	Sq root AS/E	0.110	10	0.915
	E	0.428	10	0.678
	Ln duration (mins)	1.326	10	0.214
RP3	Ln AS	0.744	10	0.474
	Sq root AS/E	-0.484	10	0.639
	E	2.901	10	0.016
	Ln duration (mins)	0.174	10	0.866

Do pairings differ in their level of aggression?

There were no significant differences in aggression levels among pairing treatment (Figure 6.5, Table 6.11).

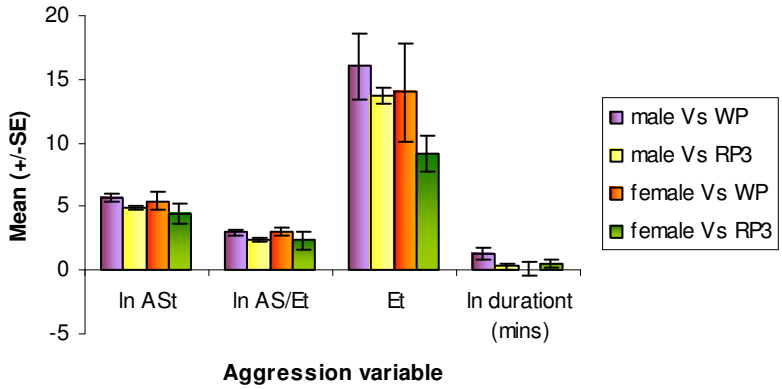


Figure 6.5. Mean (+/-) aggression levels displayed within each treatment.

Table 6.11. Results of One-way ANOVAs comparing aggression levels between treatments.

Aggression Variable	F	df	p
Ln AS	0.874	3	0.471
Ln AS/E	0.933	3	0.443
E	1.371	3	0.280
Duration (mins)	1.291	3	0.305

Are males more aggressive than females?

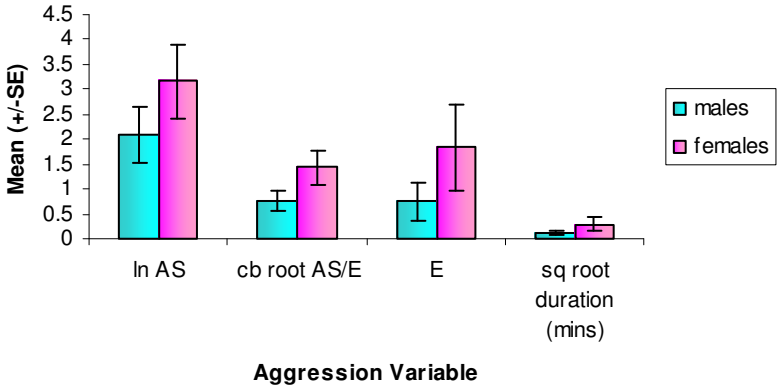


Figure 6.6. Mean (+/-) aggression levels displayed by males and sexual females.

In order to determine if the sexual population gains an advantage from having 'aggressive' males, aggression levels in males and sexual females were compared (Figure 6.6). There were no significant differences (Table 6.12).

Table 6.12. Results of independent t-tests comparing aggression levels between males and sexual females.

Aggression Variable	t	df	p
Ln AS	-1.146	1	0.264
Cb root AS/E	-1.670	1	0.109
E	-1.146	1	0.270
Sq root duration (mins)	-1.191	1	0.246

Social Status

Do treatments differ in the proportion of pairings that produce a clear subordinate dominant relationship?

Of the total 24 pairs studied in the novel environment, a clear dominance rank was seen in 19 pairs. Dominance could not be determined in the remaining 5 pairs. In two of these pairs (1x male v RP3, 1x sexual female v RP3) there were only very low levels of aggression. In the three pairs (1x male v RP3, 2x sexual female v RP3) both lizards within the pair exhibited similar levels of aggression. In trials involving WP parthenogens, all pairs produced a clear dominant subordinate relationship, while only 50% of pairs involving sexual female and RP3 parthenogens produced a clear relationship (Figure 6.7). Despite this, there was no significant difference among treatments in the proportion of pairs that produced a clear dominant – subordinate relationship (Fisher's Exact test=5.811, *df*=3, p=0.111).

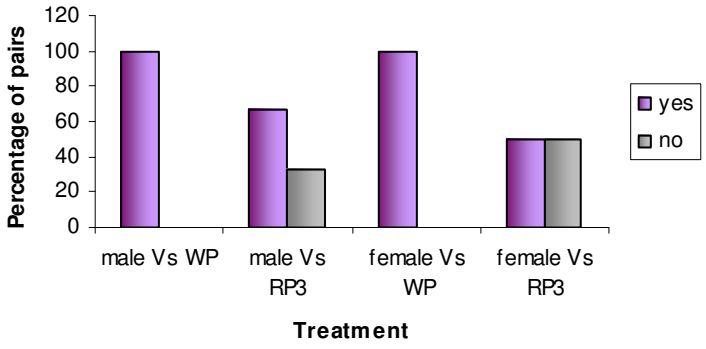


Figure 6.7. Percentage of pairings that produced or did not produce a clear dominant - subordinate relationship within each treatment.

Are parthenogens dominant more often than sexuals?

WP parthenogens were always dominant to sexuals. In pairs in which a clear dominant subordinate relationship was evident, RP3 parthenogens were also always dominant to sexuals (Figure 6.8). This difference in status among the four

types was significant (Fisher's Exact test= 48.366, p<0.001). When pooled parthenogens were dominant significantly more often than sexuals (X^2= 38.000, *df*=3, p<0.001) (Figure 6.9).

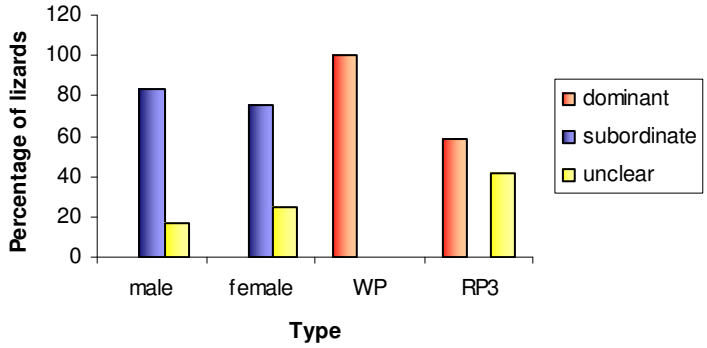


Figure 6.8. Percentage of males, sexual females, WP parthenogens and RP3 parthenogens that were dominant, subordinate or unclear.

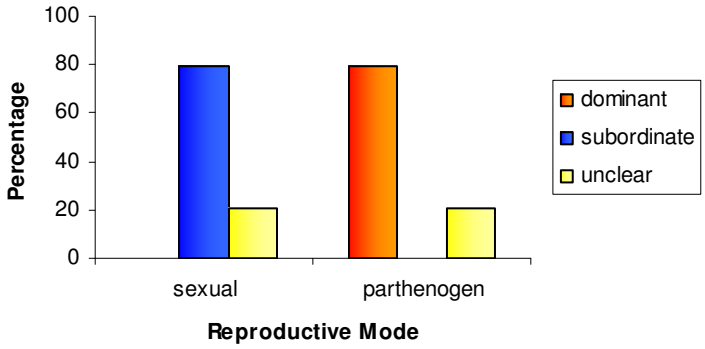


Figure 6.9. Percentage of sexual and parthenogens that were dominant, subordinate or unclear.

Advantage to Dominance

Does the dominant lizard in the pair gain more food items?

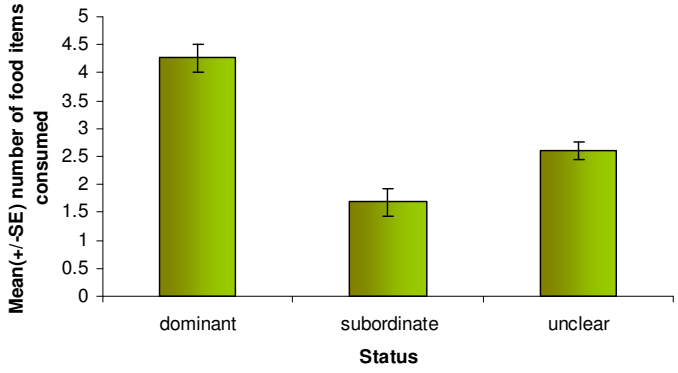


Figure 6.10. Mean (+/-SE) number of food items consumed by lizards of each social status.

Food acquisition was affected by status (Figure 6.10), with a significant differnce being found in the number of food items consumed by lizards of each status (One-way ANOVA; F= 32.74, df=2, p<0.001). Bonferroni multiple comparisons test showed that dominant lizards consumed significantly more food items, than both subordinate lizards and lizards (Table 6.13).

Table 6.13. Results of Bonferroni Post Hoc test comparing food consumption among lizard of each social status (dominant, subordinate, unclear).

Lizard 1	**Lizard 2**	**p**
Dominant	Subordinate	<0.001
Dominant	Unclear	<0.001
Subordinate	Unclear	0.057

Repeated Measures ANOVAs were used to compare the number of food items consumed by a) each reproductive mode (sexual or parthenogens) and b) each lizard type (male, sexual female, WP, RP3) across the three feeding sessions.

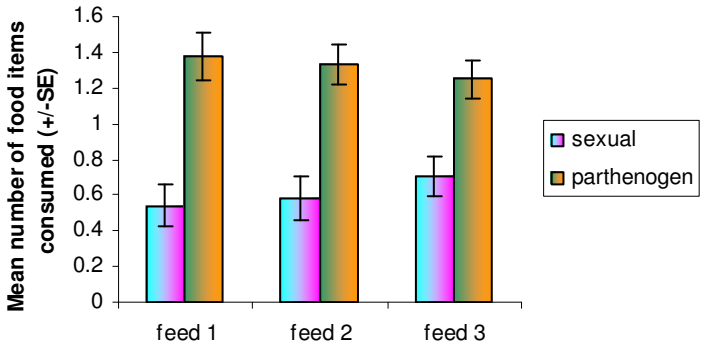


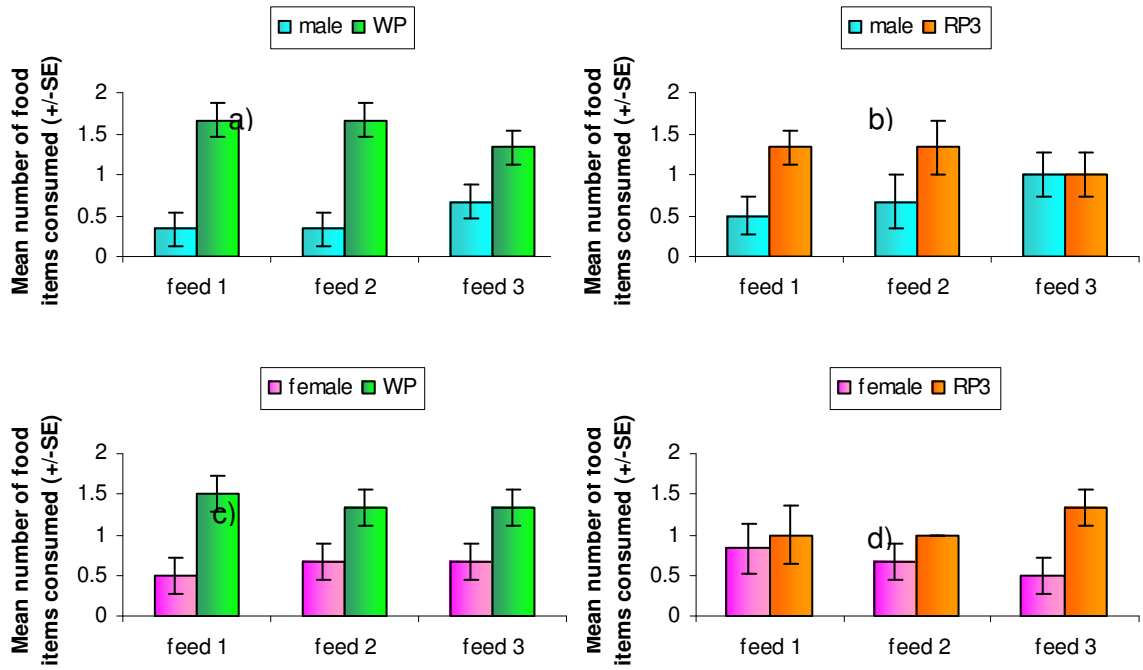
Figure 6.11. Number of food items consumed (+/-SE) by sexual lizards (males and females pooled) and parthenogen lizards (WP and RP3 lizards pooled) in each feeding session.

Results (Table 6.14, Figure 6.11) showed that parthenogens consumed significantly more food items than sexuals and this was consistent across the three feeding sessions.

Table 6.14. Results of Repeated Measures ANOVA comparing food acquisition between sexuals and parthenogens.

		df	**F**	**p**
Within	Feed	2	0.023	0.978
	Feed*Reproductive Mode	2	0.886	0.416
Between	Reproductive Mode	1	45.912	<0.001

When each lizard type was examined separately (Figure 6.12), results showed a significant difference among lizard type in food acquisition (Table 6.15).



parthenogens, and d) sexual females and RP3 parthenogens in each feeding session.

A Tukey multiple comparisons test revealed that both parthenogens consumed significantly more food items than males (WP, $p<0.001$; RP3, $p=0.001$) and sexual females (WP, $p<0.001$; RP3, $p=0.004$), and this was consistent across the three feeding sessions.

Table 6.15. Results of Repeated Measures ANOVA comparing food acquisition between each lizard type.

		df	F	p
Within	Feed	2	0.023	0.978
	Feed*Lizard Type	6	0.866	0.523
Between	Lizard Type	3	17.748	<0.001

Does the subordinate lizard lose more weight than the dominant lizard?

Change in weight (g) was affected by status (Figure 6.13), with a significant difference being found in change in weight (g) among lizards of different status (One-way ANOVA; F= 5.974, *df*=2 p=0.005). Subordinate lizards lost significantly more weight than dominant lizards. This result however, is

inconclusive since there was no significant difference in weight change detected between lizards of unclear social status and both dominant and subordinate lizards (Table 6.16).

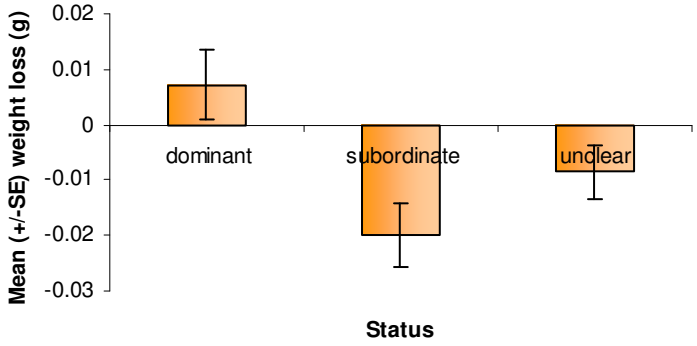


Figure 6.13. Change in weight (g) against status. Where a status = 1 is dominant, a status = 2 is subordinate and a status = 3 is unclear.

Table 6.16. Results of Bonferroni Post Hoc test comparing change in weight (g) among lizards of differing social status (dominant, subordinate, unclear).

Lizard 1	**Lizard 2**	**p**
Dominant	Subordinate	0.004
Dominant	Unclear	0.313
Subordinate	Unclear	0.702

Overall, sexuals lost weight over the course of the study while parthenogens gained weight (Figure 6.14). This differences in change in weight between sexual and parthenogenetic *M. greyii* was significant (paired t-test, t=-2.938, *df*=23, p=0.007).

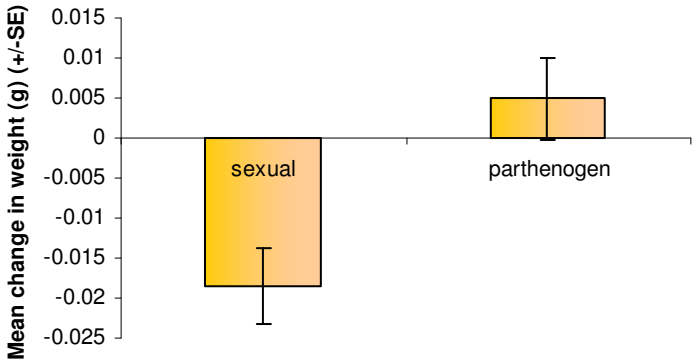


Figure 6.14. Mean (+/-SE) change in weight of sexuals (males and females pooled) and parthenogens (WPs and RP3s pooled) over the course of the experiment.

When each type was examined separately, results showed that WP parthenogens gained weight over the course of the experiment, while sexuals lost weight and RP3 parthenogens had very little change in weight (Figure 6.15). One-way ANOVA revealed that there was a significant difference in the change in weight (g) among lizard type (F=4.491, *df*=3, p=0.008). A Tukey multiple comparisons test revealed that WP parthenogens lost significantly less weight than males and sexual females. However, there was no significant difference in the change in weight between RP3 parthenogens and sexual individuals (Table 6.17).

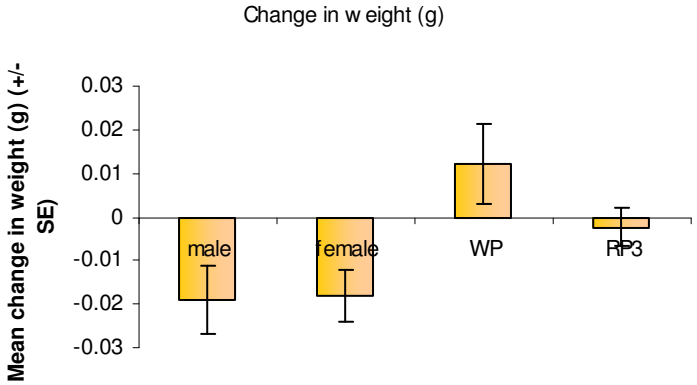


Figure 6.15. Mean (+/-SE) change in weight of males, sexual females, WP parthenogens and RP3 parthenogens over the course of the experiment.

Table 6.17. Results of Tukey Post Hoc test comparing change in weight (g) among lizards of each type.

Lizard 1	**Lizard 2**	**p**
Male	WP	0.017
Male	RP3	0.592
Sexual female	WP	0.022
Sexual female	RP3	0.697

Summary

Aggression

Parthenogen *M. greyii* were more aggressive than sexual *M. greyii*.

Social Status

This higher level of aggression enabled the parthenogens to dominate the sexuals, in a novel environment.

Advantage of Dominance

Dominance translated into a clear advantage to the parthenogens, with parthenogens acquiring significantly more food items than the sexuals.

Furthermore, a reduction in food intake translated into a clear fitness disadvantage for the sexuals, with sexuals losing significantly more weight than the parthenogens.

Competition in a Resident vs Intruder Environment.

Aggression Levels

Repeated measures ANOVAs with status (i.e. resident v intruder) as the within subjects factor and resident reproductive mode (sexual or parthenogen) as the between subject factor were used to compare aggression, food acquisition and change in weight (g) between residents and intruders. Independent t-tests were then used to compare aggression levels between parthenogen and sexual residents and between parthenogen and sexual intruders.

Are sexual residents more aggressive towards parthenogen intruders than parthenogen residents are towards sexual intruders?

a) Comparing aggression levels between sexual residents (males and females pooled) and parthenogen residents (WPs and RP3s pooled).

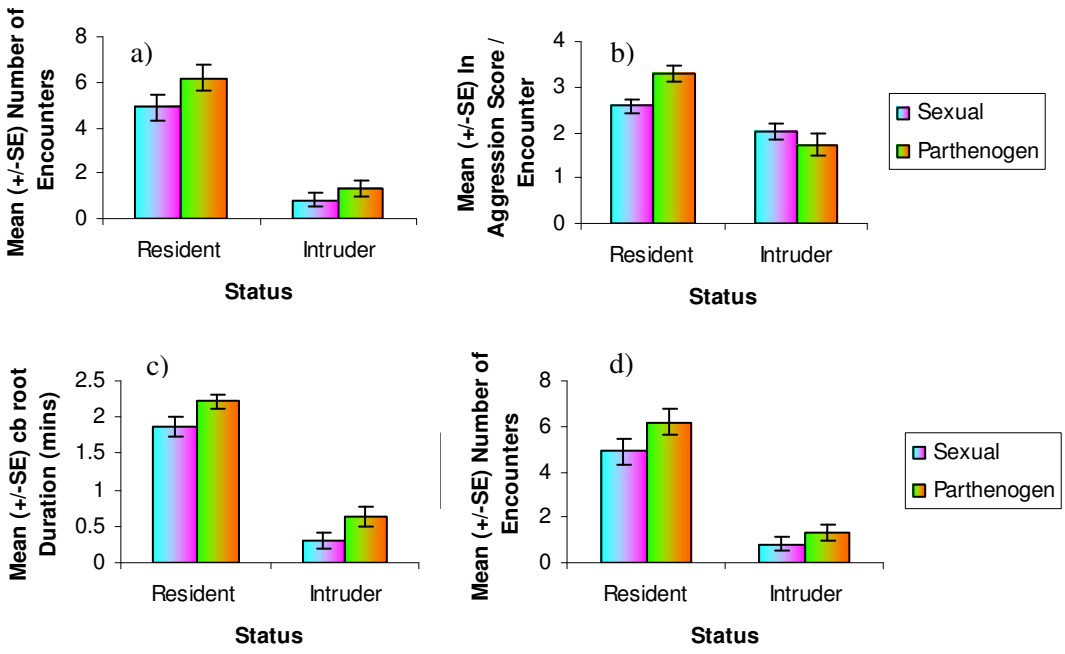


Figure 6.16. Mean aggression levels of residents and intruders for treatments with sexual residents and parthenogen intruders and treatments with parthenogen residents and sexual intruders. a)cb root aggression score (AS), b) ln aggression score per encounter (AS/E), c) cb root duration of aggressive encounters (mins) and d) number of aggressive encounters (E).

Figure 6.16 shows the overall aggression score (AS), aggression score per encounter (AS/E), the duration of aggression encounters (mins) and the number of aggressive encounters (E) for residents and intruders.

For each of the variables it was necessary to use transformed data in order to fit the assumptions of the Repeated Measures ANOVA. The transformation used in each case was the one that best produced normality, sphericity and homogeneity in the data. Results of the repeated measures ANOVAs are shown in Table 6.18.

For aggression score (AS), aggression score per encounter (AS/E), and the number of aggressive encounters (E) the interaction effect was not significant. This suggests that the difference between resident and intruder for these measures of aggression was consistent for trials with parthenogen residents and sexual intruders and trials with sexual residents and parthenogen intruders. Sexual residents were more aggressive than parthenogen intruders and parthenogen residents were more aggressive than sexual intruders, for all variables measured. Pairings (combining both resident and intruder) with parthenogen residents and sexual intruders involved more aggressive encounters (E) and produced higher aggression scores overall (AS) and per encounter (AS/E) than pairings with sexual residents and parthenogen intruders.

When considering the duration of aggressive encounters, there was a significant interaction effect. Results showed that residents initiated longer aggressive encounters than intruders in both sets of trials (i.e. trials with sexual residents and parthenogen intruders and trials with parthenogen residents and sexual intruders). However, parthenogen residents initiated longer aggressive encounters than sexual residents, but sexual intruders initiated longer aggressive encounters than parthenogen intruders, producing the interaction effect.

Independent t-tests showed that parthenogen residents showed significantly higher levels of aggression overall (AS) and per encounter (AS/E) towards sexual intruders than sexual residents did towards parthenogen intruders. Parthenogen residents also engaged in longer aggressive encounters with sexual intruders than sexual residents did with parthenogen intruders. There was no significant

difference in the number of aggressive encounters initiated by each type of resident (Table 6.19).

Parthenogen intruders showed the same level of aggression towards sexual residents as sexual intruders did towards parthenogen residents (Table 6.19).

Table 6.18. Results of Repeated Measures ANOVA comparing aggression of residents and intruders between trials with sexual residents and parthenogen intruders and trials with parthenogen residents and sexual intruders.

Aggression Variable			df	F	p
Cb root (AS)	Within	Status	1	37.920	<0.001
		Status*Reproductive Mode Resident	1	3.812	0.057
	Between	Reproductive mode of Resident	1	12.790	0.001
Ln (AS/E)	Within	Status	1	35.633	<0.001
		Status*Reproductive Mode Resident	1	1.516	0.224
	Between	Reproductive mode of Resident	1	587.062	<0.001
Cb root Duration (mins)	Within	Status	1	189.035	<0.001
		Status*Reproductive Mode Resident	1	8.898	0.005
	Between	Reproductive mode of Resident	1	340.392	<0.001
Sq root (E)	Within	Status	1	68.645	<0.001
		Status*Reproductive Mode Resident	1	2.685	0.108
	Between	Reproductive mode of Resident	1	68.645	<0.001

Table 6.19. Results of independent t-tests comparing aggression levels between sexual residents and parthenogen residents and between sexual intruders and parthenogen intruders.

	Aggression Variable	N	t	p
Between Residents	Cb root AS	24	-3.990	<0.001
	ln AS/E	24	-3.180	0.003
	Cb root duration (mins)	24	-2.057	0.045
	Sq root E	24	-1.663	0.103
Between Intruders	Cb root AS	24	1.865	0.069
	ln AS/E	24	0.909	0.368
	Cb root duration (mins)	24	-1.799	0.079
	Sq root E	24	-1.104	0.275

Do residents differ in the level of aggression they display towards each intruder type?

a) *Comparing aggression levels of sexual residents towards WP intruders and RP3 intruders.*

There appears to be very little difference in the aggression showed towards each intruder type by sexual residents (Figure 6.17). Results showed that sexual female residents engaged in more aggressive encounters with RP3 intruders than WP intruders. There were no other significant differences in aggression (Table 6.20).

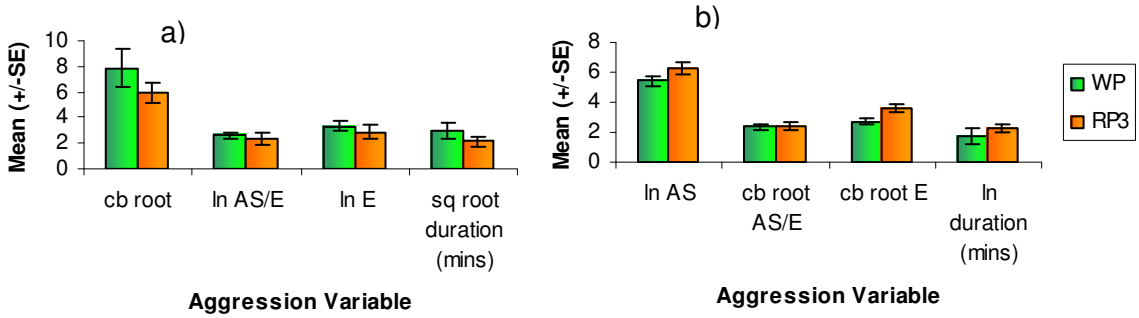


Figure 6.17. Mean (+/-) aggression levels displayed by a) resident males towards WP and RP3 intruders and b) sexual females towards WP and RP3 intruders.

Table 6.20. Results of independent t-tests comparing aggression of sexual residents towards WP intruders and sexual residents towards RP3 intruders.

Resident	Aggression Variable	N	t	*df*	p
Male	Cb root AS	6	1.199	1	0.267
	Ln AS/E	6	6.858	1	0.506
	Ln E	6	9.170	1	0.558
	Sq root duration (mins)	6	8.798	1	0.279
Female	Ln AS	6	-1.539	1	0.156
	Cb root AS/E	6	-0.069	1	0.031
	Cb root E	6	-2.536	1	0.946
	Ln duration (mins)	6	-0.974	1	0.364

b) Comparing aggression levels of parthenogen residents towards male intruders and sexual female intruders.

Figure 6.18 demonstrates the level of aggression directed towards each sexual intruder type by parthenogen residents. WP residents were more aggressive per encounter towards male intruders than female intruders. There were no other significant differences in aggression (Table 5.21).

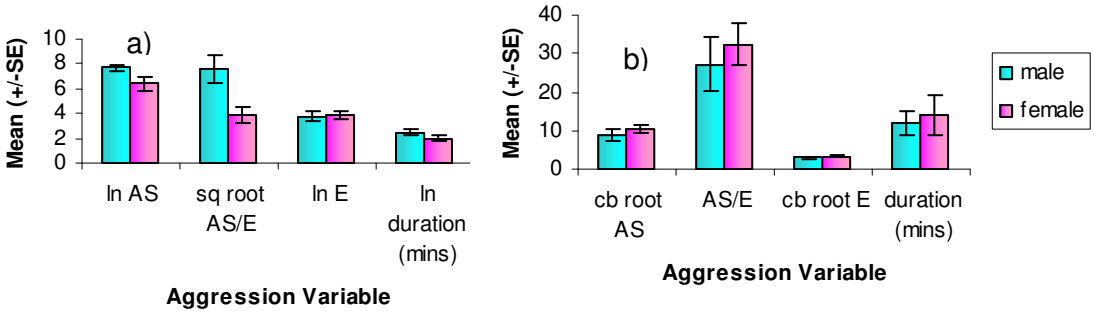


Figure 6.18. Mean (+/-) aggression levels displayed by resident WP and RP3 parthenogens towards male and sexual female intruders.

Table 6.21. Results of independent t-tests comparing aggression of parthenogen residents towards male intruders and parthenogen residents towards female intruders.

Resident	Aggression Variable	N	t	*df*	p
WP	Ln AS	6	2.025	1	0.097
	Sq root AS/E	6	2.574	1	0.018
	Ln E	6	-0.218	1	0.832
	Ln duration (mins)	6	1.729	1	0.120
RP3	Cb root AS	6	-0.990	1	0.348
	AS/E	6	-0.591	1	0.568
	Cb root E	6	-1.208	1	0.259
	Duration (mins)	6	-0.351	1	0.734

For the remainder of the analyses I compared parthenogens and sexuals without considering each sexual (male or female) and parthenogen (WP or RP3) type separately.

Social Status

Do treatments differ in the proportion of pairings that produce a clear dominant - subordinate relationship?

Those treatments that had parthenogen residents and sexual intruders produced clear dominant – subordinate relationships significantly more often than

treatments with sexual residents and parthenogen intruders (X^2= 8.545, *df*=1, p=0.003) (Figure 6.19).

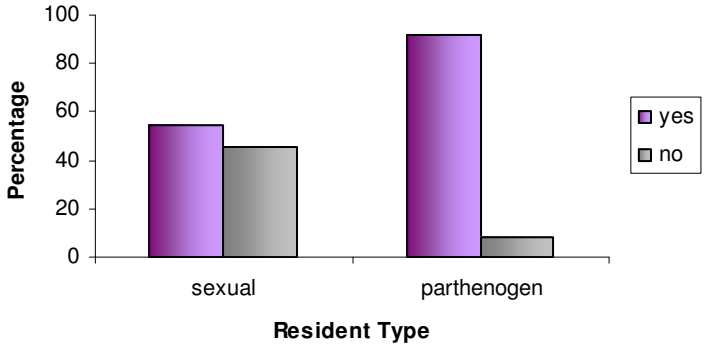


Figure 6.19. Percentage of pairings that produced a clear dominant – subordinate relationship for treatments with sexual residents and parthenogen intruders, and treatments with parthenogen residents and sexual intruders.

Are residents dominant significantly more often than intruders?

Lizards within a dyad were classified as either dominant, subordinate or of unclear status. Results for all three classifications are discussed below, however, analyses only included animals of clear status (i.e. dominant or subordinate).

a) Comparing social status between residents (pooled) and intruders (pooled).

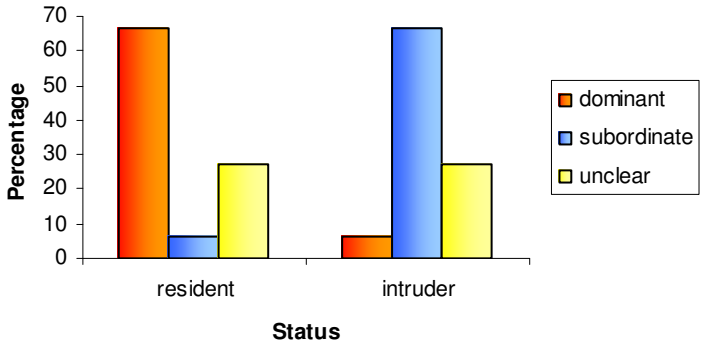


Figure 6.20. Percentage of residents and intruders (pooled for all treatments) that had a social ranking of dominant, subordinate or unclear.

Of the total 48 pairs studied in the resident vs intruder environment, a clear dominant – subordinate relationship was seen in 35 pairs (approx. 73%), (Figure 6.20). Of these trials of clear rank, residents were dominant in 91.4% of the pairings while intruders were dominant in 8.6% of trials. This difference in rank between residents and intruders was significant (X^2= 48.057, *df*=1, p=0.001).

Dominance could not be determined in the remaining 13 pairs. In eight of these pairs we detected very low levels of aggression, while in the remaining five pairs both lizards within the pair exhibited similar levels of aggression.

b) comparing dominance between residents and intruders for each reproductive mode

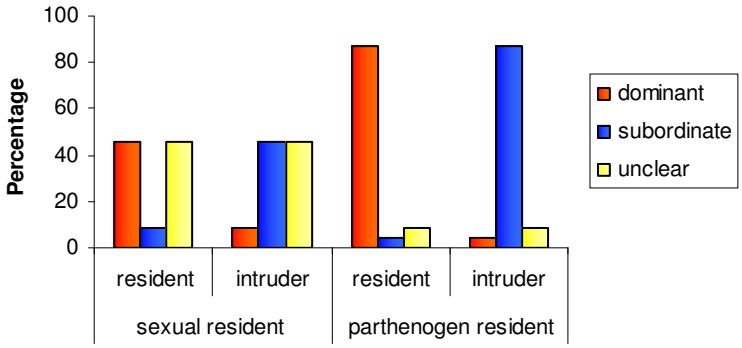


Figure 6.21. Percentage of residents and intruders that had a social ranking of dominant, subordinate or unclear for trials with sexual residents and parthenogen intruders and trials with parthenogen residents and sexual intruders.

In treatments with sexual residents and parthenogen intruders a clear dominance – subordinate relationship was evident in only approximately 54% of pairings (Figure 6.21). Within these pairs of clear rank, sexual residents were dominant over parthenogenetic intruders significantly more often than parthenogenetic intruders were dominant over sexual residents (X^2= 12.462, *df*=1, p<0.001).

In treatments with parthenogen residents a clear dominance – subordinate relationship was evident in approximately 92% of pairings (Figure 6.21). Within these pairs of clear rank, parthenogenetic residents were dominant over sexual intruders significantly more often than sexual intruders were dominant over parthenogenetic residents (X^2= 36.364, *df*=1, p<0.001).

Are parthenogen residents dominant significantly more often than sexual residents.

Parthenogen residents were dominant to sexual intruders more often than sexual residents were to parthenogen intruders (Figure 6.22). This difference in rate of dominance was significant (X^2= 9.689, *df*=2, p=0.008).

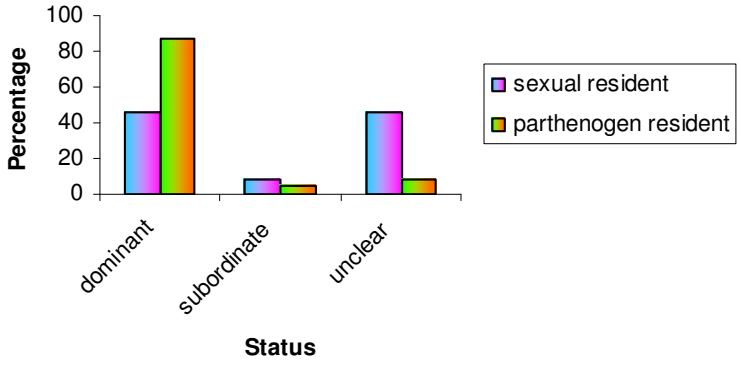


Figure 6.22. Percentage of sexual and parthenogen residents that were dominant or subordinate.

Advantage of Dominance

Do residents gain more food items than intruders?

Comparing food consumption between residents (pooled) and intruders (pooled).

Figure 6.23 shows the number of food items consumed by residents and intruders for trials with sexual residents and parthenogen intruders and trials with parthenogen residents and sexual intruders.

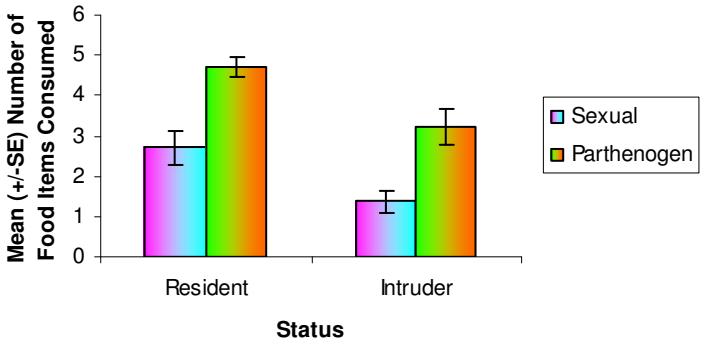


Figure 6.23. Mean number of food items consumed by residents and intruders for trials with sexual residents and parthenogen intruders, and trials with parthenogen residents and sexual intruders.

Repeated measures ANOVA showed a significant Status*Reproductive Mode of Resident Interaction effect (Table 6.22). This indicates that the difference between resident and intruder in the number of food items consumed is not consistent for trials with parthenogen residents and sexual intruders and trials with sexual residents and parthenogen intruders. In trials with sexual residents and parthenogen intruders, intruders gained slightly more food items than residents

(3.21 vs. 2.71). In contrast, in trials with parthenogen residents and sexual intruders, residents gained more food items than intruders (4.71 vs. 1.38). As a result, parthenogen residents consumed significantly more food items than sexual residents and parthenogen intruders consumed significantly more food items than sexual intruders (Figure 6.23) (Table 6.23).

Table 6.22. Results of Repeated Measures ANOVA comparing food consumption of residents and intruders for trials with sexual residents and parthenogen intruders and trials with parthenogen residents and sexual intruders.

Resident Type			df	F	p
Change in weight (g)	Within	Status (resident or intruder)	1	8.186	0.006
		Status*Reproductive Mode	1	14.984	<0.001
	Between	Reproductive Mode Resident (sexual or parthenogen)	1	2.706	0.107

Table 6.23. Results of independent t-tests comparing food consumption between sexual and parthenogen residents, and between sexual and parthenogen intruders..

	Aggression Variable	N	t	p
Between Residents	Number of food items	24	-4.155	<0.001
Between Intruders	Number of food items	24	-3.570	0.001

Does a reduction in food intake result in a loss of weight?

Determining change in weight for residents (pooled) and intruders (pooled).

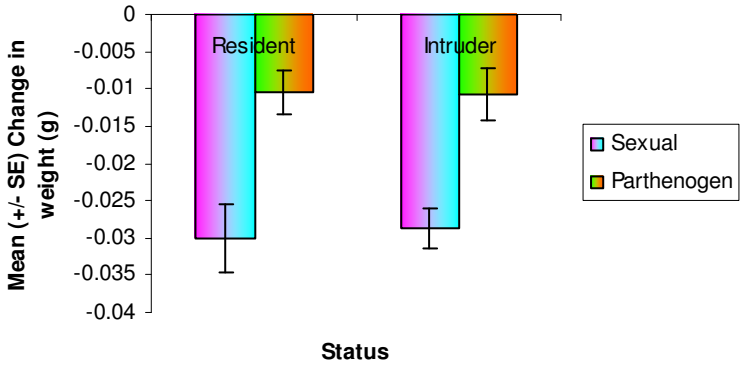


Figure 6.24. Change in weight of residents and intruders for treatments with sexual residents and parthenogen intruders and treatments with parthenogen residents and sexual intruders.

Figure 5.25 shows the change in weight (g) of residents and intruders for trials with sexual residents and parthenogen intruders and trials with parthenogen residents and sexual intruders. Overall, both residents and intruders lost weight over the course of the trial.

Repeated measures ANOVA showed a significant status*resident reproductive mode interaction effect (Table 6.24). This indicates that the difference between resident and intruder in change in weight (g) is not consistent for trials with parthenogen residents and sexual intruders and trials with sexual residents and parthenogen intruders. In trials with sexual residents and parthenogen intruders, residents lost more weight than intruders. In contrast, in trials with parthenogen residents and sexual intruders, intruders lost more weight than residents. As a result, sexual residents lost significantly more weight than parthenogen residents and sexual intruders lost significantly more weight than parthenogen intruders (Figure 6.24, Table 6.25).

Table 6.24. Results of Repeated Measures ANOVA comparing change in weight (g) of residents and intruders between trials with sexual residents and parthenogen intruders and trials with parthenogen residents and sexual intruders.

Variable			df	F	p
Change in weight (g)	Within	Status	1	0.021	0.885
		Status*Reproductive Mode Resident	1	27.516	<0.001
	Between	Reproductive mode of Resident	1	0.051	0.822

Table 6.25. Results of independent t-tests comparing change in weight (g) between sexual and parthenogen residents and between sexual and parthenogen intruders.

Variable		N	t	p
Change in weight (g)	Between Residents	24	-3.568	0.001
	Between Intruders	24	-4.127	<0.001

Summary

Aggression

Parthenogen residents were more aggressive towards sexual intruders, than sexual residents were towards parthenogen intruders. Parthenogen and sexual intruders did not differ in their level of aggression towards residents.

Social Status

In nearly 50% of trials with sexual residents and parthenogen intruders, there was no clear dominant-subordinate relationship formed. In the trials that did produce a clear relationship, the residents were dominant. In 92% of trials with parthenogen residents and sexual intruders, clear dominant – subordinate relationships were formed, with residents being dominant in 90% of trials.

Advantage to dominance

Clear dominance of parthenogen residents resulted in parthenogen residents acquiring more food items than sexual intruders. The greater aggression shown by parthenogen residents compared to sexual residents also resulted in parthenogen residents acquiring more food items than sexual residents.

The high occurrence of unclear relationships in the sexual resident and parthenogen intruder treatments resulted in sexual residents and parthenogen intruders acquiring the same number of food items. Furthermore, parthenogen intruders obtained significantly more food items than sexual intruders.

These differences in food acquisition resulted in both sexual residents and sexual intruders losing significantly more weight than parthenogen residents and parthenogen intruders.

Discussion

Aggressive Behaviours Observed

Aggression between sexual and parthenogenetic *Menetia greyii* was detected in the current study. Results demonstrate that parthenogens exhibit aggression towards sexuals and sexuals exhibit aggression towards parthenogens, suggesting that aggression is an important social behaviour in both reproductive modes.

The acts observed in *M. greyii* during agonistic interactions ranged from non-contact behaviours (approach, supplant, tail movement, back arch, flee), to low level contact (move over, straddle), to attack (lunge, nip, bite, wrestle) and elevated aggression (lock jaw and chase). All of the behaviours observed, or

behaviour similar to these have been previously recorded in lizards (e.g. Carpenter and Ferguson 1977).

Each of the four types (males, sexual females, WP and RP3 parthenogens) displayed the same range of aggressive behaviours, however, the circumstances under which they displayed these behaviours did differ. In a novel environment, when sexuals engaged in aggressive acts with parthenogens, they were more likely to engage in less violent interactions than were parthenogens. The more aggressive attack behaviours (biting and wrestling) and the escalated aggression (lock jaw and chasing) seen directed by parthenogens towards sexuals were not performed by sexuals towards parthenogens. However, as residents, sexuals displayed a wider range of aggressive behaviours than when in a novel environment, suggesting that prior ownership was an important determinant of aggression level in sexual *M. greyii*. In contrast, parthenogens were equally aggressive in both a novel environment and as residents suggesting that prior ownership does not determine the level of aggression displayed by this reproductive mode.

In this study social status was also a major determinant of subsequent behaviour, with differences in aggressive behaviour seen between dominant and subordinate lizards. Several aggressive behaviours were only performed by the dominant lizard in the pair, including low contact behaviours (straddle and supplant), attack behaviour (wrestle) and all elevated aggressive behaviours. The most common behaviour observed in subordinate lizards (and rarely seen in dominants) was fleeing. An important aspect of agonistic interactions is the ability of one of the opponents to retreat from the conflict, and has been observed in subordinates of other lizard species such as *Ctenosaura hemilopha* (Carothers 1981), and *Heteronotia binoei* (Ryhorchuk 2002).

In trials in which a clear dominant-subordinate relationship was formed, rank was usually established early on in the interactions, and once established rank did not change throughout the behaviour session or the subsequent feeding trials. This observation is similar to that for *Anolis aeneus* (Stamps 1983, Stamps and Krishnan 1995, 1998), *Hemidactylus frenatus* and *Lepidodactylus lugubris* (Petern

et al 1993) and *Heteronotia binoei* (Ryhorchuk 2002). Even after the dominant relationship had been established, although overt displays of aggression did reduce, aggression of the dominant on the subordinate did generally continue throughout the trial, and was probably due to the inability of the subordinate lizard to escape from the immediate vicinity of the dominant lizard. Recurring aggression of dominants on subordinates has been observed in other studies (Saylor Done and Heatwole 1977, Grassman and Crews 1987, Ryhorchuk 2002), but in studies on wild reptile populations, the levels of aggressiveness tend to decrease once dominance has been asserted (Carothers 1981, Stamps 1983, Bolger and Case 1992).

Both sexual and parthenogen *M. greyii* tended to direct bites towards the tail region, and to a lesser extent towards the jaw and neck region of their opponent. Neck and jaw biting generally occurred within the more aggressive attacks that included jaw locking. Specificity in targeting certain body parts for attack by an individual has been documented. For example, Jaeger (1981) found that *plethodontid* salamanders directed their biting at their opponent's snout in an attempt to "chemically blind" them by damaging the nasolabial grooves, and Jennings and Thompson (1999) found that *Ctenotus fallens* directs attacks to the tail region. It is suggested that this is because they store fat reserves in the tail. The implications of tail autotomy caused by social interactions could be severe and has been found to cause a reduction in fitness parameters such as fecundity (Smyth 1974, Wilson and Booth 1998). The frequency of tail biting in the current study may have been facilitated by the behaviour of the subordinate lizard through tail wagging and twitching. Tail movements have been described for other autotomy capable lizards as a method of displacing predatory attacks from the body to the more expendable tail (Cooper 1998). Although, *M. greyii* also potentially store fat reserves in the tail and as a result tail autotomy may have serious consequences on fitness, not a single case of tail loss was observed in the trials and therefore tail autotomy may not be a common cost of social interactions, making it the preferred target of attack for the subordinate lizard.

Competitive Ability

The primary objective of this study was to test the hypothesis that at Bundey Bore, *sexual* Menetia greyii *are behaviourally dominant to parthenogenetic Menetia greyii, and this dominance translates into an increase in the acquisition of a resource for the sexuals (or reduction in acquisition of a resource for the subordinate parthenogens).*

This hypothesis was not supported for either the novel or resident vs. intruder conditions.

In a novel environment

In a novel environment, aggression was asymmetric in favour of WP and RP3 parthenogens, and this behavioural dominance allowed the parthenogens to acquire significantly more food items than the sexuals. As a consequence the sexuals suffered a significant reduction in fitness, losing more weight than the parthenogens. A loss in weight can have serious repercussions, and has been shown to affect important traits in lizards such as survival and reproductive success (Ballinger 1977).

The sexual taxon failed to even accrue a small advantage through having aggressive males. If males had been more aggressive than sexual females this would have presented the sexual taxon with some degree of advantage in producing males. However the two sexes were found to be equally aggressive, and less aggressive than the parthenogens. However, males could potentially still harass parthenogens for matings and could use passive aggressive methods.

Thus, in a novel environment, parthenogen *M. greyii* were superior competitors to sexual *M. greyii*.

It is worth noting that in a novel environment there appears to be differences between the two clonal types in their aggressive behaviour towards sexuals. When paired RP3 clones and sexual females did not differ in their aggression score or aggression score per encounter. In contrast WP clones were clearly more aggressive towards sexual females than sexual females were towards WP clones

When comparing dominance, WP clones were always the dominant type when paired with either sexual females or males. In contrast in a number of pairings of RP3 clones with sexual males or females it was not clear who the dominant form was.

Therefore in the context of the proposed genetic basis of variation in aggression it would be interesting to examine (in future studies) among- versus within– clone interactions.

Residents vs. Intruders

As mentioned above, prior ownership was important in determining the level of aggression displayed by sexual *M. greyii*, with sexual residents showing higher aggression than sexuals in a novel environment. However, this increased aggression did not lead to competitive success for the sexual residents against parthenogen intruders. Therefore, prior ownership did not determine the outcome of contests.

Sexual residents were more aggressive than parthenogen intruders and sexual were dominant over parthenogen intruders in trials with a clear dominant – subordinate relationship. However, a clear relationship could not be determined in approximately 46% of trials. This lack of clear rank allowed the parthenogen intruders access to a similar number of food items in feed 1, and slightly more food items in feed 2 and 3, as the sexual residents. As a result of this lower food intake, sexual residents incurred a fitness cost, losing significantly more weight than the parthenogen intruders. This loss in weight may, in part, be due to the higher level of energy exerted in aggressive behaviour by the sexual residents compared to the less aggressive intruders.

Staged encounters between parthenogen residents and sexual intruders were more aggressive than encounters between sexual residents and parthenogen intruders. Again, the aggression seen was asymmetric in favour of the residents. In contrast to trials with sexual residents, however, in trials with parthenogen residents and sexual intruders, unclear relationships were only evident in approximately 8% of trials. Parthenogen residents were dominant in 90% of all trials observed. This clear behavioural dominance allowed the parthenogen residents access to the

majority of the food items presented and reduced food acquisition in the sexual intruders. Reduced food intake translated into a fitness cost for the sexual taxon with the intruders losing significantly more weight than the parthenogen residents. In addition, the higher aggression of parthenogen residents and the higher incidence of clear dominant relationships in trials with parthenogen residents, compared to sexual residents, resulted in parthenogen residents acquiring more food items than sexual residents, and parthenogen intruders consuming more food items than sexual intruders.

Thus, in a resident vs. intruder environment, both parthenogen residents and parthenogen intruders gained a competitive advantage over sexual residents and sexual intruders.

The difference in competitive ability between parthenogens and sexuals suggests that there is genetically based variation in competitive ability within the Bundey Bore population. Genetic analysis has determined that the sexual taxon found at Bundey Bore (SAS) appears to be the parental ancestor of the RP3 parthenogen, but neither ancestor of the WP parthenogen. It is possible that the maternal ancestor of the RP3 parthenogen and the sexual *Menetia* taxon from which WP parthenogens arose are more aggressive than SAS, and the parthenogen taxa examined in this study may reflect the behaviour of these sexual ancestors.

I have not examined all of the behavioural interactions possible between these two reproductive modes, and what was observed in the laboratory experiment does not necessarily predict what would happen in the field. For example, aggressive behaviour may increase the risk of predation in nature but not in the lab. However, I did get a consistent result across two separate studies (novel and resident) using predominantly two distinct groups of lizards. I also recognise that other mechanisms could underlay a reduction in weight in competing lizards such as the triggering of stress hormones (Downes and Bauwens 2002).

It must be mentioned that dominance was tested on adults only in an artificial situation of forced interference. Free-ranging sexual individuals may have a

competitive edge in resource exploitation whilst avoiding direct confrontation with parthenogens,

The implications of these results on coexistence between sexual and parthenogen forms at Bundey Bore are discussed in the general discussion.

Chapter 7

Parasite prevalence in parthenogenetic and sexual Menetia greyii, testing the Red Queen Hypothesis.

Introduction

An alternate short-term advantage to sexual reproduction that may offset the reproductive advantage held by the parthenogens (Maynard Smith 1971, Williams 1975, Maynard Smith 1978), and allow the persistence of the sexual taxa is differential parasite infestation. Higher mortality in the parthenogens due to a higher parasite load would provide an advantage to the sexual form.

A parasite based theory of the maintenance of sexual reproduction in populations was introduced by Jaenike (Jaenike 1978a) and Hamilton (1980), and the idea was later labeled the Red Queen hypothesis (Bell 1982). Since a single host cannot resist all of the different kinds of parasites, nor can one parasite strain infect all the potential hosts, selection will favour parasites that can exploit the most common host phenotype (Hakoyama 2001, Howard and Lively 2003), thus creating a time-lagged, frequency dependent selection (Lively 1996). And because parasites adapt to the most common host genotype, evolution will favour hosts with a rare combination of resistant genes. Therefore, the advantage of sexual reproduction under the Red Queen stems from the ability to produce offspring with rare genotypes, which are more likely to escape infection by coevolving parasites (Glesner and Tilman 1978, Jaenike 1978a, Bremermann 1980, Lloyd 1980, Hamilton 1982, Hamilton et al. 1990). Genetically identical parthenogenetic lineages, in contrast, are more vulnerable to parasitism as they can only create rare genotypes through mutation. Computer simulation experiments have demonstrated an advantage to a sexual subpopulation in an asexual / sexual system after the introduction of parasites (Jaenike 1978a, Hamilton 1980,

Hamilton et al. 1990, Ladle et al. 1993, Parker 1994, Peters and Lively 1999, Martins 2000).

The principal underlying assumptions of the Red Queen Hypothesis are;

1) that there is genetic variation in the parasites or pathogens for infectivity and that there is genetic variation in the host population for resistance to specific strains of parasites (Lively 1992). Such genetic variation has been shown for different host-parasite systems (Burdon 1980, de Nooij and Van Damme 1988, Lively et al. 1990, Grosholz 1994);

2) that there is parasite mediated selection against common genotypes. Studies have shown that parasites track common hosts and that parasites develop local adaptation (Antonovics and Ellstrand 1984, Lively 1989, Dybdhal and Lively 1995b, Lively 1996, Lively and Jokela 1996, Dybdhal and Lively 1998, Lively and Dybdhal 2000b, Dybdhal and Krist 2004). In addition, increasing genetic diversity in a population has been shown to reduce the risk of infection among individuals (Lively et al. 1990, Baer and Schmid-Hempel 1999).

3) that the parasites must have a strong negative effect on host fitness (Howard and Lively 1998). Parasites have been shown to have a negative impact on host reproduction (Read 1990, Loye and Zuk 1991), growth rate and subsequent adult size (Flynn 1973, Symons et al. 1982) and survival. In lizards, parasites can cause integumental lesions (Goldberg and Bursey 1991), and lizards with parasites have had poorer body condition (Dunlap and Mathies 1993, Sorci and Colbert 1995), increased mortality (Sorci and Colbert 1995), reduced social status (Dunlap and Schall 1995), lower reproductive output (Sorci et al. 1996), a potential reduction in predation efficiency (Moritz et al. 1991), slower running speed (Oppliger et al. 1996, Main and Bull 2000), less endurance and smaller home ranges (Main and Bull 2000) and poorer competitive ability (Schall 1992) than those lizards without parasites.

Given these assumptions, the central prediction of the Red Queen Hypothesis is that asexual hosts should be more prone to infection by pathogens and parasites than sexual hosts. Direct comparison of parasite loads of several syntopic asexual and sexual taxa have found that parasitism is higher in asexual than sexual

individuals (Lively et al. 1990, Moritz et al. 1990, Hakoyama 2001, Kearney and Shine 2005).

Additional studies on asexual and sexual fresh water snails (*Potamopyrgus antipodarum*) have tested the prediction of the Red Queen Hypothesis that the prevalence of sex is correlated with the risk of infection (Lively 1987, Lively 1992, Jokela and Lively 1995). These studies suggest that parthenogens have been successful at replacing sexual individuals in areas where parasites were rare, and parasites have prevented clones from replacing sexual populations in those areas where the risk of infection is high (Lively 1992).

The Red Queen Hypothesis also provides a mechanism whereby multiple clones can coexist (Hamilton et al. 1990, Howard and Lively 1994), since it predicts temporal dynamics in clonal composition, where the most common clones alternate depending on the differences in the relative parasite pressure (Antonovics and Ellstrand 1984). Thus parasites prevent the long term dominance of a single clone.

At Bundey Bore, the RP3 parthenogen was more commonly encountered than the WP parthenogen in all three years of the study (based on capture rates; 2000- WP=10, RP3=13; 2001- WP=7, RP3=15; 2002- WP=11, RP3=13), suggesting that at the time of the study the RP3 parthenogen was the most common asexual form at Bundey Bore. Furthermore, genetic analysis has indicated that the WP lineage is highly heterozygous while the RP3 lineage exhibits lower levels of clonal diversity (Adams et al. 2003). Heterosis has been hypothesised to increase host resistance to parasites (Potts et al. 1991, Ritte et al. 1991). The higher abundance of, and lower genetic diversity within, the RP3 lineage may render RP3 parthenogens more susceptible to parasite infection than the less abundant more genetically diverse WP parthenogens.

Since the development of the Red Queen Hypothesis, several authors have argued that frequency-dependant selection, by itself cannot eliminate parthenogenetic lineages (Lively and Howard 1994, Judson 1997, Lythgoe 2000). In order to generate an advantage to the sexuals great enough to overcome the two-fold

reproductive cost of sex, the Red Queen needs to work in conjunction with some other factor such as competition for resources (Hamilton et al. 1990, Ladle et al. 1993) or mutation accumulation (e.g. Muller's Ratchet) (Howard and Lively 1994, 1998, West et al. 1999).

Hypotheses, Aims and Predictions

The aim of this study was to test the Red Queen Hypothesis as a mechanism contributing to the maintenance of sexual reproduction in *Menetia greyii* at Bundey Bore by addressing the following three questions;

1) Are the parthenogens more susceptible to infection by parasites than the sexuals?

I predicted that either the WP parthenogens and / or the RP3 parthenogens will have a higher endoparasite infestation rate than the sexual subpopulation.

2) Are the parasites infecting the most common genotype within the population?

I predicted that the more common RP3 parthenogens will exhibit higher levels of parasite prevalence than the WP parthenogens.

3) Does parasite infestation have a negative impact on the fitness of the host?

I predicted infected lizards would have lower fitness than uninfected lizards.

Methods

A total of 60 *M. greyii* were tested for endoparasite infestation. This included 12 males, 13 sexual females, 16 WP parthenogens and 19 RP3 parthenogens. Lizards were tested for the presence of gut endoparasites by examining the scats of individual lizards. Endoparasites include those parasites that are confined within the hosts body, and include protozoans, digeneas, cestodes, nematodes and acanthocephalans.

Field scats were collected from individuals caught in the 2002 and 2003 seasons. When caught, each lizard was placed in an individual 'holding container' awaiting transportation to Flinders University. These containers were checked every two

hours each day for four days until two scats were collected for each lizard. Parasites often have intermittent passage, therefore to increase the probability of finding organisms it is suggested that 2-3 scat specimens, collected at 2 to 3 day intervals, should be examined for field samples (Garcia 2003). Only those lizards that produced two scats before being given their first feed in the laboratory (4-5 days after capture) were utilised.

Scats were collected using forceps that were cleaned with alcohol after each collection. Each scat was placed into an individual centrifuge tube and the tube was labelled with the lizard number and date. The scats were preserved in SAF fixative within one hour of passage (Yang and Scholten 1977). An equal volume of 1X concentrated SAF fixative was added to each scat suspension. SAF will preserve helminths, eggs and protozoan with minimal shrinkage (Yang and Scholten 1977).

Scats were scanned for endoparasites using a direct wet preparation smear and sedimentation technique (Garcia 2003). For diethyl ether sedimentation, a suspension of 8 ml of scat (scat + SAF) layered with 2 ml of diethyl ether, was capped and shaken vigorously for 1 minute. The suspension was then centrifuged at 500 x g for 2 minutes. Supernatant fluid was discarded and the pellet examined microscopically. Each suspension was then passed through a 50 mm diameter stainless steel filter with a 30 µm mesh, to remove any extraneous particulate matter. The filtrate was collected in a 10 ml plastic centrifuge tube and allowed to sediment for 10 minutes before removing the top 8 ml of the suspension. The remaining 2 ml of sediment was resuspended to 8 ml with distilled water then layered with 2 ml of diethyl ether. The tubes were capped and shaken vigorously for 1 minute followed by centrifugation at 500 x g for 2 minutes (Garcia 2003). The supernatant fluid was discarded and the remaining pellet was suspended in one drop of 10% Lugol's iodine (Garcia and Bruckner 1993) then examined microscopically.

The endoparasites were recorded as helminthes or protozoa, but were not identified to species or genus. No attempt was made to quantify the infection intensity. For the purpose of this study, each individual lizard tested was either

scored as 'not infected' or 'infected'. A score of 'not infected' indicated that both of the scats collected from that lizard contained no endoparasites, while a score of 'infected' indicated that one or both of the scats from that lizard contained one or more endoparasites.

Statistical Analyses

Fisher's exact test was utilised to compare parasite prevalence between each pair of taxa.

Results

Parasite Prevalence

Two major kinds of endoparasites, helminth worms and protozoa, were found within the scats of *M. greyii*. Examples of some of these parasites are shown below in Figure 7.1.

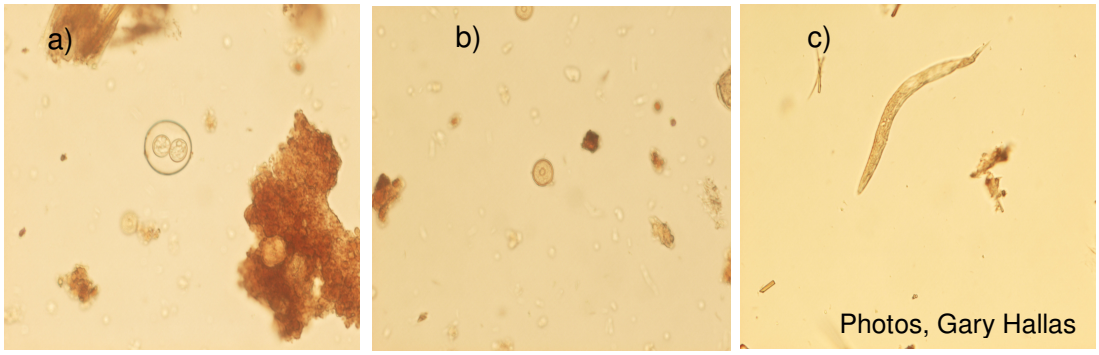


Figure 7.1. Plates of parasites identified within the scats of Menetia greyii*; a) Eimeria (protozoa), b) Entomoeba Cyst (protozoa) c) worm (helminth). a) and b) 40X, and c) 20X)*

Only one lizard, a WP parthenogen was infected with both kinds of parasites. Half of the remaining infected WP parthenogens were infected with protozoa and the other half were infected with helminths. Only helminths were detected in the scats of sexual *M. greyii*, while only protozoa were detected in the scats of RP3 parthenogens (Table 7.1).

Table 7.1. Number of males, sexual females, WP parthenogens and RP3 parthenogen infected with helminthes, protozoa or both forms of parasites.

Lizard Type	N	# lizards infected with;		
		helminths	protozoa	both parasites
Male	12	1	0	0
SAS female	13	2	0	0
WP	16	3	3	1
RP3	19	0	3	0

Are the parthenogens more susceptible to infection by parasites than the sexuals?

For analyses both kinds of parasites detected were pooled and the lizards were scored as either 'infected' or 'not infected'.

Sexual males and sexual females did not differ significantly in prevalence of parasite infection (two-tailed Fisher's exact test, p=1.000), therefore males and sexual females were pooled as 'sexuals'.

Prevalence of endoparasite infection of sexual and parthenogenetic *Menetia greyii* at Bundey Bore is shown in Table 7.2.

Table 7.2. Number of sexual (males and females pooled), WP parthenogen and RP3 parthenogen M. greyii *with endoparasites.*

Taxa	n	INFECTED		Proportion of lizards parasitised (%)
		No	Yes	
Sexuals	25	22	3	12
WP parthenogens	16	9	7	43.8
RP3 Parthenogens	19	16	3	15.8

When comparing sexuals and RP3 parthenogens, there was no significant difference in the proportion of individuals infected with endoparasites (two-tailed Fisher's exact test, p=1.000).

WP parthenogens had a significantly higher prevalence of endoparasites than sexuals (two-tailed Fisher's exact test, p=0.030).

Are the parasites infecting the most common genotype within the population?

RP3 parthenogens exhibited a lower parasite prevalence rate than WP parthenogens (15.8% Vs 43.8%) (Table 7.2). However, this difference was not significant (two-tailed Fisher's exact test, p=0.132).

Does parasite infection have a negative impact on the fitness of the host?

Sprint speed is generally supposed to be a fitness-linked trait in reptiles (Bennett and Huey 1990). Due to the high rate of infestation of endoparasites shown in WP parthenogens, sprint speed was compared between infected and uninfected animals of the WP lineage to determine if there is a fitness cost associated with higher parasite loads. Nine of the 16 WP parthenogens tested for parasite infestation were also tested for sprinting ability in Chapter 5. Five of these WP parthenogens were infected, while four were not infected. Maximum velocity (Vmax) was compared between infected and uninfected individuals (Figure 7.2).

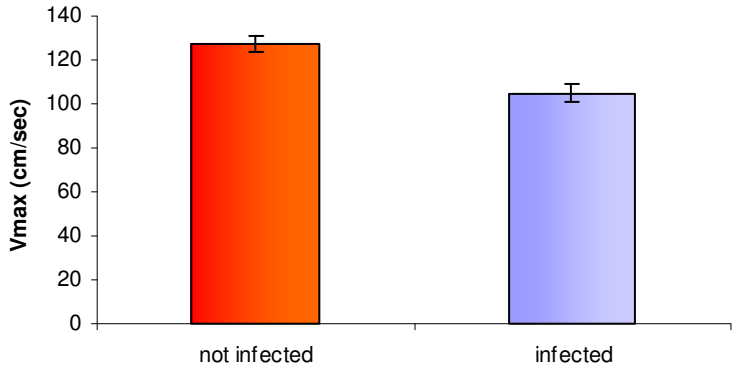


Figure 7.2. Maximum sprint speed (Vmax) (±SE) achieved by infected and uninfected WP parthenogens.

Results showed that WP parthenogens infected with endoparasites ran significantly slower than uninfected WP parthenogens (t-test for independent samples t=3.953, n=9, p= 0.006). However, the sample size was small for this comparison and the result should be taken conservatively.

Conclusion

Endoparasites were more prevalent in the WP parthenogens than sexual *M. greyii* at Bundey Bore. In addition parasite infestation causes a reduction in maximum

sprinting ability in WP parthenogens. These results are consistent with the Red Queen hypothesis.

However, endoparasite infestation was not more prevalent in RP3 parthenogens than WP parthenogens suggesting that the parasites were not tracking the most common host genotype in the population as predicted under the Red Queen. Possible reasons for this outcome are discussed below.

Discussion

Are Parthenogens more susceptible to endoparasite infestation than sexuals?

As predicted under the Red Queen hypothesis, one of the parthenogens, WP, did exhibit higher endoparasite infestation than the sexual taxon. However, it can not be conclusively said that this difference in parasitism is attributable solely to parthenogens being more susceptible than sexuals to parasites, since we have not specifically tested whether susceptibility to endoparasites is genetically based. It is also possible that non-genetic environmental or physiological factors (or a combination of genetic and non-genetic factors) influence the outcome of host-parasite interactions (Little and Ebert 2000). Trade-offs between immune defense and other fitness components might lead to greater infection in hosts. Such tradeoffs have been demonstrated in a variety of systems (Sheldon and Verhulst 1996, Martens and Schon 2000, Pioiani et al. 2000, Rigby et al. 2002). It is possible that WP parthenogens at Bundey Bore have invested more energy than sexuals into physiological performance (in Chapter 5, WP parthenogens were shown to be significantly faster than the other forms), or competitive ability (WP parthenogens were found to be competitively superior to sexuals in chapter..), which renders them more susceptible to parasite infection due to a trade-off between competitive ability or physiological performance and resistance to infection.

Are parasites tracking the most common host genotype?

At the time the study was conducted, RP3 parthenogens were the most common host genotype at Bundey Bore. However, a greater number of WP parthenogens were infested with endoparasites than RP3 parthenogens, although this difference was not significant. This lack of a significant difference may be due to the small

sample size, or due to the timing of the study. The WP lineage is the most geographically widespread of the *M. greyii* parthenogenetic lineages studied to date (Adams et al. 2003), and therefore, on a broader geographic scale is the most common host genotype in *M. greyii*. The host-parasite system is a time-lagged process and therefore the susceptibility of parthenogens should be cyclic. Therefore, since the second most common parthenogen was generally higher in infection rate, this result may be an indirect indication of a time-lagged, parasite-host dynamic. It may be that the more widespread WP parthenogen may have been more frequent in the past and the most common genotype at Bundey Bore, but had been driven down in number due to parasite infection, while the rarer RP3 parthenogen was becoming more abundant, and the parasites as yet have not caught up with it. A similar result was found by (Michiels et al. 2001) in parthenogenetic flatworms. Alternatively, I only examined the presence of gut endoparasites. These lizards may also be infested with other parasites, although no ectoparasite mites were ever observed.

Do parasites cause a large enough reduction in fitness to compensate the 2-fold cost of sex?

Parasite infestation in the WP parthenogens was shown to coincide with a reduction in sprint speed ability. A similar fitness cost has been shown in other lizard species (e.g. *Tiliqua rugosa* (Main and Bull 2000)). Sprinting is often used by lizards to escape predators (Hertz et al. 1988), and due to their small size, *M. greyii* potentially form part of the diet of several predators including other lizards, birds and small or juvenile snakes. Therefore, a reduction in sprint speed could result in an increase in mortality due to predation. Sprint speed may also be important in social interactions. In Chapter 6, chasing was identified as one of the most aggressive behaviours observed in staged encounters between sexual and parthenogen *M. greyii* and may have partly contributed to the dominance of WP parthenogens over sexuals. Therefore a reduction in sprint speed may cause a reduction in competitive ability. However, whether these costs to asexuals are large enough to compensate the two-fold reproductive cost of sexuals is difficult to gage. WP parthenogens were found to be significantly faster than the other *M. greyii* forms at Bundey Bore (see Chapter 5), therefore a reduction in sprint speed may not render them slower than the sexuals. Although parasitism may cause a

reduction in chasing ability, it is unlikely that this would cause a large effect on competitive ability as sprint speed is unlikely to be an important component of the other highly aggressive behaviours observed including biting, wrestling and jaw locking. However, reduced sprint speed may be symptomatic of reduced vigour in other activities, such as fighting. Therefore a reduction in sprint speed due to parasitism is unlikely to cause a large enough increase in mortality due to predation or reduction in competitive ability to compensate for the two-fold cost of sex. Alternatively, it is possible that parasite infestation may cause an alternate fitness reduction that may compensate the sexual taxon to a higher degree.

Conclusion

Although inconclusive, these results suggest a possible role of parasites in the maintenance of sex within *Menetia greyii*. This theory is discussed further in Chapter 8.

Chapter 8
General Discussion

Summary of results

We examined ecological, physiological and morphological niche relationships in parthenogenetic and sexual forms of *M. greyii* in an attempt to determine differences between individuals of each reproductive mode that might reduce competition and allow the apparent observed coexistence.

Similarities Between Reproductive Modes

Results suggested that the four types studied are morphologically and ecologically similar, overlapping extensively in time, space and physiological niche dimensions. The potential use of similar habitats suggested by the field data was supported by the laboratory study in which sexual and parthenogen *M. greyii* showed the same habitat selection with respect to ground cover and light intensity. Additionally, there was very little difference in thermal biology detected among the four types, a factor that largely restricts habitat use (Schall 1977, Grant and Dunham 1988). For example, Adolph (1990) found that *Sceloporus occidentalis* and *S. graciosus* converged on similar microhabitats in sympatry, because both species responded similarly to the thermal conditions characteristic of the habitats. Likewise, microhabitat differences between some sympatric *Anolis* lizards reflect differing temperature preferences (Roughgarden et al. 1981). Further to this, a major proportion of the ecological and behavioural activities of animals is linked with morphology (Pianka and Pianka 1976), suggesting that ecological segregation may be limited in this morphologically similar complex.

My study failed to find any major differences among the different taxa that would indicate they are partitioning resources and could explain how the sexual and parthenogenetic forms are coexisting. Similarity in key ecological traits has been found in other studies comparing sympatric sexual and asexual forms (Echternacht 1967, Medica 1967, Casas-Andreu and Gurrola-Hidalgo 1993,

Jokela et al. 1997a, Jokela et al. 1997b, Paulissen 2001). As a consequence of these similarities, the study also failed to find conclusive evidence supporting any of the hypotheses explaining coexistence between sexual and parthenogenetic animals due to differences in resource use. This included hypotheses based on the generalist view (General Purpose Genotype and Spontaneous Heterosis hypotheses) and the specialist view (Frozen Niche Variation and Tangled Bank models).

In addition to similar resource use, sexual and parthenogenetic females within the study population differed very little in their reproductive effort and output, indicating that RP3 and WP parthenogens possess a reproductive advantage over sexual females as a result of not having to produce males (Williams 1975, Maynard-Smith 1978, Bell 1982). For the sexual females, assuming the observed bias in the sex ratio is real, this means realising a lifetime production of more than one, but something less than two viable offspring compared to the one for the parthenogen. The evidence from chapter 4 of similar reproductive success of gravid females of the two reproductive modes raises the question of how the sexual type compensates for having some portion of each litter comprising males that don't themselves produce offspring.

Superimposed on that, parthenogens may gain an additional advantage over sexuals from faster sprint speeds to escape predators. Moreover, parthenogens were behaviourally dominant to sexuals and showed competitive superiority when competing for food items.

These factors together would suggest that the parthenogens should exclude the sexuals from Bundey Bore. Despite this, the parthenogenetic females at Bundey Bore do not outnumber the sexual subpopulation. This raises the question of how the sexual taxon is persisting, and what allows the two reproductive modes to coexist?

If we consider the models of ecological coexistence within the Lotka -Volterra framework (Pound *et al*. 2002), then the intrinsic two-fold cost (or in this case possibly a cost slightly less than two-fold) to the sexual populations growth rate is

reduced due to density regulation of recruitment. Although the realised lifetime production of offspring shows a two-fold difference even at the coexistence equilibrium (each sexual female producing two offspring in a 1:1 sex ration, for each parthenogens single offspring), the cost of this difference is less than two-fold under density-regulated recruitment. The realised cost of males can be very small for productive species (e.g. Daphnia: Tagg et al. 2005), because parthenogens must compete for limited recruitment opportunities not only with the sexual type but also amongst themselves.

In this study the cost may be met in competitive release provided by one or more of the small differences observed between sexual and parthenogenetic *Menetia greyii*. These differences included: the sexuals posses a slightly broader niche than the parthenogens (Chapter 3), the sexuals posses a shorter incubation time than the parthenogens (Chapter 4), the slight differences in microhabitat and activity (Chapter 5) or the lower susceptibility to parasites observed in sexuals compared to parthenogens (Chapter 7). The latter difference is discussed in more detail below.

Parasites are reducing numbers of parthenogens,

Coexistence could still occur, even if competition was intense, if dominant parthenogen taxa were maintained at low densities by some other factor. Climate, parasites or predators can maintain levels below the carrying capacity of resources, reducing the importance of competition.

Although inconclusive, results suggested that sexual reproduction in this population of *M. greyii* may be maintained, at least in part, by parasites. WP parthenogens suffered a significantly higher parasite load than sexual individuals, and parasite infestation was shown to cause a reduction in fitness of the host. Thus parasite infestation may maintain parthenogen numbers at a low enough capacity to render competition unimportant and may prevent the parthenogens from completely eliminating the sexuals at Bundey Bore.

RP3 parthenogens also had higher numbers of parasites than sexuals, although the difference in parasite load was not significant. This may have been due to the

small sample size, or alternatively, it may have been evidence that parasite-mediated selection was also contributing to the maintenance of local clonal diversity. The infection rate in WP and RP3 lineages may be oscillating over time, preventing the long term dominance of a single clone.

In addition to maintaining numbers of parthenogens, higher parasite rates may also reduce the competitive dominance of parthenogens due to their effect on the fitness of the host. Under stressful conditions, such as intense competition, the greater infection rate in the parthenogens could have a negative impact on the health of the parthenogens and reducing their performance in contests with sexuals (Hamilton et al. 1990).

However, parasite load alone does not accurately predict that WP parthenogen *M greyii* are more prone to infection because of their clonal mode of reproduction. They may be more infected because they trade-off parasite resistance with aggressiveness and competitive ability. Alternatively, aggression may result in the production of immunosuppressive hormones (Moore et al. 1991) and consequently cause an increase in parasite infestation in the parthenogens. Determining if parthenogen *M. greyii* are more prone to infection than the sexuals due to their parthenogenetic mode of reproduction is important in assessing if the Red Queen Hypothesis is a plausible explanation for coexistence in this system.

Alternatively, the cost may be met by the sexuals, or coexistence may be allowed through other means discussed below, some of which were not tested in the current study. These include:

Higher Juvenile or Adult Survival in the Sexuals

Since both types have similar frequency of reproduction, the sexual females may compensate for their lower intrinsic capacity for population growth by realising a relatively higher juvenile or adult survival. Survival advantages could accrue through a number of factors including competitive dominance (unlikely due to the results of the current study -Chapter 6), better evasion of predators, superior efficiency in resource exploitation or lower susceptibility to parasites (as discussed above).

Better evasion of predators seems unlikely since in this study, rate of tail loss was similar for both sexuals and parthenogens indirectly suggesting that rates of predator avoidance is similar in both reproductive modes. Results suggest that due to their higher sprint speed ability parthenogens may in fact be better able to avoid predators than sexuals.

While in this study, parthenogens expressed superior interference competitive abilities, the sexual population may express superior exploitation capabilities that would allow them to better utilise resources.

Destabilising Hybridization is reducing reproductive output in the parthenogens

The presence of tetraploid males (SASmt) in the population suggests that mating between sexual males and WP parthenogens may be happening and is leading to the production of offspring. This would result in the WP parthenogens having a reduced representation of parthenogen offspring in the next generation, and suggests that the WP parthenogens are potentially suffering a disadvantage due to destabilising hybridization (Lynch 1984). Destabilising hybridization happens through the occasional matings of parthenogenetic lizards by their sexual congeners which leads to higher levels of polyploidy and sterility (Cueller 1977). This may also be occurring with RP3 parthenogens, but as yet has not been identified. Destabilising hybridization has been cited in other parthenogen / sexual systems as a potential method for sexually reproducing individuals to, at least, reduce the two-fold reproductive advantage of the parthenogens. Examples include the geckos *Heteronotia binoei* (Whittier et al. 1994) (Moritz 1984), and *Lepidodactylus lugubris* (Hanley et al. 1994).

Although this behaviour must reduce the reproductive output of WP parthenogen females to some extent, tetraploid males appear to be rare in the population and it seems unlikely that this cost alone would balance the potential two-fold reproductive disadvantage, but it may be a contributing factor.

Alternatively, coexistence may be occurring for reasons that were tested but went undetected in the current study, such as:

The potential advantages to the sexuals or disadvantages to the parthenogens discussed above would also have to counteract the behavioural dominance exhibited by the parthenogens (Chapter 6). If this behavioural dominance is expressed in free-ranging *Menetia*, it could substantially raise the level of competitive release required for persistence of sex.

The sexuals and parthenogens are partitioning resources, but it was not detected.

Another possibility is that the sexuals and parthenogens are partitioning resources, but it was not detected in this study. It may be that, in the field, there are habitats within each of the areas searched, upon which the different forms might specialise, but the existence of these microhabitats is not obvious at the present time. Results were based on capture rates and therefore may not be a true indication of the habitat use of the different forms. Alternatively, the measures necessary for detectable resource partitioning may involve factors not considered in this study, for instance, differences in seasonal activity. Or it may be that to detect differences, niche dimensions need to be examined on a finer scale. For example, sprinting ability was measured over a range of temperatures separated by 5^{o}C, it may be that we needed to conduct it at a range of temperatures separated by 2^{o}C. Also, much of the study was based on data collected in the laboratory, which may not truly reflect what is going on in nature. Due to the difficulty with studying this small cryptic species in the field, investigations based purely on field studies would be difficult to undertake.

Competition levels are low or competition is not occurring (i.e. populations below carrying capacity)

A possibility for why parthenogen forms do not appear to outnumber sexual forms at Bundey Bore, at the present time, is that interference competition is not occurring, or interference competition is occurring, but has not yet reached a level where the parthenogens have complete monopoly. It may be that none of the resources for which these types compete has been in short enough supply to produce intense competition. Interestingly, the field component of this project ran over three years (2000-2003), one of which (2002) was a drought year. In the year following the drought year (2003), parthenogen numbers remained steady, while capture rates of sexual males and females was greatly reduced. One potential

theory for this is that, due to the drought, food became a limited resource in 2003 resulting in intense competition for prey among the taxa. Perhaps then, in the 2003 season, the behaviourally dominant parthenogens were able to outcompete the sexuals for the limited food available, resulting in the maintenance of numbers of parthenogens, but a reduction in the number of sexuals. If this is the case, then the sexual taxa may have persisted at Bundey Bore because food has not become limited for a sufficiently long period of time to cause their elimination by the competitively superior parthenogens. Dunham (1980) found a similar result in competing iguanid lizards, and predicted intense competition should occur in years in which lizard populations experience a reduction in prey availability induced by drought. Mortality due to drought has also been found to influence population size in *Cnemidophorus* lizards (Fitch 1958). Alternatively, adult sexual *M. greyii* may be more prone to dehydration than parthenogen adults. Or the eggs of sexuals may be more susceptible to dehydration than parthenogen eggs thus reducing recruitment in the sexual subpopulation. To determine if the fluctuations in abundance observed at Bundey Bore are due to the parthenogens competitively excluding sexuals from food, a study of the abundance of each of the taxa over a period of time and correlating this with climatic conditions and food abundance could be undertaken.

When competition between sexual and parthenogen *M. greyii* is prompted by such resource shortages, the limits of the respective ecological niches of sexual and parthenogen *M. greyii* may become more apparent and ecological differences may occur that were not detected in this study. For instance, food habits might be altered, or a shift in time at which one taxon is active might occur.

In Summary

The results appear to suggest that, at least in this population, the parthenogen lineages have a competitive and reproductive advantage over the sexuals. The sexuals may counteract this (at least with the WP parthenogen) through destabilizing hybridization, greater resistance to parasite infestation or through the minor differences detected in ecology. In the short-term, this may allow coexistence between sexual and parthenogen *M. greyii* at Bundey Bore. In the longer-term one of the following could occur at Bundey Bore. Firstly, coexistence

could be stable in which case, differences in resource utilisation may become apparent between the reproductive modes. If coexistence is stable between parthenogen and sexual *Menetia* it would be expected that other mixed assemblages would occur across the geographical range of *M. greyii*. Secondly, coexistence may be dynamic, and eventually either the parthenogens would eliminate the sexuals or the sexuals would eliminate the parthenogens from Bundey Bore. If an important resource such as food becomes limited for a sufficiently long period of time, the parthenogens may be able to eliminate the sexuals if the determining factor is aggression and dominance. If parasites and destabilising hybridization allow coexistence to occur for a sufficient amount of time, the accumulation of mutations (for example, by Muller's ratchet), may eventually cause the demise of the parthenogens. If one form is likely to replace the other, then coexistence between sexual and parthenogen forms is unlikely to be a common trait in the *M. greyii* complex. Determining the outcome would require a longer term study that examines the abundance of each of the taxa, and determining how the dynamics change over time.

Although this study is limited in temporal and geographical scope, I hope that the data has provided some knowledge of the basic ecological, behavioural and physiological characteristics of sexual and parthenogen *Menetia greyii*, and provided some insight into the interactions of sympatric parthenogen and sexual *Menetia*. More notably, I hope that this study will prompt many more questions regarding the ecological properties and interactions of parthenogen and sexual *M. greyii*, and as a result research will continue on this intriguing complex. Below, I outline just some of the many possible future studies that could be undertaken on the *M. greyii* complex.

It is worth noting that estimation of competitive impacts requires clearly distinguishing intrinsic attributes from those realised in the presence of competition. Described results are a mixture of the two. Logistical difficulties often prevent direct measurement of competition from the comparison of realised to intrinsic measures. The resulting interpretive weakness should be acknowledged and the limitations to evaluating the role of competition.

Future Directions

An important component of examining asexual and sexual organisms is having a strong genetic background for the complex. Therefore, a major part of future work should be further investigation into the genetic relationship of the different forms across the entire range of *M. greyii* in Australia. This includes determining the number of distinct sexual and parthenogen lineages present within the complex, and the potential ancestral parental species for the different parthenogens.

This would allow the ecological comparison of sexual and asexual *M. greyii* taxa from both an evolutionary and ecological perspective. An evolutionary approach would involve comparing parthenogens with the sexual forms which gave rise to them. An ecological approach would involve comparing parthenogens with the sexual forms they either coexist with, (or occur in local allopatry with) irrespective of their evolutionary relationships. This would also allow for the determination of whether coexistence between sexual and parthenogen forms is widespread in this complex, or whether the coexistence observed in this study was unusual for *M. greyii*, and perhaps just an artifact of timing (i.e. one form had not yet eliminated the other).

Geographical Parthenogenesis

- Determine the geographical distribution of the different sexual and parthenogen *M. greyii* lineages. Ascertain if this complex displays a similar pattern of geographical parthenogenesis as was seen by Kearney et al. (2003) in their study on several parthenogenetic and sexual complexes within the arid interior of Australia.

Spontaneous Heterosis

- The higher levels of heterozygosity seen in the WP and RP3 parthenogens resulted in superior physiological performance in comparison to the sexuals. For a more robust test of heterozygosity the parthenogens should be compared with their parental species.

Demographics

It is also important to determine a life table for the sexual and parthenogenetic forms. For example, as mentioned in Chapter 4, a key to the persistence of sexual taxa at Bundey Bore may be the survivorship of females (an unexplored variable). Field enclosures could be used to examine the long-term demographics of sexuals versus parthenogens.

There may also be substantial differences between juveniles of each reproductive mode that went undetected in this study, which warrants further investigation.

Resource Partitioning

- Examine the differential use of resources across several mixed populations (if they occur) of sexual and parthenogen *M. greyii*. If possible, also compare these results with sexual and parthenogen lineages occurring in allopatry. This will give an indication of firstly, whether resource partitioning is a factor in the observed coexistence, and in what way it is influencing coexistence.
- If differences in niche utilisation are detected, then the General Purpose Genotype and Frozen Niche Variation hypotheses can be further investigated. Are parthenogenetic *M. greyii* individuals ecological generalists relative to sexuals? Or are parthenogens more specialized relative to sexuals?

Competition

- The current study only investigated interference competition. Further study could attempt to measure exploitation competition and total resource competition (exploitation plus interference).
- Evidence of the presence or absence of competition can require controlled field experiments in which one species is removed and the response of the other species is noted. Since this would be very difficult with *Menetia*, laboratory based arenas that mimic natural conditions could be used.
- In a similar vain, through manipulation, competition could be introduced into laboratory based colonies (for example by increasing lizard densities

or reducing food). In such a study, the limits of the respective ecological niches of sexual and parthenogen *M. greyii* may become more apparent and ecological differences may occur that were not detected in this study. For instance, food habits might be altered, or a shift in time at which one taxon is active might occur. Experiments manipulating food abundance can also test the mutational deterministic model (MD). Lively et al. (1998) tested this model by performing an experiment that relies on the prediction that mutation load at mutation-selection balance should respond to variation in the harshness of the environment (Kondrashov 1995). If sex is maintained under the MD model, clones should suffer more under severe starvation stress than sexuals, and a decrease in the proportion of clonal individuals should be observed (Lively et al. 1998). A similar experiment could be performed in *Menetia*.

- Given the possible differences in aggression of WP and RP3 clones observed in the current study, it would be interesting to examine among- versus within- clone aggression of these two forms.
- To investigate the interspecific competition model proposed by Doncaster et al. (2000) and Pound et al. (2002 and 2004) both intra-specific competition (competition between individuals within a sexual lineage, and competition between individuals within a parthenogen lineage) as well as inter-specific competition (competition between the sexual and parthenogen lineage) should be examined.
- Determine if dominance is a common trait in *Menetia* parthenogens, by examining the competitive abilities of other sexual and parthenogen lineages across a range of habitats. This can then be correlated with the biogeographical distribution of *M. greyii* populations. A similar experiment was done in *Artemia*, where the competitive hierarchy was found to be Old World sexual < parthenogen < New World sexual (Browne and Halanych 1989). Biogeographic distribution supported this, where in the New World reproduction was purely sexual but in the area of the world where Old World sexual and parthenogens are both found, parthenogens dominate (Browne and MacDonald, 1982).

- Investigate the Impact of competition on clonal diversity. Does the aggressiveness of WP and RP3 parthenogens also provide these lineages with an advantage over other parthenogenetic *Menetia* lineages? If so, it may prevent the establishment of other parthenogen lineages in areas where WP and RP3 parthenogens occur.

Parasites

Determining if a higher prevalence to infestation is due to their parthenogenetic mode of reproduction

- One method of testing this would be to determine if there is a correlation between competitive ability and endoparasite infection.
- Another method would be to investigate the correlation between parasite load and parthenogenesis on a geographical scale. In areas with high parasite densities, sex is expected to prevail and any parthenogen forms arising should quickly acquire high parasite loads, leading to local extinction. When parasite density is low, the costs of sex outweigh the benefits and parthenogens should thrive (Jokela and Lively 1995). This will also test if parthenogens are more susceptible because they are hybrid and polyploidy rather than due to their mode of reproduction.
- Lively and Dybadhl (2000b) tested this in freshwater snails by comparing the susceptibility of infection of rare and common clones when exposed to sympatric, allopatric and hybrid sources of parasites. The trade-off hypothesis would predict that the most common clones would be significantly more infected than rare clones, independent of the source of parasites. The Red Queen Hypothesis predicts common host genotypes would be more susceptible to only the sympatric source of parasites. A similar experiment could be performed with *Menetia*.

Other studies on parasite susceptibility

- Determining whether parasites are tracking the most common genotype, by comparing parasite loads across several populations containing both sexual and parthenogenetic *M. greyii*.
- Acquire a greater knowledge of the fitness effects of parasite on the host. This could involve experimental manipulation of parasite load.

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