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# Reproductive Ecology and Impact of the Invasive Praying Mantis *Miomantis caffra*

Murray Peter Fea

A thesis submitted in fulfilment of the requirements for the degree of Master of Science in Biology,  
The University of Auckland, 2011

# Abstract

This thesis concerns the two species of praying mantis in New Zealand, the introduced *Miomantis caffra* and native *Orthodera novaezealandiae*. The aims of this research are to: 1) predict the potential future distribution of *M. caffra* in New Zealand and to test the modelling procedure used for this purpose, 2) examine the influence of relatedness and body mass on the rate of cannibalism in juvenile *M. caffra* and 3) assess the potential for impact of *M. caffra* upon *O. novaezealandiae*. The first of these goals was approached using the computerised species distribution modelling package Maxent, as well as a field test of *M. caffra* ootheca viability in the South Island. The second was examined by captive observation of *M. caffra* nymphs in groups with differing body mass and relatedness. Y-maze experiments were used to assess the possibility of heterospecific attraction and mating observations were carried out to quantify copulatory cannibalism and examine the possibility of interspecific impact. Modelling results suggest that *M. caffra* will be able to colonise much of the eastern half of the South Island and assessment of Maxent indicates that it is robust to low levels of input data, supporting its usefulness as a tool for predicting the spread of invasive species. The test of oothecae indicate that these are resilient to most of the winter conditions which the New Zealand environment presents and consequently should be able to facilitate the widespread dispersal of *M. caffra*. It was found that juvenile *M. caffra* do not show kin-biased discrimination in their cannibalism, although this was influenced by size heterogeneity. The males of *O. novaezealandiae* are attracted to heterospecific females, more so in fact than conspecifics, a behaviour which exposes them to the risk of copulatory predation from *M. caffra*, which was found to be commonplace. This identifies a possible mechanism for the purported displacement of *O. novaezealandiae* by *M. caffra* and suggests that *M. caffra* is a threat to *O. novaezealandiae*, possibly responsible for the widespread decline of the former in New Zealand and likely to cause further loss of *O. novaezealandiae* abundance in the future.

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# 1. General Introduction

## 1.1 Invasive species

Exotic organisms that establish and spread in new environments are currently one of the greatest threats to global biodiversity (Park, 2004; Ficetola, *et al.*, 2007). These cause diverse impacts in their introduced ranges, often with disastrous consequences for the native biota there (Wilcove, 1998). Such organisms have played a key role in the decline of many New Zealand species from a wide range of taxa (Brockerhoff, *et al.*, 2010). Here the definition of Falk-Peterson *et al* (2006) will be used, describing invasive organisms as “established and are expanding their range in an area where they previously did not occur” (Falk-Petersen, *et al.*, 2006 pp. 1415). Of these pests, invasive invertebrates are among the most threatening, due to their ease of transport (accidental or otherwise), cryptic nature and potential to reach large numbers rapidly and unnoticed (Mack, *et al.*, 2000).

The main ways in which invasive organisms negatively affect their recipient ecosystem include herbivory, predation, competition with guild members and ecological engineering (Mack, *et al.*, 2000; Brockerhoff, *et al.*, 2010). Where invasive species are predatory or herbivorous, their feeding can lead to extinction of native biota simply by direct population reduction (Nuñez, *et al.*, 2009; Wilson, *et al.*, 2009). In cases of intraguild predation by invasive species, the invader receives the added benefit of reducing the populations of its competitors (Snyder & Hurd, 1995). Such impacts are often exacerbated by the naive nature of native species in regards to their introduced enemies (e.g., Taraschewski, 2006). Because they have no evolutionary experience with the new organism, they lack adaptations to defend themselves and are especially vulnerable to extirpation (Park, 2004). For example, the yellow-spotted goanna (*Varanus panoptes*) is susceptible to mortality from introduced cane toads after attempting to eat the toxic amphibians, because they have no behavioural avoidance or resistance mechanism to protect them from this new prey source (Ujvari & Madsen, 2009). This type of impact is also associated with an invasive insect: the glassy-winged sharpshooter (*Homalodisca coagulata*) in French Polynesia (Suttle & Hoddle, 2006). Native predatory invertebrates that feed on the sharpshooter succumb to what is presumed to be a chemical defence compound or toxic bacterial symbiont carried by the insect (Suttle & Hoddle, 2006). Because *H. coagulata* has reached very high densities in this region, its poisoning of a wide variety of native organisms has the potential to severely affect community structure and ecosystem

functioning. In North America the same species is also a serious pest, due to its propensity to vector the bacterium *Xylella fastidiosa* which is the cause of Pierce's disease of plants and a major threat to agriculture and natural ecosystems (Hummel, *et al.*, 2006). This species provides a good example of the range of impacts and complexity of interactions with native biota which an invasive organism can have.

In addition to primary impacts, exotic species often have indirect effects on native species, with effects proceeding through a number of intermediary species before reaching the population in question (e.g., Mattos & Orrock, 2010; Nelson, *et al.*, 2010). In some cases, the suppression of one species by an introduced enemy may release a native competitor or prey species from regulation (Fagan, *et al.*, 2002), which in turn causes new negative impacts. Exotic organisms can also compete with similar species in their introduced range, likewise driving them to extinction or causing the release of their natural enemies (Van Riel, *et al.*, 2007). This competition can also be direct (interference), indirect (by exploitation of a common limiting resource) or apparent. The latter refers to a situation where the proximal effect occurs through the action of another species, such as facilitation of a natural enemy of the native (Brockerhoff, *et al.*, 2010). For example, invasive plants can compete with natives by providing refugia for herbivores to which they are more resistant than those around them, facilitating apparent competition (Sessions & Kelly, 2002; Orrock, *et al.*, 2010).

The engineering of ecosystem processes is also a way in which an exotic species may cause significant damage (Sousa, *et al.*, 2009). For example, the mussel *Musculista senhousia* which is invasive in aquatic systems of North America, forms a dense mat of shell on the benthos, thereby altering substrate composition and complexity. This differentially affects native species assemblages, changing the structure of the benthic community (Crooks & Khim, 1999). In addition to the potential for ecological disruption, invasive species can have large economic impacts if they affect crops, livestock, human health or infrastructure, which they often do (Mack, *et al.*, 2000). Other potential causes of impact include vectoring diseases, hybridizing with natives, altering nutrient cycles and interfering with pollination systems (Brockerhoff, *et al.*, 2010; Hershberger, *et al.*, 2010; Yara, *et al.*, 2010). Because of this, invasive species are described by Walker and Steffen (1997) as the second greatest cause of biodiversity loss (only behind direct habitat destruction) occurring globally. This problem threatens to create a more homogenous global biota, consisting largely of widespread cosmopolitan species, thus reducing the diversity upon which ecosystem health and function depends (Mack, *et al.*, 2000).

### Invasive arthropod predators

Of the damaging invasive invertebrates worldwide, many are arthropod generalist predators, or AGPs (Snyder & Evans, 2006). The large number of trophic links that these species often have (Fagan, *et al.*, 2002) can make their ecological effects widespread and varied, affecting numerous taxa from different feeding guilds (Snyder & Evans, 2006; Crowder & Snyder, 2010). The main ways in which AGPs cause ecological damage include displacement of and direct feeding on native predators, altering plant community structure by suppressing herbivores and forming mutualisms with other invasive species (Snyder & Evans, 2006; Crowder & Snyder, 2010)

Such influence on native species may have consequent flow-on impacts to the entire ecosystem if the native species is a keystone organism (Park, 2004). This is often especially pronounced for insular ecosystems where the impacts on prey species are generally greater (Dulloo, *et al.*, 2002; Wagner & Van Driesche, 2010). Both these features are exemplified by the complete alteration of the Christmas Island environment by the introduced yellow crazy ant (*Anoplolepis gracilipes*). There the ant preys upon the dominant ecosystem engineer, the red land crab (*Gecarcoidea natalis*), altering forest successional structure because the crab usually suppresses seedling growth through herbivory, creating a distinct, open understory (Green, *et al.*, 1999). The yellow crazy ant also tends an (invasive) scale insect (*Tachardina aurantiaca*), the sugary excrement of which leads to outbreaks of sooty mould fungi which destroy the forest canopy (Abbot & Green, 2007). The chain reaction of impacts on this island led Green *et al* (2003) to refer to the situation as invasional meltdown, the result of the varied interactions one exotic AGP can have with multiple local species.

Another example of an AGP which affects native biota in a different way is the red swamp crayfish (*Procambarus clarkii*) which has been introduced to Spain from North America (Gil-S'anchez & Alba-Tercedor, 2002). This species was introduced in 1973 to provide commercial fishing stock and became widespread throughout the Iberian Peninsula (Habsburgo-Lorena, 1979). This crayfish is a common vector of the pathogenic fungus (*Aphanomyces astaci*) which is lethal to European crayfish species (Gil-S'anchez & Alba-Tercedor, 2002). This has caused the destruction of many Spanish populations of the white clawed crayfish (*Austropotamobius pallipes*), the only native found in the region (Holdich & Lowery, 1988). Another aquatic AGP with a different mode of impact again is the European green crab (*Carcinus maenas*), which is a successful global invader (Griffiths, *et al.*, 1992). One of the impacts this species has had is the alteration of shell morphology in prey species due to increasing predation pressure upon those with thinner shells, permanently altering these species' evolutionary trajectories (Trussel, 1996). It also impacts on its guild member the Dungeness crab (*Cancer magister*), native to the northeast Pacific, by driving juveniles from their protective habitat of benthic shell refuse. This then exposes them to greater fish and bird

predation in open areas and results in population decline (Griffiths, *et al.*, 1992). The kinds of impacts described above for these three AGPs can completely alter the composition of the biotic community in the invaded system (Van Riel, *et al.*, 2007; Chiba, 2010). The type and severity of impacts that these organisms can have are also compounded by the propensity of arthropods to reach new areas beyond their native range; there is estimated to be over 2,500 exotic arthropods in the USA alone for example (Parker, *et al.*, 1999). Insect generalist predators in particular have received disproportionately little research relative to other taxa (Kenis, *et al.*, 2009), given the widely recognized threat which they pose to native species and the large portion of the worlds exotic fauna which they comprise (Rodder & Lotters, 2010).

## 1.2 Study species

### *Miomantis caffra*

*M. caffra* is a praying mantis of the family Mantidae, native to South Africa (Ramsay, 1990). It was discovered in Auckland, New Zealand in 1978, but has since spread throughout the North Island and recently become established in Nelson, as well as being reported as present in Christchurch (I. Stringer, pers. comm.). This spread is most probably facilitated by the accidental transport of oothecae (egg cases) by humans, rather than by individual adult dispersal which is generally gradual (Ramsay, 1990). This is unsurprising as the species is commonly found in and around human structures, modified habitats and disturbed sites, often laying oothecae on or inside buildings or other structures (Ramsay, 1990).



Photo: Bryce McQuillan

Figure 1.1 Female *M. caffra* depositing an ootheca on a fence.

It is a sexually dimorphic species with females having a mean body length of 43 mm and males 40 mm. Females are also more heavily built, having larger forelimbs, strongly sclerotised and waxy forewings and vestigial hind wings, whereas adult males are slender and bear functional fore- and hind wings, although they are not strong fliers (Ramsay, 1990). Males also have more well developed ocelli and larger eyes. Both vary in colour from green to brown and possibly adapt their colouration according to their environment during development (Ramsay, 1990). They are univoltine, hatching in the spring and rapidly developing to adulthood in several months. Soon afterwards, egg laying commences and continues as long as females survive, which is usually until the onset of winter (Ramsay, 1990). Each female produces up to 5 oothecae which overwinter and hatch the following spring, releasing approximately 100 nymphs each over a period of several weeks.

Adults rarely survive the winter, so the oothecae are a vital link between successive generations. These are coated in a pale cream coloured foam produced by the female's accessory glands and although mostly lozenge shaped, are highly variable in size and dimensions, usually conforming to the shape of their substrate (see Figure 1.1). Underneath the protective foam coating is a robust case containing multiple egg chambers, each containing up to 6 eggs which are themselves enclosed in an individual membranous cell. The choice of attachment site for the oothecae is largely variable, with oothecae being laid on any available surface, whether it is natural or artificial (Ramsay, 1990). After hatching, the exopterygote nymphs measure around 5 mm long but quickly develop through 6 instars (sometimes more with large females) to adulthood, with males winged and females flightless. This reproductive cycle results in a typical r-selected life history *sensu* MacArthur and Wilson (1967); having little parental care of offspring, high fecundity, rapid maturation and short life spans. They are capable of regenerating limbs lost during earlier instars, although sometimes resulting in smaller or distorted replacements with fewer segments (Ramsay, 1990).

*M. caffra* are indiscriminate ambush predators, sitting motionless (usually in their preferred perch of the underside of a leaf or twig) until a prey item is spotted. To suit this hunting strategy they have cryptic colouration, wings that can be held close to the abdomen by hinged sclerites and large well-developed eyes allowing 360 degree visibility (Ramsay, 1990). The pronotum is flexibly connected to the mesothorax and the head is mobile which allows the insect to turn and attack items to either flank, above or below themselves with relative ease. Once a prey item is identified they are aggressive hunters, often charging and sometimes leaping onto prey, which constitute virtually any moving invertebrate small enough to be grasped by the insect's forelimbs (Ramsay, 1990). The instinct to attack is strong enough to cause them to also strike and attempt to eat objects such as blades of grass, twigs or leaves if they are stirred by the wind or otherwise moved about (pers. obs.).

Their primary form of defence is crypsis, but they also possess some behavioural responses to threats. They will run, leap (especially nymphs) or fly, make an intimidatory display (body held upright with fore-legs raised to either side, sometimes accompanied by regurgitation of fluid) or display thanatosis (feigned death) (Ramsay, 1990).

Conspecifics are also a common food item for this species, with all instars capable of killing and consuming one another (Ramsay, 1990). Cannibalism is also associated with reproduction in *M. caffra*, with males often being eaten before, during or after copulation, which may explain why males appear to decline from the population rather rapidly (Ramsay, 1990). Such cannibalism is common among some species of arthropod and is often attributed to female foraging tactics (Rabaneda-Bueno, *et al.*, 2008). This appears to be a significant source of mortality for males in the *M. caffra* population (Ramsay, 1990).

### *Orthodera novaezealandiae*

*O. novaezealandiae* is a praying mantis also in the family Mantidae, native to New Zealand and likely originating in Australia (Ramsay, 1990). This species is the only native praying mantis in New Zealand, and together with the introduced *M. caffra* comprises the entire mantid fauna of two species (Ramsay, 1990). *O. novaezealandiae* are similar to *M. caffra* in regards to their r-selected life history, generalist diet, foraging strategy and use of oothecae to overwinter. They are however less sexually dimorphic, with males and females similar in size and both capable of flight, although females are more reluctant to do so (Ramsay, 1990). They are a bright green colour over their entire body, with the exceptions of a conspicuous blue spot on the anterior side of the fore femur and an occasional reddish tinge to the upper surface of the eyes and lateral edges of the pronotum (Ramsay, 1990). The pronotum is broad, extends anteriorly to slightly overlap the head capsule and comprises over 20% of the insect's body length. The femur and tibia are armed with a ventral row of 14 and 10 spurs respectively and the tibia possessing an additional outer row of 14 spurs. The forewings are more sclerotised in females and completely cover the transparent, membranous hind wings at rest (Ramsay, 1990).

Like *M. caffra*, females produce up to five oothecae, but these differ in that they are uniformly shaped and not usually placed in crevices or other irregular surfaces. The *O. novaezealandiae* ootheca is tapered towards the dorsal surface and flat-sided, dark brown in colour and houses two parallel rows of egg chambers, which are capped with a paler coloured foam, giving the appearance of a stripe running the length of the dorsal surface (Ramsay, 1990). Each egg chamber contains a vertical stack of three eggs, separated into individual membranous cells. The total number of eggs per case varies between two and 70 and the approximately 6-7 mm long nymphs emerge in the

spring. These proceed through six instars over the following 3-6 months to reach maturity around February to March and senesce by June, a slightly slower development than the exotic, which usually reaches maturity by January or February (Suckling, 1984; Ramsay, 1990). Dissimilarly to *M. caffra*, the nymphs of each ootheca emerge synchronously, all within one or two days of each other (Suckling, 1984). *O. novaezealandiae* are also ambush predators, but much less aggressive in their foraging than *M. caffra* (Ramsay, 1990). This extends to conspecific predation, which is much less common and rarely associated with copulation in this species (Suckling, 1984), meaning that non-cannibalistic mortality accounts for the loss of most individuals from the population (Suckling, 1984; Ramsay, 1990). *O. novaezealandiae* prefer open shrubland to dense forest and appear to enjoy sun-lit rather than shaded habitat. Additionally, they do not take to habitation of human structures as readily as *M. caffra*, with an occasional visit to a lit window being the closest most will venture into a building and females not known to deposit oothecae indoors (Ramsay, 1990).

### 1.3 Range prediction

The estimation of the potential distribution of species is clearly of high value to the management of invasive organisms (Simberloff, 2008). This is especially so because of the importance of pre-emptive control in minimising the damage that occurs, due in part to the extreme difficulty of eradicating noxious species once they are well established (Mack, *et al.*, 2000; Ficetola, *et al.*, 2007). A promising tool in the pursuit of predictive ability is the use of species distribution models (SDMs) to simulate the range of an organism in a remote time or place (Guisan & Zimmermann, 2000; Rodder & Lotters, 2010). However, there are several drawbacks to the use of SDMs in invasion biology, as well as a number of core assumptions which are especially important in this field (Guisan & Thuiller, 2005; Zurell, *et al.*, 2009). *M. caffra* has not yet spread far into the South Island of New Zealand, so predicting its potential for range expansion there will be valuable in determining the level of threat it poses to *O. novaezealandiae*. Most interesting is the extent of overlap between the current distribution of the native species and the future range of the invasive and this is examined in Chapter 2.

### 1.4 Cannibalism

Cannibalism is an interesting behaviour because it is conceivably maladaptive, especially in the cases of filial and pre-copulatory sexual cannibalism, yet it is widespread across multiple kingdoms (Agarwala & Dixon, 1992; González-Pastor, *et al.*, 2003; Mehliis, *et al.*, 2010). The occurrence of cannibalism is not only of interest in terms of understanding its own evolution, but it can also

explain the basis of other traits such as keen kin recognition abilities (Avise, *et al.*, 2002) and sophisticated signalling adaptations (Uetz & Roberts, 2002). Cannibalism is also a strong driving force in population structure of many predators (Rudolf, 2008) with flow on effects for whole biological communities (Wahlström, *et al.*, 2000; Rudolf, 2007). This implicates it as a potential factor in population limitation of mantids and therefore of relevance to our understanding of their basic ecology (Krebs, 2002). Because of this, examining the behaviour throughout the developmental stadia of *M. caffra* may also be informative regarding its establishment and spread in New Zealand. Cannibalism is also especially interesting in cases where there is potential for predation of relatives, because of the fitness consequences which are expected to result from this behaviour (West & Gardner, 2010). *M. caffra* provides a useful study species for this topic because it is strongly cannibalistic throughout its developmental stadia, has intrinsic size variation within broods and displays sexually-associated and siblicidal cannibalism (Ramsay, 1990; Crumrine, 2010). In addition, its high fecundity and modular egg configuration make specimens plentiful and relatedness easy to determine.

## 1.5 Displacement

Competitive exclusion is the ejection of a species from its range (or part thereof) due to direct or indirect competition with another species (Reitz & Trumble, 2002). This is the ultimate consequence of intense interspecific competition, which drives resources below the minimum required to support populations of one of the species (Crowder & Snyder, 2010) and is widespread among many taxa, including invertebrates (Van Riel, *et al.*, 2007) and more specifically, insects (Crowder & Snyder, 2010). Because of this, the outcome of invasion by an AGP is often the complete expulsion of similar native fauna (Snyder & Evans, 2006; Laparie, *et al.*, 2010), especially if the species in question are closely related (Parker, *et al.*, 1999; Reitz & Trumble, 2002; Van Riel, *et al.*, 2007). Such competitive displacement is one of the key ways in which arthropod predators may affect native communities (Snyder & Evans, 2006), but the mechanism of competition driving them is variable and may consist of any combination of interference, exploitative or apparent competition (Reitz & Trumble, 2002). This is especially true of impacts occurring between species of the same trophic level (Parker, *et al.*, 1999) and displacement is more likely between species that share similar ecological niches (Van Riel, *et al.*, 2007; Crowder & Snyder, 2010). In agreement with this, anecdotal reports suggest that *M. caffra* is gradually replacing *O. novaezealandiae* as it expands its range in New Zealand (Brockhoff, *et al.*, 2010). The changing distribution of *M. caffra* also corresponds with Elton (1958) and Falk-Peterson *et al.*'s (2006) definition of invasiveness; geographic (and demographic) spread of the population in the introduced range.



However, to date there has been no assessment of whether or not *M. caffra* has any specific ecological impact or is affecting *O. novaezealandiae* in particular, beyond anecdotal testimony.

## 1.6 Current study

In this study, three separate but related topics pertaining to these species' biology are examined : the potential range of *M. caffra* in New Zealand, cannibalism in juvenile *M. caffra* and the possible impact of *M. caffra* upon *O. novaezealandiae*.

In regards to these areas the following specific questions are addressed:

1. Where in New Zealand is *M. caffra* likely to be able to establish, based on its known spatial occurrence? (Chapter 2)
2. Which of these areas is *M. caffra* able to disperse to by human transport of oothecae? (Chapter 2)
3. How much of the current range of *O. novaezealandiae* is likely to fall within the eventual extent of *M. caffra* distribution? (Chapter 2)
4. Is the cannibalism frequency in *M. caffra* nymphs influenced by their relatedness or body mass? (Chapter 3)
5. Do either species use non-visual, airborne cues to locate mates? (Chapter 4)
6. Do either species respond to the cues of heterospecific females and thus create potential for reproductive interference? (Chapter 4)
7. Is copulation-associated predation a significant cause of mortality for *O. novaezealandiae* males in heterospecific pairs? (Chapter 4)

These are approached with computer and field-based distribution modelling, behavioural study of *M. caffra* nymphs in the laboratory and Y-maze experimentation with adults of both species.

Because they address separate aspects of the species' biology, one chapter is dedicated to each of the three general topics of range prediction for invasion biology, kin selection on cannibalism and impact of *M. caffra*, with individual introductory and discussion material for each. A short general discussion is provided to synthesise the areas where their results have overlapping relevance and conclude the thesis.

## 2. Range Prediction and Field Validation for *Miomantis caffra* in New Zealand

### 2.1 Introduction

#### Range Prediction

Predicting the trajectory of biological invasions has been described as the Holy Grail of modern invasion biology (Simberloff, 2008). A promising tool in this endeavour is ecological modelling, which attempts to elucidate basic ecosystem functions through the use of simulation. Applications of ecological modelling include predicting alteration of communities due to future climate change (Zurell, et al., 2009; Gibson, et al., 2010), aiding the location of populations of cryptic species (e.g., Jackson & Robertson, 2010), examining drivers of spatial population structure (Rudolf, et al., 2010), identifying areas of high conservation priority (Mateo-Tomás & Olea, 2010) and predicting the spread of invasive species (Guisan & Thuiller, 2005; Pearson, et al., 2007). Computerised species distribution models (SDMs) are an important tool in this pursuit (Phillips & Dudík, 2008; Carroll, et al., 2010) and their use to assess potential future distributions, including for evaluation of potential invasive species establishment and spread is a growing field (Phillips, et al., 2006; Elith, Phillips, et al., 2010; Rodder & Lotters, 2010). This is in part due to the growing availability of global scale climate and land use data sets, the development of new modelling techniques and the success that these techniques have demonstrated in the field (Ficetola, et al., 2007; Elith, Phillips, et al., 2010).

This is a pertinent area of research because invasive species are a leading cause of biodiversity loss world-wide (Mack, et al., 2000) and one which promises to become more prevalent as global trade and travel continue (Perrings, *et al.*, 2010). Additionally, because the eradication of established populations of exotic organisms is usually an impossibility (Mack, *et al.*, 2000; Baxter, *et al.*, 2008) prevention of establishment of the highest risk species is a priority (Ficetola, *et al.*, 2007; Vander Zanden, *et al.*, 2010) and ecological modelling is a tool which can help identify them.

Here, the SDM Maxent (short for maximum entropy) is used to create an image of the potential range of *M. caffra*, an invasive praying mantis in New Zealand and is combined with the results of a practical range test in order to assess the agreement of the computer based technique with an

independent prediction, as well as create an overall estimate of the species' potential to spread. The term "range" shall be used from here onwards to refer to the area a species occupies, rather than distribution, to avoid confusion with the statistical meaning of that term. "Potential range" refers to the area that a species could occupy with a self-perpetuating population if it were to reach it by dispersal (by its own mobility or otherwise), i.e., the geographic component of its fundamental niche.

Ecological modelling generally makes use of a comparison between the climatic conditions in the native and introduced range of the species in question, as similar climates are considered essential for the successful establishment of an introduced species (Richardson & Thuiller, 2007 but also see; Ibáñez, *et al.*, 2009). Although other factors (such as propagule pressure and biotic interactions (Sakai, *et al.*, 2001)) play a role in determining the range of a population or species (Stohlgren & Schnase, 2006; Godsoe, 2010), climatic match far outweighs them in both importance and the availability of data (Ficetola, *et al.*, 2007; Pino, *et al.*, 2009). From an analysis of 24 studies addressing variables that effect establishment, Hayes & Barry (2008) found 3 characteristics that were reliable for animals: climatic match, establishment success elsewhere and propagule pressure. For *M. caffra*, establishment success in other locations has not been reported and propagule pressure is equal to net reproductive output since the species is already established. Consequently, climate remains the best predictor for the potential range of *M. caffra* in New Zealand. Additionally, because the study area (the South Island of New Zealand) has a very small native mantid fauna (one species: *O. novaezealandiae*), the success of *M. caffra* is less likely to be influenced by interspecific competition, adding weight to the relative importance of climatic variables in the prediction of its potential range. To examine the influence of climate on limiting the range of *M. caffra* in the South Island, ootheca of that species are tested for their ability to overwinter there.

#### Realised vs. potential range

Following Soberon & Peterson (2005), the fundamental niche is defined as the entirety of conditions under which a species population growth rate can be  $\geq 1$ . The potential range is the spatial component of this term, i.e., the entire geographic area where this is possible. The realised niche/range is the portion of the fundamental which is actually occupied. SDMs make heavy use of niche concepts in their operation, so a major limitation of predictive range models comes from the disparity between the fundamental and realized range which organisms usually do occupy (Rodder & Lotters, 2010). Indeed, that species do not occur everywhere they could is one of the core recognitions of biogeographic theory (Glaubrecht, 1999). This has consequences for both the assumptions which are made about the input data (discussed further in 2.4 below), and the interpretation of the output (Rodder & Lotters, 2010). The latter is the case because current

modelling techniques do not usually incorporate data about the host of biotic and abiotic conditions that might act to restrict the species to its realized niche when generating their predictions of species range (Guisan & Thuiller, 2005; Zurell, *et al.*, 2009; Godsoe, 2010). In other words, they only present a picture of the suitability of habitat, not an estimate of the likelihood that the species in question will actually colonise there successfully. The missing piece in that pursuit is the inclusion of dispersal estimates, or restrictions to the output where barriers to movement are known to occur (Soberon & Peterson, 2005). However, attempting to hone predictions by the inclusion of such information is a hitherto underutilized approach (Zurell, *et al.*, 2009), but see Midgley *et al* (2006).

This is especially relevant to invasive species, since they are almost always in a state of population expansion during the time of interest, and thus have a restricted realized niche. This is in contrast to other applications which may be investigating the range of a species which has had years to reach every corner of its native region (e.g., Jackson & Robertson, 2010) and thus is more likely to occupy (or realize) a greater proportion of its fundamental niche or range.

Here, because the species' primary form of dispersal is likely to be the transport of oothecae by humans and because the viability of these oothecae under different environmental conditions is easily observable, it is possible to make an estimate of the areas into which *M. caffra* is unlikely to be able to migrate. As a result, an opportunity is provided to trim the output of a SDM by comparison with dispersal information. Human mediated transport of oothecae is the most likely mode of long range dispersal in this species, as they are often laid on human materials and vehicles, while adults are generally sedentary and females are flightless (Ramsay, 1990). Therefore, ootheca survival is an important factor in the ability of the species to colonise a particular locale; if the oothecae die then it will be unlikely to ever reach the area, even if adults can easily survive there.

#### Computer modelling for invasion biology

Here, an SDM is used in the context of biosecurity. Predictive techniques are valuable in this field because they have the potential to allow prioritisation of species management (e.g., Gutierrez, *et al.*, 2010). This is because a large component of invasion risk is the range an invader might attain in the introduced region (Mack, *et al.*, 2000; Sakai, *et al.*, 2001). Therefore, knowing which species have the greatest potential to spread within the area of concern can inform choices about where to allocate control effort (e.g., Downey, *et al.*, 2010). Another benefit modelling can yield is understanding of how invasive populations behave spatially, in order to optimize control effort and inform pre-emptive protection of vulnerable locales (e.g., Thum & Lennon, 2009; Fabre, *et al.*, 2010). Because of the tremendous cost involved in suppressing noxious species (Hulme, 2006), preventative action and strategic application of resources to the task are essential (Mack, *et al.*, 2000; Ficetola, *et al.*, 2007).

In addition to the benefits for biosecurity, modelling of invasive species establishment also contributes to our understanding of founder population dynamics (Sakai, *et al.*, 2001) and changes in niche properties (Rodder & Lotters, 2010). This is beneficial because most natural colonization events go unnoticed and unstudied, meaning they usually have to be examined *post hoc* (e.g., Toon, *et al.*, 2010). Invasive species however are often the subjects of intense scrutiny, which can contribute insight into rates of successful dispersion (Harris, *et al.*, 2007; Buckley, 2008), trends in habitat vulnerability (Chytry, *et al.*, 2008) and pathways of establishment in natural dispersal events (Anderson, *et al.*, 2010) leading Sakai *et al.* (2001) to describe them as valuable natural experiments.

However, despite their great potential for use in this field, computer models have several limitations when used for invasive species range prediction. We do not have the luxury of choosing which species are to be examined, so there is often a paucity of data regarding their ecology at the time that range prediction is relevant (Buckley, 2008; Strubbe & Mathysen, 2009). Ecological information is important to have in order to appropriately tune the model to the species (e.g., Elith, Kearney, *et al.*, 2010), as they are not a one-size-fits all tool (Elith, Phillips, *et al.*, 2010). Having information about which variables are important to the success of the species also allows refinement of the predictor set in order to improve model performance (Moilanen, *et al.*, 2009). Because of those factors, SDMs are often asked to run under sub-optimal, generalised conditions when used for predicting invasive species establishment. Occurrence data are also often limited, because we rarely have thorough surveys of the species range ahead of time (Crall, *et al.*, 2010). This often means using a limited sample with which to train the model, making it more difficult to confidently estimate the relationship between the presence of the species in a particular location and the environmental variables there (Barry & Elith, 2006). This factor also complicates the acquisition of independent data against which to test the model results (Pearson, *et al.*, 2007). Models also tend to display greater performance when examining specialist rather than generalist species, possibly due to tighter niche association in the former (Zurell, *et al.*, 2009; Rodder & Lotters, 2010). However, invasive species are typically generalists, due to the advantage this trait gives in dispersing to and succeeding in new habitats (Snyder & Evans, 2006).

In addition to these drawbacks, the model is also asked to make a prediction for the species range in an area distant from the location (and often time) from which training data are drawn. Thus the study area may differ in many aspects of climate, geography, land use practices, biological community and the host of other factors which may interact to limit species range (Elith, Kearney, *et al.*, 2010; Rodder & Lotters, 2010). Therefore, there are many assumptions regarding whether the same environmental variables are limiting in the native and introduced range which need to be kept in mind. This means that the model's prediction may be more questionable when used for this

purpose (Elith, Phillips, *et al.*, 2010) and pre-selection of a more ecologically relevant set of predictor variables is even more important (Moilanen, *et al.*, 2009).

Despite the statistically demonstrated accuracy of many ecological modelling techniques, these estimates are often based on the same data set that is used to train the model. In such cases, the model may be shown to perform well while predicting the range of a species within the area from which locality data are drawn, but it can be problematic to evaluate its accuracy in distant regions with different conditions (Ficetola, *et al.*, 2007; Elith, Phillips, *et al.*, 2010). For this reason, their usefulness has been brought into question (e.g., Hulme, 2006) and external data sets are desirable for validation purposes (Ficetola, *et al.*, 2007; Elith & Graham, 2009). A common approach is to combine the results of multiple modelling methods and use their agreement to define a final prediction (Elith, Kearney, *et al.*, 2010). A similar manner of testing is carried out here, although comparing the results of a practical test to those of an SDM.

In the current study, the SDM is also used to make a prediction of potential range for an invasive species under the sub-optimal conditions typical of studying a newly arrived organism.

A separate validation of the potential range of *M. caffra* is also attempted here by examining its overwintering ability in different regions of the study area. This is not usually possible for invasive species because of the obvious drawback of spreading the organism beyond its currently invaded range in order to observe this. However in this case, we have the opportunity to do so, due to the species' use of an ootheca, which must survive the winter in order to maintain the population into the following season (Ramsay, 1990). Because of this it is possible to use the hatching success of the oothecae in different areas as a proxy measure for the species' ability to establish a viable population there. If the oothecae are unable to survive the winter, the insect will be unable to create a breeding population even if the adults are able to withstand the climate (Ramsay, 1990).

Furthermore, as the ootheca represents the most resistant stage of the organism's life cycle, it is not expected that free living instars could survive in areas where the egg case cannot. However, the reverse of this is that oothecae may survive in areas where adults cannot, thus predicting some regions as potential habitat areas despite not being suitable. Therefore this approach favours commission over omission, depicting a worst case scenario, which is desirable in the context of invasive species management and biosecurity (Guisan & Thuiller, 2005; Ward, 2007).

SDMs are increasingly being used to make predictions into areas beyond the training data, an application with arguable accuracy and many implicit assumptions (Carroll, *et al.*, 2010; Elith, Phillips, *et al.*, 2010). Therefore, I seek to investigate the performance of maxent in projecting species distribution into an area remote from the source landscape of South Africa and using

evaluation data drawn from that same area. A Maxent run is also carried out using added presence records from the invaded range (North Island of New Zealand), to evaluate the effectiveness of including this data where available, as suggested by Beaumont *et al* (2009).

In many cases, the availability of locality data is highly restricted, especially when dealing with species of high conservation priority (Pearson, et al., 2007). Because of the correlation between the usefulness of modelling to conservation and the paucity of presence/absence records for species of conservation concern, the evaluation of prediction techniques when used with small sample sizes is important (Pearson, et al., 2007). Therefore the technique is used here with reduced subsets of the full complement of available input data in order to examine its performance under those conditions.

### Presence-only modelling

Maxent is an example of a presence-only method, meaning that it does not require specific absence data (that is, confirmation that a species is not present in a given locale (Elith, Phillips, *et al.*, 2010)). This class of SDMs is useful because herbarium and museum collections comprise the greatest source of occurrence data for most species (Scott, et al., 2002), but these typically do not contain information about where a species *is not* found (Phillips, *et al.*, 2004). This is especially true of invasive species, as they are unlikely to occupy all of the suitable habitat available to them (Kadoya, *et al.*, 2009). Hence, a practical benefit of this approach is that it avoids the difficulty of obtaining reliable absence data, which is typically unavailable for most species (Phillips, et al., 2006; Phillips & Dudík, 2008). The presence-only approach is also more closely associated with the fundamental niche rather than the realized niche of the species, which is more valuable for predicting potential range (Guisan & Zimmermann, 2000). On the other hand, the use of absence data restricts the prediction of suitable habitat because of dispersal limitations and historical factors such as extinction (Anderson, *et al.*, 2003), which are less relevant to the study of invasive species establishment (Elith, Phillips, *et al.*, 2010). This is because invasive species may not be subject to the same restrictions (such as anthropogenic influences, competition and abiotic conditions) in their introduced range and the maximum potential range (i.e., the worst case scenario) is of more interest to biosecurity managers (Ward, 2007).

### Current scenario

*M. caffra* appears to be displacing *O. novaezealandiae* as it expands its range (Ramsay, 1990; Chapter 4), which is the main concern regarding the impacts of this introduced AGP (Brockerhoff, *et al.*, 2010). However, a large part of the native species' range is located in the South Island (see Figure 2.1), where *M. caffra* has yet to establish widely. Because of this, the extent of *M. caffra*'s potential distribution in the South Island is a major component of the threat posed to *O. novaezealandiae*. Therefore, key questions to be addressed in this chapter are: 1) How much of

the South Island might *M. caffra* occupy and 2) in light of this, will there be a refugium for *O. novaezealandiae*? This is approached using the modelling package Maxent. Unfortunately, there is very little ecological or distributional information about *M. caffra* in its native range of South Africa (Ramsay, 1990), which is a hindrance to evaluating the potential for distribution of any exotic species. Thus in the process of approaching this subject, the performance of the chosen method under the low-input conditions typical of invasion biology is also assessed.

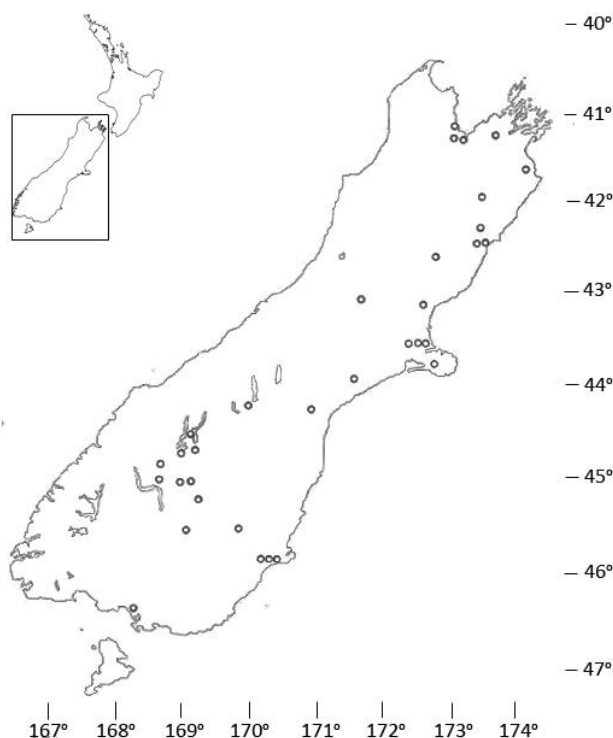


Figure 2.1 Known distribution of *O. novaezealandiae* in the South Island of New Zealand, after Ramsay (1990).

### Maximum entropy

The modelling technique used here is a machine-learning method that can be used to describe the potential range of a species based on known occurrence data (Phillips, *et al.*, 2004). It is a presence-only technique as it uses background (or pseudo-absence) data in place of specific absence records to evaluate its output (Elith, Phillips, *et al.*, 2010). Its default setting is to use 10,000 randomly selected points for this purpose and it has demonstrated performance on par with other techniques that do incorporate absence data (Ficetola, *et al.*, 2007). Entropy refers to the quantity of information held by a random variable and the Maxent software aims to identify the probability distribution which places the least constraint upon it (i.e., it finds the distribution of maximum entropy). Maxent was selected as it has been shown to perform better than other common packages



(Elith, *et al.*, 2006; Phillips, *et al.*, 2006; Ficetola, *et al.*, 2007), including when used in New Zealand specifically (Ward, 2007) and its application is widespread in invasive species research (Hoffman, *et al.*, 2008; Ficetola, *et al.*, 2009; Jarnevig & Reynolds, 2010). It has also been shown to perform well when used with small sample sizes (e.g., Pearson, *et al.*, 2007), in part because it operates in a generative rather than discriminative manner (Phillips & Dudík, 2008), which provides better results under such conditions (Ng & Jordan, 2001). The model is used to predict the range of *M. caffra* in the South Island of New Zealand only, as the insect is already well established throughout the North Island.

## 2.2 Methods

The overwintering success of *M. caffra* oothecae was tested by placing them outdoors in locations spread throughout the study area, but within a container from which nymphs are unable to escape upon hatching. The spatial data that this produced was used to assess agreement between the simulated Maxent projection and the physical survival of *M. caffra* and to provide further insight into the potential range of the species in the South Island of New Zealand. The number of correctly classified presences and absences achieved by a model is the most commonly used measure of its accuracy (Fielding & Bell, 1997) and this was determined by agreement with the ootheca data in this case. Thus in addition to the standard approach of testing the model against a subset of the training data, this was also carried out using the data on oothecae success as proxies for presence and absence in the potential invaded range.

### Computer modelling software

The Maxent model package version 3.3.3 (most recent as at June 2010) available at <http://www.cs.princeton.edu/~schapire/maxent/> was used. The Bioclim climate layers produced by Hijmans *et al* (2005) and available at <http://www.worldclim.org/> were used as features. These include the derived variables of annual mean temperature, mean diurnal temperature range, isothermality, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, annual temperature range, mean temperature of the wettest and driest quarters, mean temperature of the warmest and coldest quarters, annual precipitation, precipitation of wettest and driest months, precipitation seasonality, precipitation of wettest and driest quarters and precipitation of warmest and coldest quarters (denoted as 1- 19 in that order). The highest resolution layers available (30 arc seconds, or approximately 1 km<sup>2</sup>) were used for all features. 18 presence records from South Africa (the native range) and seven from the North Island of New Zealand (introduced range) were used as locality input.

### Maxent methods

The Maxent algorithm requires the estimated range to agree with all known data without applying any unsupported restrictions to it (Pearson, et al., 2007). This approach is based on the Gibbs probability measure, which describes the probability of a random variable having a certain value. This measure uniquely has the effect of maximizing entropy and thus it is the source of this property in the Maxent approach (Kindermann & Snell, 1980). Maxent thus estimates the probability distribution of occurrence at maximum entropy (closest to uniform) while still being subject to the limitations of the environmental variables used (Phillips, *et al.*, 2006). The model identifies correlation between the species presence records and patterns in environmental variables then compares the similarity of each grid square in the projected area to this information. This produces an estimate of similarity between the area of interest and the conditions where the species is known to occur, described by a numerical output ranging from 0 (unsuitable habitat) to 1 (highly suitable habitat) for each cell (Phillips and Dudík 2008). This can then be plotted on a map of the area in question to produce a visual representation of the potential range of the species there. Because every factor that influences the ability of an exotic species to become established cannot be quantified and modelled, the output of these techniques cannot be interpreted as absolute measures of risk, but indicators of which areas are more or less vulnerable to colonisation (Pearson, et al., 2007). For each run the data were partitioned, with 25% of presence records used for testing and the remaining records used for model training (the split sample approach (Van Houwelingen & Le Cessie, 1990)). Output format was set to logistic, as this provides greater performance than the alternative (cumulative) and creates a probabilistic output (Phillips & Dudík, 2008) that is considered easier to interpret (Wang, *et al.*, 2010).

There is very little published information available regarding *M. caffra*, meaning that there was little justification for alteration of model parameters from default settings, and little opportunity to tune its operation or select predictor variables to suit the organism. Similarly, only 18 native-range presence records are available for training and testing, which is far from optimal but typical of the kind of data that may be available without undertaking an extensive survey. The species in question is a generalist and the study area (the South Island of New Zealand) is also distant from and very different to the native range of the species from which the presence records are drawn. Thus the model was run under fairly sub-optimal conditions, so its performance was expected to be somewhat impaired.

Output file type was set to \*.grd. All Bioclim layers were used for each run and jackknifing was used to evaluate their relative importance. Other than this, all settings were left at recommended defaults: convergence threshold  $10^{-5}$ , maximum iterations 500, auto features enabled and

background points at 10,000. This was carried out once using only native range presence records and once using both native range and New Zealand range records. To assess the performance of the model with different amounts of training data, an additional 3 runs were made using a random subset of 15, 10 and 5 presence records from South Africa and none of the records from New Zealand.

In order to convert the continuous logistic outputs into binary predictions of suitable and unsuitable habitat, a threshold of minimum training presence (MTP) was used. This equates to the lowest predicted value which applies to a cell containing a known presence record (Phillips, *et al.*, 2006). The result is that cells on the projection area are identified as suitable if they are at least as suitable as locations where the species is known to occur. Because of this feature, the estimate is as conservative as possible without allowing omission of presences in the training data (Pearson, *et al.*, 2007). Unless otherwise noted, this threshold is used in all instances here. Note that for outputs using reduced subsets of training data, the MTP value is also drawn from that subset, rather than the entire sample. As a result the MTP value is likely to be different for each run.

The MTP threshold map from the best estimate Maxent run using all available data was overlaid with the map of known *O. novaezealandiae* populations in order to ascertain the degree of overlap that might occur and thus whether or not there is a refugium for the native species where *M. caffra* is unlikely to colonise.

#### Field test materials

Forty one *M. caffra* oothecae laid in the lab and seven wild caught oothecae were used. These were placed into standard plastic 35 mm diameter vials which were modified in the following way: a 2.5 cm diameter hole was cut in the lid and this was covered with fine (< 1 mm mesh gauge) nylon screen, secured by placing it between the threads of the lid and vial such that there was a 4 mm distance between the top of the lid and the outer surface of the mesh. Approximately 130 holes (< 1 mm diameter) were made in the base of the vial with a heated needle to provide further ventilation. A further 30 similar holes were made in the side of the vial 2 cm from the base, aligned horizontally to surround the vial, so that any water could drain out regardless of vial orientation. A nylon cord approximately 12 cm long was tied around the top of the vial. Several layers of insulation tape were placed around the cord and cap to secure them in place. A canvas label was tied to the end of the cord furthest from the vial. The oothecae were left attached to their substrate (the inside of the plastic cup they were laid in) and this was cut into a size appropriate to be wedged securely into the vial, with the ootheca suspended as close to the centre of the vial as possible. Oothecae not attached to a substrate were affixed to a thin piece of pine board with a small twist of stainless steel wire, secured gently to prevent damage to the egg case. This was wedged into the

centre of the vial. All oothecae were placed into the vial so as to not touch the sides, in order to prevent contact with any condensate. Vials were secured to their attachment site by stainless steel staples applied to the nylon cord with a Black and Decker Inc. Powershot® stapler.

#### Field test methods

##### Test of vial insulation:

Oothecae vials were checked for divergence from ambient temperature with a Raytek® Ti30 Thermo-view™ thermal imager in Auckland. Vials were placed outdoors in the same fashion and at the same height that they were attached to their locality substrate and left for 3 hours before measurement to allow them to equalize at their innate temperature. Emissivity correction was set to 0.95 and the temperature at the centre of the vial and at a point immediately next to the vial was captured. This was repeated with 30 different vials, once during daylight (1200 hours) and once during night conditions (2400 hours) for each vial. The difference between temperatures within and beside the vials was compared with a t-test for both the day and night set.

##### Field experiment:

In late June 2010, 48 oothecae vials were taken to the South Island of New Zealand. These were distributed over a 10 day period into the locations described in Figure 2.2 below. This distribution was chosen as the closest to an even spread allowable by the location of main roads. At each position, two vials were attached to separate objects within 1-2 m of one another. Each vial was secured to the northern side of a tree or fence post at approximately 1.5 m height from the ground, in order to mimic as closely as possible the natural position in which they are usually attached. They were connected by tying their cord to the tree/post, then applying several staples to the cord, one as close as possible to the vial in order to minimize its freedom to swing. The cord was pulled through this staple to draw the vial against the attachment surface then stapled in place. Locations were chosen in urban fringes (where *M. caffra* tend to proliferate (Ramsay, 1990)) and the vials were placed away from any structures or other features which could cause a local microclimate effect, or be susceptible to interference from people. All pairs included at least one lab produced ootheca.

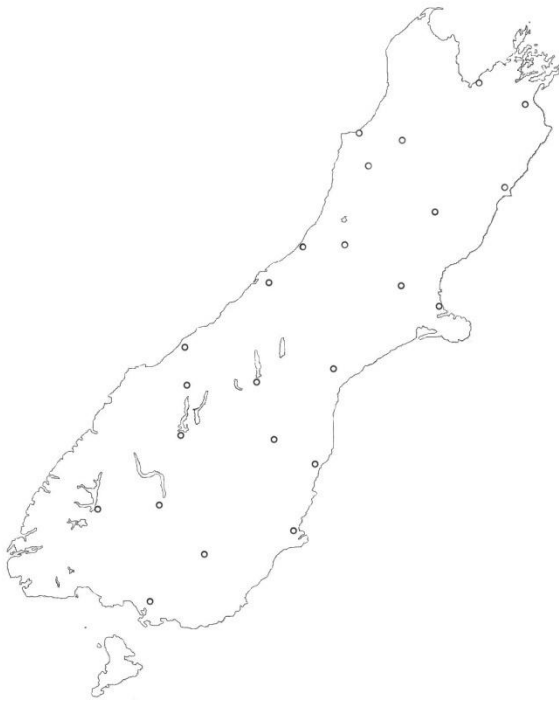


Figure 2.2 Locations of oothecae used for survival test.

Each location was photographed, its description recorded and marked by GPS coordinates in order to ensure future relocation (Appendix 1). A northern direction of travel from the initial site of Christchurch was chosen in order to prevent exposure of all the oothecae to potentially fatal colder temperatures in the southern areas while in transit. As an added precaution, the vials were transported in an insulated container, from which only the vials to be used at each location were ever removed and which itself was never removed from the vehicle. The oothecae were recollected over a 10 day period in late January 2011, after seven months in their location. The vials were retrieved in the same order and over the same length of time as they were distributed, so each was in the field for the same number of days. At the time of

collection the hatching status of each ootheca was recorded, as well as the number of surviving nymphs, if any. The oothecae were counted as having successfully hatched if at least one nymph was present in the vial, alive or dead. There is a visibly clear difference in appearance between hatched and unhatched oothecae, so it is not considered that any may have hatched and been recorded as unhatched.

The results of the oothecae hatching success were compared with the best estimate prediction of the Maxent software and used qualitatively to suggest which areas appear less likely for *M. caffra* to disperse into.

Data on climatic variables in the locations where oothecae hatched were drawn from the National Climate Database through CliFlo (available at <http://cliflo.niwa.co.nz>), provided by the National Institute of Water and Atmospheric Research (NIWA).

### Statistics

One-tailed t-tests were used to check for any difference between internal and ambient temperature of the vials.

The binomial (sign) test was used to compare the agreement between Maxent and the oothecae hatching success with a null hypothesis of 0.5 probability of agreement.

Maxent implements a one-tailed binomial test of omission to determine the probability of having at least  $t(1 - r)$  successes out of  $t$  trials, each with probability  $a$ , where  $t$  is the number of test localities,  $r$  is the omission rate and  $a$  is the proportional predicted area, equal to the fraction of all pixels predicted as suitable for the species (Phillips, *et al.*, 2006). This provides an indication of the confidence that the model performed better than it would if using random selection. Maxent also makes use of the receiver operating characteristic (ROC), which describes the true positive rate relative to the false positive rate, giving a measure of sensitivity (Phillips, *et al.*, 2004). “Operating characteristic” refers to the performance of an agent (“receiver”) in classifying dichotomous values. This is created by plotting the true positive fraction against the false positive fraction for all available thresholds (Fielding & Bell, 1997). The area under the ROC curve (AUC) that this generates gives a measure of the model’s accuracy in terms of its ability to resolve presence from absence, ranging from 0 to 1 (with one being perfect discrimination). With presence only data however, grid cells without occurrence records are interpreted as absences (Phillips, *et al.*, 2004) meaning that the maximum AUC is always less than one (Wiley, *et al.*, 2003).

AUC values greater than 0.5 indicate superior performance to random selection; a score of 0.5 would indicate that there is a 50% chance that a presence record randomly selected from those used to test the model will have a suitability score greater than a random selection from the background values. Generally, a model with AUC score greater than 0.75 is considered potentially useful (Elith, 2002). Because of the way the ROC is obtained (i.e., across all thresholds (Phillips, *et al.*, 2004)), the AUC score is independent of any particular threshold (Fielding & Bell, 1997). In order for Maxent to calculate these statistics, the input data must be partitioned into training and testing subsets. This results in a trade-off between having a large training set and small testing set (higher accuracy and higher variance in error estimates) or a small training set and large testing set, giving lower accuracy but more precise estimates of error (Fielding & Bell, 1997). Here 25% of each input set is used for testing and 75% for training.

In addition to the evaluation statistics mentioned above, Maxent also makes use of a procedure referred to as jackknifing to quantify the value of the environmental features used. This can then give an indication as to which of them are important to the study organism’s invasion success (Peterson & Cohoon, 1999; Wang, *et al.*, 2010). This is carried out by building models in a leave-one-out fashion (Pearson, *et al.*, 2007), firstly with a given feature in isolation, then with all other features except the one in question and comparing the results in terms of gain (Peterson & Cohoon, 1999). Gain is a likelihood statistic the exponent of which describes the mean probability of presence samples relative to pseudo-absences and is the measure of overall model fit used by Maxent. It is thus possible to compare which features contribute the most gain when included and

reduce gain the most when excluded, to rank them in terms of the predictive power they provide to the model (Pearson, *et al.*, 2007). In this way the environmental variables which are most and least important to delineating the species range can be revealed.

## 2.3 Results

### Model output

Confidence measures:

*P* values for the binomial test of omission for each model run as well as their corresponding AUC scores are reported in Table 2.1 below.

Table 2.1 Performance statistics for models using different levels of input data. *P* values are against the null hypotheses that the model performed no better than random. AUC scores quantify the model's ability to correctly classify presence and absence in the locality data, with values > 0.5 indicating superior performance than random selection. The test AUC is most telling in regards to the model's predictive power, as it represents fit to the test data partition.

| Input localities      | <i>P</i> | Test AUC | Training AUC |
|-----------------------|----------|----------|--------------|
| All available records | <0.0001  | 0.985    | 0.998        |
| All SA records        | <0.0001  | 0.956    | 0.997        |
| 15 SA records         | <0.0015  | 0.945    | 0.997        |
| 10 SA records         | 0.0136   | 0.967    | 0.958        |
| 5 SA records          | 1.0      | 0.715    | 0.981        |

Graphic outputs:

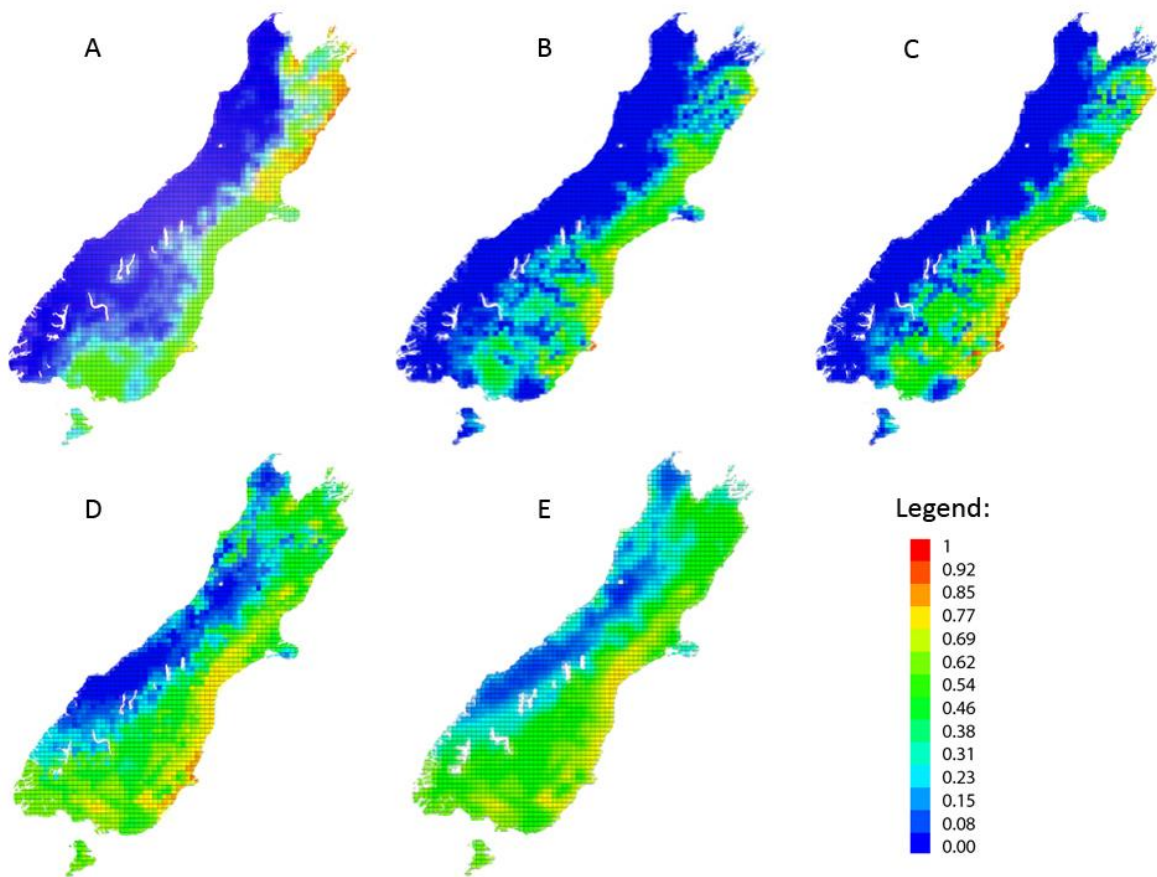


Figure 2.3 Logistic output maps of habitat similarity in the South Island using the full complement of available data (A), only native range data (B) and random subsets of 15 (C), 10 (D) and 5 (E) South African locality records. The legend indicates probability that conditions are suitable, based on similarity to presence records in the input data. Reds represent highly suitable areas, middle values (shades of green) indicate typical conditions where the species is found and blues indicate unsuitable habitat.

One of the greatest impacts of reducing input data was the affect on the MTP threshold value. This caused the value to range from 0.308 (all available data) to 0.674 (15 South African localities), resulting in large differences in the area predicted as suitable on threshold maps (see Figure 2.4 below).



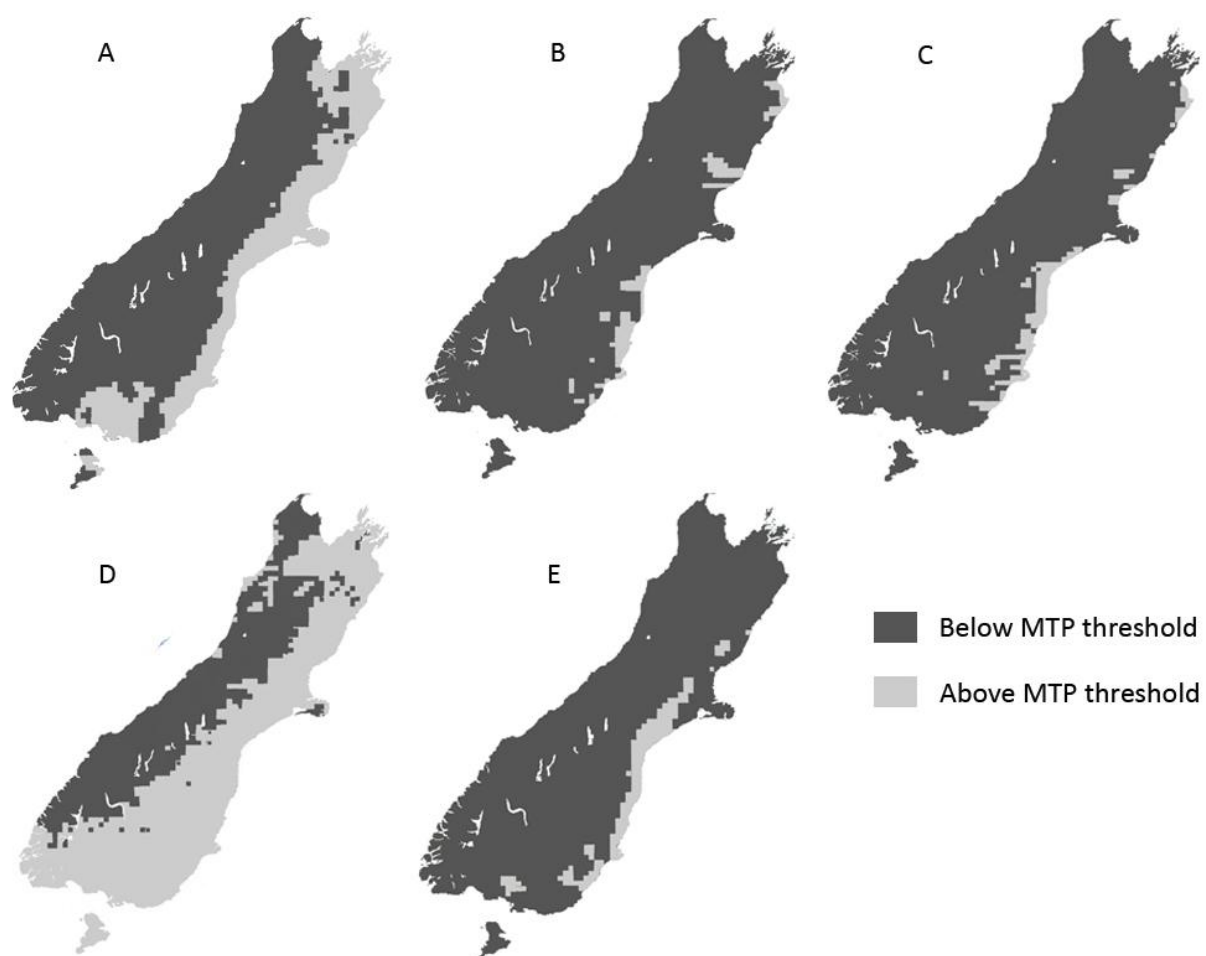


Figure 2.4 Graphic outputs from the same Maxent runs as used in Figure 2.3 above, with a threshold rule applied. Each is divided into the habitat which falls above or below the MTP value drawn from its own input data set: 0.308 (A), 0.586 (B), 0.674 (C), 0.431 (D) and 0.652 (E).

### Feature importance

The jackknife protocol on training data identified temperature seasonality, mean temperature of driest quarter, and annual temperature range as being the most important three features (in that order) in determining the range of the mantis. These variables contributed the most gain to the model when used in isolation and reduced gain the most when omitted. The variables of mean temperature of wettest quarter, mean diurnal range (calculated as the mean of maximum monthly temperature minus minimum monthly temperature) and precipitation seasonality had low predictive power, altering training gain little (see Figure 2.5).

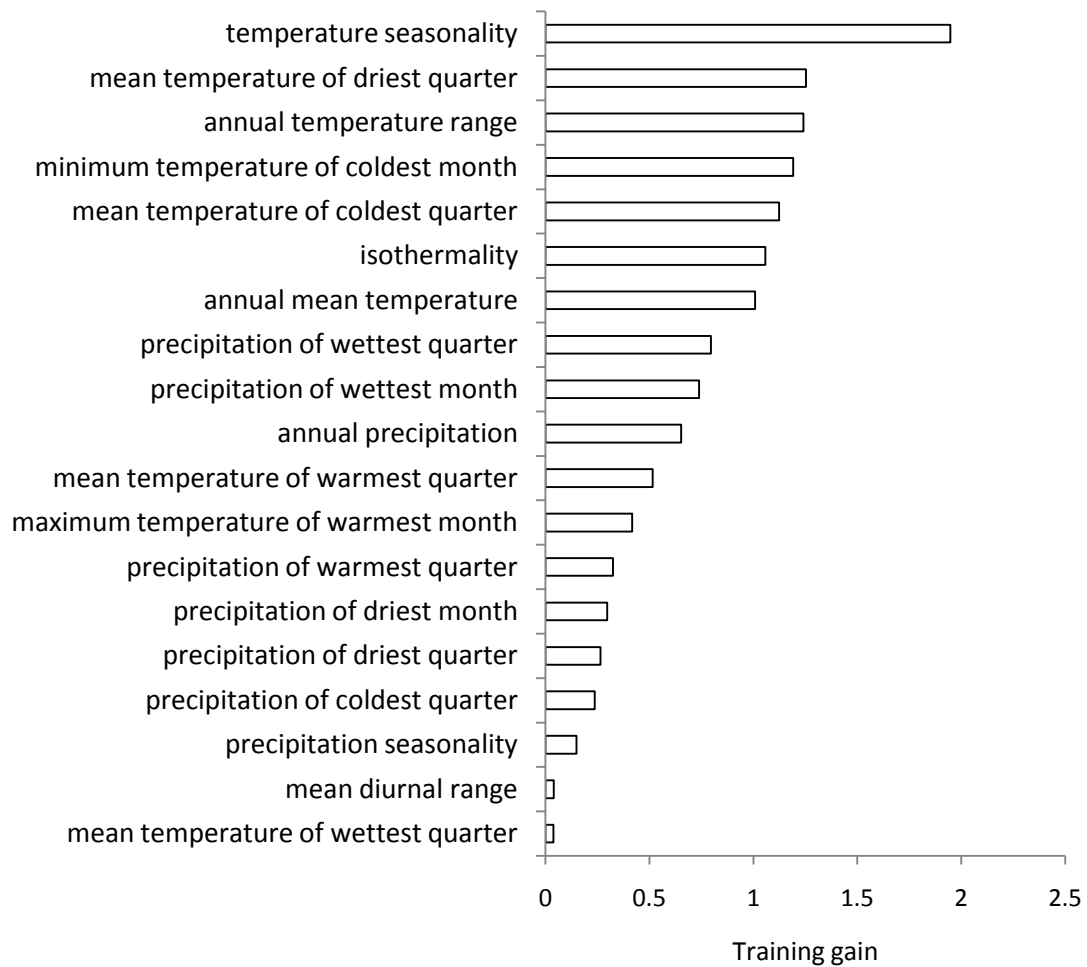


Figure 2.5 Contribution of bioclimatic features to overall model fit when used in isolation, according to the jackknife procedure. Taken from model using all available presence localities, including New Zealand North Island data.

### Range overlap between species

The threshold map output of the best estimate (i.e., maximum input data) run from Maxent was combined with the map of known *O. novaezealandiae* locations taken from Ramsay (1990) to give the estimate of potential overlap given in Figure 2.6 below.

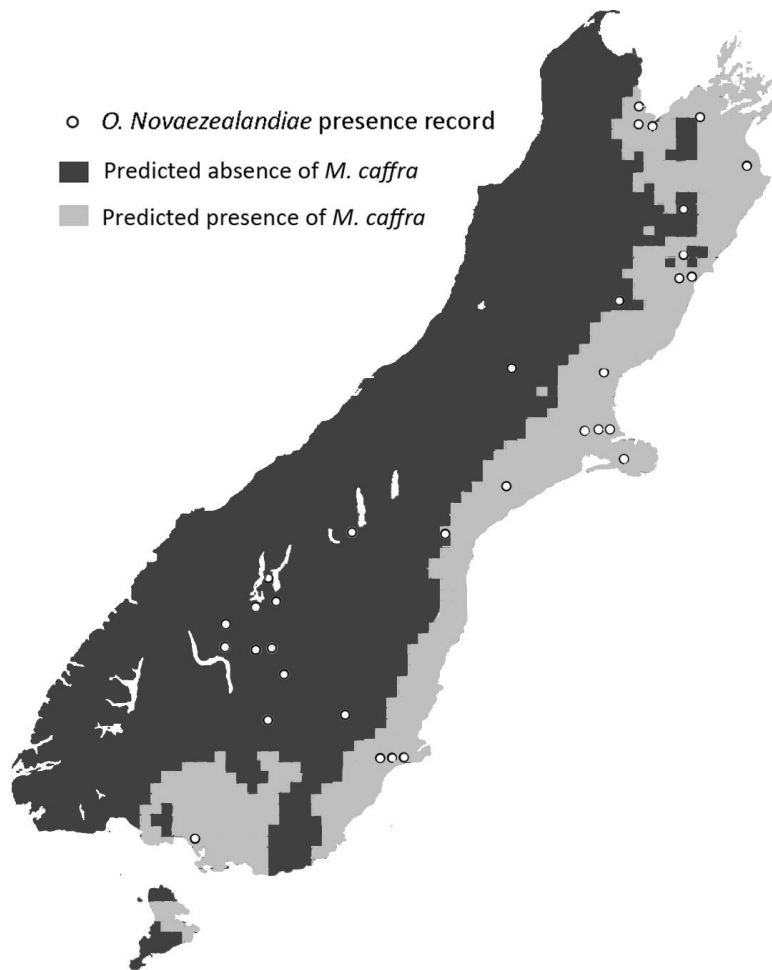


Figure 2.6 Distribution of *O. novaezealandiae* as reported in Ramsay (1990), relative to areas predicted as having suitable habitat for *M. caffra* by Maxent.

### Oothecae results

#### Influence of vials:

According to t-tests there was no significant difference between the internal and external temperature of the vials during daylight ( $t = 0.716$   $P = 0.474$ ) or night ( $t = 1.744$   $P = 0.149$ ), indicating no insulating effect that might have protected the oothecae.

#### Success of oothecae:

All ootheca vials were recovered undamaged and securely attached to their substrate, no vials showed signs of removal, or tampering. One unhatched ootheca (11a, Franz Joseph) was attacked by an unidentified fungus and excluded from further analysis.

The oothecae survived a variety of conditions, including temperatures well below freezing (see Table 2.2), for the seven month period in the field and hatched as far south as Oamaru (see Figure 2.7).

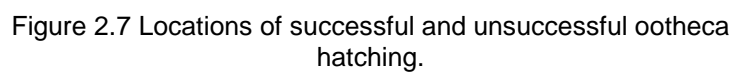


Table 2.2 Environmental conditions in locations where oothecae successfully hatched. Bold text denotes the most extreme value for each variable. All data are draw from NIWA's CliFlo database.

| Location  | Maximum<br>temperature<br>(°C) | Minimum<br>temperature<br>(°C) | Maximum<br>daily rainfall<br>(mm) | Maximum<br>relative<br>humidity (%) | Minimum<br>relative<br>humidity (%) | Altitude<br>(m) |
|-----------|--------------------------------|--------------------------------|-----------------------------------|-------------------------------------|-------------------------------------|-----------------|
| Blenheim  | 31.0                           | -4.9                           | 47.4                              | 100                                 | 40.3                                | 42              |
| Haast     | 20.9                           | -1.2                           | 103.8                             | 100                                 | <b>19.9</b>                         | 15              |
| Kaikoura  | 30.9                           | 2.7                            | 34.2                              | 100                                 | 38.1                                | 58              |
| Murchison | 32.4                           | -5.1                           | 61.4                              | 98                                  | 40.0                                | 144             |
| Oamaru    | 27.0                           | -2.7                           | 37.8                              | 100                                 | 40.5                                | 49              |
| Otira     | 25.6                           | -6.6                           | <b>141.6</b>                      | 98                                  | 44.0                                | 248             |
| Oxford    | <b>32.8</b>                    | -4.3                           | 26.0                              | 97                                  | 37.0                                | 253             |
| Reefton   | 26.3                           | <b>-10.6</b>                   | 83.6                              | 98                                  | 35.0                                | 248             |
| Twizel    | 30.4                           | -8.6                           | 79.8                              | 100                                 | 42.3                                | <b>477</b>      |
| Wanaka    | 31.4                           | -5.2                           | 50.6                              | 100                                 | 49.7                                | 318             |

#### Agreement between maxent and oothecae

Overlaying the hatching success of the oothecae with the threshold prediction from the best estimate Maxent output gives an indication of the agreement between the approaches (see Figure 2.8). Less than half (11 of the 24) of the locations match in their prediction (oothecae hatched and Maxent predicts suitability  $N = 4$ , or oothecae didn't hatch and Maxent predicts unsuitability  $N = 7$ ), a clearly non-significant difference between this and random (0.5 probability) assignment (binomial  $P = 0.419$ ).

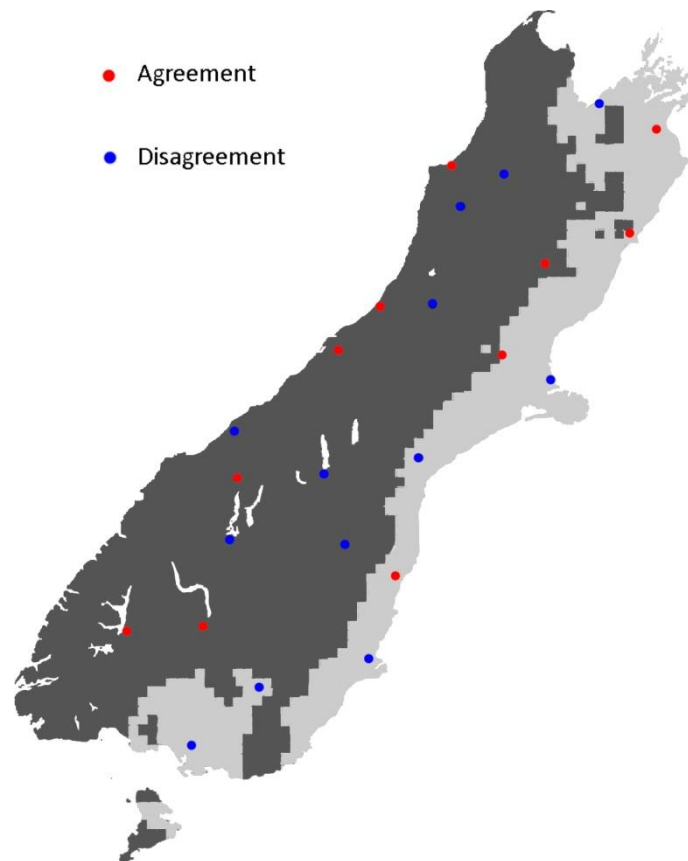


Figure 2.8 Distribution of points of agreement and disagreement between the best estimate Maxent output and the survival of oothecae.

## 2.4 Discussion

### Best estimate projection

The Maxent run using all available input data created a projection with high confidence (see Table 2.1) and predicted a general pattern of unsuitable habitat in the western half of the island and suitable habitat in the east (Figure 2.3 A). According to the model, there are areas of high suitability for *M. caffra* in coastal Marlborough, especially between Blenheim and Kaikoura and predictions of fairly suitable habitat also apply to large areas north of the Banks Peninsula and to the east of the Southern Alps. Despite a trend of greater suitability in the north, there are still large areas of moderately suitable conditions in the most southern regions, including a pocket of high climatic match around the Otago peninsula. Even the mid latitude areas of Stewart Island are identified as hospitable to *M. caffra* (Figure 2.3 A). While not indicating probability of occurrence, these values do suggest which areas are relatively more or less likely to be suitable for *M. caffra* and as such, which areas are most at risk of establishment. The most striking aspect of the projection is the

longitudinal division of the projection area into western and eastern halves. This may relate to the generally wetter conditions experienced west of the Southern Alps, suggesting that humidity or precipitation may be highly correlated with presence records in the input data for *M. caffra*.

Interestingly however, the jackknife procedure of Maxent mainly identified temperature-based features as being the most important, with precipitation having less effect on gain.

When a threshold of MTP is applied to this prediction, similar patterns are visible in the map because the run includes the true MTP record for the entire input data set (Figure 2.4 A). As the most informed projection, this run is used as the actual prediction of Maxent and the threshold version is used to compare agreement with the field data. Future monitoring of the continued expansion of *M. caffra* into the study area would be revealing in terms of the accuracy of this projection.

### Reduced input projections

The Maxent results using reduced input data sets all show variations on a theme, with the east coast being highly suitable relative to the west and pockets of suitable habitat around Nelson, Kaikoura and Dunedin. Similarly, some isolated areas of unsuitable habitat are suggested in Christchurch and south east of Gore (See Figure 2.3 B through E). The spatial prediction fluctuated quite widely between high and low input runs, but the variation was in favour of commission at low sample sizes, with smaller areas of potential habitat identified as unsuitable as the input levels were reduced. This is the lesser of two evils in the context in invasive species range prediction, as it indicates that error in the model is in favour of false positives rather than false negatives. Therefore, Maxent appears robust to the un-calibrated, low-input conditions which it was required to perform under in these cases, suggesting that it is a suitable tool for the use it is commonly put to in assessing the potential ranges of invasive species.

AUC scores deteriorated at low sample sizes because of the lack of representation in both the training and test data set. For example, with only 5 input localities and a 25% test partition, only one presence record is available to evaluate model performance. Nevertheless, AUC remained high in all but the lowest data conditions, indicating excellent capability of the model to distinguish real presences and absences. Unsurprisingly model confidence was low under these conditions however (see Table 2.1).

The greatest effect of reducing the input data was the impact on the MTP value of the presence data, evidenced by widely fluctuating areas of predicted suitability under this threshold (see Figure 2.4). This is the result of the particular combination of presence records used, showing that missing one vital presence record with a low value can drastically change the prediction. Continued testing of

SDMs under these data-scarce conditions will provide improved evaluation of their usefulness in the field of invasion biology, an application which is becoming commonplace.

#### Range overlap between species

The best estimate Maxent output suggests a large overlap between the potential range of *M. caffra* and the current locations of *O. novaezealandiae* populations in the South Island, especially in the northern areas (see Figure 2.6, above). Since *M. caffra* appears to be displacing the native species as its range expands (Ramsay, 1990; Chapter Y-choice; Brockerhoff, *et al.*, 2010), this suggests that there is significant potential for further loss of *O. novaezealandiae* abundance. However, there is an area of Otago which is predicted as unsuitable for *M. caffra* but which harbours a number of the *O. novaezealandiae* records. Consequently, there is likely to be a refugium in that area where the species should remain separate and *O. novaezealandiae* might persist even if *M. caffra* expands into the entire range predicted as potentially suitable by Maxent. This is an example of the way in which SDMs can help inform biodiversity protection; if the species in question were of conservation concern one might recommend prioritisation of this area in order to maximise the effectiveness of protection measures.

#### Oothecae hatching success

The oothecae hatched in a spatially scattered manner, with little recognisable pattern in the distribution of successful and unsuccessful hatching. There were nymphs alive in the vial at warm, dry, lowland locations such as Oxford as well as semi-alpine, high-rainfall areas such as Twizel and Otira. The fact that eggs survived for seven months and emergence was possible in areas with sub-freezing temperatures and regular snow and frost is surprising in its own right considering the small, exothermic organism involved. The concomitant success of oothecae in the contrasting conditions of northern Marlborough suggests a great resilience of the oothecae to climatic extremes. However, it is interesting to note that oothecae hatched in areas where the temperature dropped well below freezing (see Table 2.2) but not at any sites south of Oamaru (see Figure 2.7), where low temperatures would presumably be the limiting factor. This may be explained if the oothecae can easily survive extremes of temperature but fail to hatch if certain favourable conditions aren't met, such as a minimum number of warm days or daylight hours in order to trigger emergence. In other words it could be the case that oothecae failed to hatch in those locations because of a lack of the right conditions, rather than an excess of harmful ones. Alternatively, this could be due to extended periods of unfavourable conditions rather than singular extreme events. If there is a spatial trend in the survivability of *M. caffra* oothecae in the South Island, the sample size used here was unable to resolve it.



### Agreement between approaches

The scattered success of oothecae in the South Island indicates that there is more to the survival of the immature stages than climatic conditions. The lack of a latitudinal gradient in the survival of egg cases especially suggests that climate is not the deciding factor in whether or not hatching can occur. This may in part explain the low agreement between the field experiment and Maxent, which relies heavily on climatic data (see Figure 2.8). Although Maxent presumably uses the presence of adult individuals as locality data, unless these samples represent vagrant individuals far from reproductive populations, then the success of oothecae is also implicated. Therefore the disparity between the juvenile life stage used here and the records used by Maxent should not be responsible for these differences.

### Ootheca transport and dispersal of *M. caffra*

The range of locations in which the oothecae survived in this experiment suggest that they are able to withstand most climatic conditions that New Zealand can offer. In addition, this suggests that oothecae can remain viable in harsh climates for several months, so even discontinuous transport via the southern, alpine areas is unlikely to kill them. This is especially so since the current test was carried out during the coldest months of the year. In light of this, it is expected that live egg cases could reach any of the areas predicted as suitable by Maxent, meaning that no restriction to the model's projection is warranted based on the oothecae data. Predation of ootheca is uncommon (Ramsay, 1990), so climatic mismatch is a more likely cause of hatching failure. However, two species of unidentified hymenoptera have been found parasitizing *M. caffra* oothecae in New Zealand (Ramsay, 1990), a possible influence on their survival which cannot be quantified and included in this analysis.

### Inherent assumptions of both approaches

Due to time limitations, the oothecae survival in the South Island could only be tested over one season, which may not represent typical winter conditions due to natural climatic variation. As such it is recognised that the observed pattern of hatching success may have been different if the approach was repeated over several seasons. Regardless, if propagule pressure is maintained then only one suitable season is required for a species to become established. It is also assumed that the vials did not influence the survival of the oothecae in some way other than altering the temperature. As many steps as possible were taken to prevent them from collecting water, moving due to the wind or being exposed to adverse conditions during transit, however the influence of some factor which was not considered cannot be ruled out completely.

Because SDMs necessarily represent simplifications of natural processes, there are a number of assumptions involved in their projections as well (Guisan & Thuiller, 2005; Zurell, *et al.*, 2009).

Maxent relies on unbiased sampling to provide input (Elith, Phillips, *et al.*, 2010), however much survey data is influenced by human subjectivity and variable sampling effort, making it difficult to guarantee that a given database of species presence is unbiased (Ward-Paige, *et al.*, 2010; Michalcová, *et al.*, 2011). An especially common source of this bias is the tendency of taxonomists to survey areas which have all ready been shown to return good results, causing continued re-sampling of the same areas while other, less reliable localities are neglected (Sastre & Lobo, 2009; Wolmarans, *et al.*, 2010). The consequence of this for modelling applications is that the correlation between the locality data and the features used to train the model may not represent a true approximation of the relationship between the species and its environment (Sastre & Lobo, 2009). Subsequently, the projection based on this correlation will contain the same mismatch. This effect is likely to be especially amplified at small sample sizes, because the first records of presence which are made about a given species are likely to be the most obvious, and thus the most likely to be influenced by survey bias. In addition, these biases are especially common for hyper diverse groups such as the insects (Sastre & Lobo, 2009; Santos, *et al.*, 2010), which comprise a large proportion of the species which have become invasive globally (Crowder & Snyder, 2010). Hence, the assumption of unbiased samples is often going to be violated, and the results of SDMs need to be interpreted in light of this (Wolmarans, *et al.*, 2010).

Another important assumption inherent in SDMs is that the species in question is in a state of equilibrium with its environment in the native range (the so called equilibrium postulate (Guisan & Thuiller, 2005; Robinson, *et al.*, 2010)). Furthermore, they aim to predict a hypothetical equilibrium state in their projection (Zurell, *et al.*, 2009). Models also only take a snapshot of the species' range under the conditions that are prevalent at the time they are sampled (Guisan & Thuiller, 2005). However, the range might be altered drastically by environmental variations over time, giving highly inaccurate estimates of the factors which constrain the species spatial extent (Guisan & Thuiller, 2005). Unfortunately for invasion biologists, species that are shifting their ranges most often violate this assumption of equilibrium (Guisan & Thuiller, 2005; Elith, Kearney, *et al.*, 2010), adding another hurdle to the use of SDMs for predicting the spread of invasive species. This problem relates to the heavy reliance of SDMs on the niche concept (Guisan & Thuiller, 2005) and assumptions made about this include that the fundamental niche is spatially and temporally conservative (Rodder & Lotters, 2010). However, climatic niche shift might occur during invasion (e.g., Broennimann, *et al.*, 2007), creating a mismatch in the species behaviour between the native and invaded areas and violating basic assumptions of the approach (Elith, Kearney, *et al.*, 2010; Rodder & Lotters, 2010). This may be counteracted somewhat by the inclusion of locality records from the invasive range, as carried out presently.

In regards to Maxent specifically, the logistic output mode applied here assumes that the presence localities used as input relate to a probability of occurrence of 0.5, something that cannot be assessed without an exceedingly thorough survey of the target species throughout its range.

Fortunately, the South African presence records all fall within an area of numerous weather stations (Hijmans, *et al.*, 2005) so climatic conditions are well recorded there and this is unlikely to be a source of error in the predictions. This is unlikely to be the case for all species however, so sampling effort is also consequential regarding the climate data used in the model, as well as the species' presence records. In addition, the transferability of climatic correlation with species presence to distant locations is heavily assumption-laden. This is highlighted in this case by the projection of very unsuitable habitat in the western half of the South Island, where rainfall is very high and probably in excess of any of the locations from which the locality data are drawn. This means that the species is essentially "un-tested" as far as its survival in those conditions is concerned and the modelling algorithm is required to extrapolate from the organism's response to a different precipitation regime altogether.

Only a few studies have undertaken to assess how valid many of these assumptions actually are (Rodder & Lotters, 2010), so the interpretation of SDM outputs as gross indications of suitability rather than fine-scale predictions of presence is currently favourable. Because of these factors it is important to continue to test model performance at a variety of input levels, time frames and spatial scales (Elith, Phillips, *et al.*, 2010).

### Limitations

The results of Maxent are limited by the assumptions required in modelling species distributions from climatic correlation, as discussed above. The accuracy of these outputs is also constrained by the coverage of climate stations in both South Africa and New Zealand, as well as the resolution at which the interpolated data are mapped. These factors resulted in the minimum 1 km<sup>2</sup> grid cell size used here and the resulting coarseness of projections. The rate of dispersal of the study organism is also a factor which is currently beyond the reach of most SDMs' predictive capabilities, so the time until establishment in those areas suggested as suitable is still a completely unknown variable. The ootheca test was limited to one season by time constraints and the number of ootheca used was restricted by the productivity of the lab population of *M. caffra*, reducing the power of the test somewhat. Comparison of climatic variable importance suggested by the jackknife procedure of Maxent and the pattern of survival in the oothecae were not easily comparable, because data on the same derived features used by the model were not available for the South Island in the CliFlo data base of NIWA. The match or mismatch between these would have been interesting to examine.

## Conclusions

It appears that *M. caffra* could colonise large areas of the eastern South Island, particularly in the north-eastern quarter and some areas of the south-eastern coast. This is supported by the climatic resilience of the species' oothecae, which should allow it to reach any of these areas of the island by transport attached to human vehicles or materials. This does not bode well for the *O. novaezealandiae* which occupy the same areas, although there appears to be a likely zone of *M. caffra* exclusion in Otago where the native species is thought to occur. These results need to be taken in light of the assumptions inherent in the modelling process however, meaning that the outputs should be taken as general rather than specific predictions. Nevertheless, prediction of invasion sites is still of great interest to the study and management of invasive species (Mack, *et al.*, 2000).

This study supports the findings of Thorn *et al* (2009) and Pearson *et al* (2007) that Maxent can provide consistent predictions with very small sample sizes and little calibration, making it a useful tool for biosecurity research where presence data are especially likely to be lacking. Further development of SDMs such as Maxent for the use of predicting invasive species range is required due to the priority of prevention and pre-emptive control measures in managing these damaging organisms (Ficetola, *et al.*, 2007). Combinations of empirical and theoretical range prediction techniques are valuable tools for predicting the spread of invasive insects (Crowder & Snyder, 2010), however, use of actual specimens to validate the output of predictive software is a hitherto little-used technique (Stankowski & Parker, 2010). In this case, the results weren't particularly informative due to a lack of resolution in the approach, however external data sets are of great value for the evaluation of SDM predictions (Ficetola, *et al.*, 2007) so they should be sought wherever possible. Ongoing use of SDMs such as Maxent for invasion biology in diverse settings with many different species will provide valuable further validation and refinement of their use, improving their performance in this growing field.

# 3. Cannibalistic Siblicide in Early Instar Nymphs of *Miomantis caffra*

## 3.1 Introduction

### Kin selection

Many biological traits can be understood more easily in the light of kin selection theory (Mock & Parker, 1998). This takes into account the fact that individuals may increase their total fitness by aiding their relatives, due to the shared portions of their genome (West & Gardner, 2010). The more closely related the individuals, the greater the benefit of helping one another, a factor which may result in the evolution of so called altruistic behaviour (e.g., Nam, *et al.*, 2010). Altruism in the biological sense refers to an action that incurs a direct individual fitness cost to the actor and benefit to the receiver (Brosnan & Bshary, 2010). Such behaviours are not expected to arise under traditional natural selection alone, because of the potential to reduce the fitness of individuals performing them (West & Gardner, 2010). However, the existence of such behaviour can be explained by kin selection and the inclusive fitness benefits of helping relatives (Hamilton, 1964). The former refers to the evolution of behaviours that favour the survival of one's relatives, at a cost to one's own survival or fecundity and the latter refers to the total number of offspring and offspring-equivalents that an organism can produce (West & Gardner, 2010).

According to inclusive fitness theory (IFT), the evolution of this phenomenon is made possible by the fact that genes encoding traits which harm individual fitness may nevertheless increase in frequency throughout the population if the trait increases the fitness of the carrier's relatives, since they too are likely to carry the gene. In other words, they affect the inclusive fitness of the gene (West & Gardner, 2010). Hamilton (1964) described this with the statement that such genes should increase in frequency throughout the population when the benefit to the recipient multiplied by the relatedness of the individuals is greater than the cost to the actor. For this purpose, cost and benefit are measured in terms of reproductive output and relatedness by Wrights Coefficient, i.e., the probability that the genes of both at a randomly selected locus are identical by descent (Hamilton, 1964). This mechanism is thought to be responsible for the evolution of sociality, as well as the prevalence of seemingly altruistic behaviour in sub-social organisms. It is also of central importance to the origins of multicellularity (Nedelcu, 2009). However, there is an asymmetry between the

large body of theory which explains these observations and the paucity of empirical research supporting it (Mock & Parker, 1998; Brosnan & Bshary, 2010).

Nevertheless, the occurrence of altruistic behaviour has been demonstrated across kingdoms (Driscoll & Pepper, 2010), suggesting that kin selection is a pervasive mechanism of evolution. For example, the bacterium *Escherichia coli* when placed under antibiotic stress, shares drug resistance through the colony by the action of drug resistant mutants that produce the metabolic product indole at their own energetic cost (Lee, *et al.*, 2010). Indole is a signalling molecule involved in stress tolerance in *E. coli* and its secretion by resistant mutants protects individuals that are incapable of producing enough when under the effects of antibiotics. This allows the survival of less resistant relatives of the mutants, thus bolstering their inclusive fitness at the cost of individual fitness (Lee, *et al.*, 2010).

A plant example is given by *Impatiens pallida* which reduces its competitiveness towards kin relative to unrelated neighbours (Murphy & Dudley, 2009). These plants are able to identify related neighbours through root interactions and alter their allocation of resources to shading responses, such that they compete more strongly for light with unrelated neighbours (Murphy & Dudley, 2009). Many species of animal show altruism in a wide range of behaviours, most famously in the social hymenoptera where most of the colony forgo reproduction in favour of rearing their siblings (Crozier, 2008). However, it also occurs in sub-social animals, for example in the red squirrel *Tamiasciurus hudsonicus*, the females of which occasionally adopt orphaned extra-pair juveniles (Gorrell, *et al.*, 2010). Interestingly, the decision to adopt or not adopt an orphan in this species appears to closely follow Hamilton's rule; the mothers only adopted juveniles if their relatedness was great enough to offset the loss of fitness incurred to her own litter because of the addition of an individual. Additionally, they declined to adopt in cases where orphaned juveniles were present but not sufficiently related to increase their inclusive fitness (Gorrell, *et al.*, 2010).

Hamilton (1964) identified two ways in which kin selection may act, through kin recognition or population viscosity. Kin recognition, the ability to distinguish relatives from non-relatives, would allow discrimination to be displayed in the behaviour of the organism such that relatives are favoured over non-relatives (as in *I. Pallida*). Although this is central to kin selection, it may have initially been selected for other discriminatory reasons such as inbreeding avoidance (e.g., Metzger, *et al.*, 2010) and then been co-opted. Recognition of relatives can occur in several ways. One is self-referential phenotype matching (Gerlach & Lysiak, 2006), where organisms learn their own phenotype and then compare others to this template in order to assess similarity (e.g., Mateo, 2010). Another is to learn cues associated with siblings and parents during early development then retain this information in order to identify these specific individuals from others later in life (Sharp, *et al.*,

2005; Gerlach, *et al.*, 2008). In some cases, a combination of these may be used (e.g., Newey, 2010). Another mechanism that is independent of relatedness, known as the green-beard effect may produce a similar outcome if a recognizable phenotype is associated with the gene (or gene complex) that is responsible for altruism, such that carriers of the gene favour other carriers, thus increasing its frequency (West & Gardner, 2010). However, recognition may not be essential for kin discrimination if dispersal is limited (and population viscosity is therefore high, as in *E. coli*). In this case, interacting individuals are more likely to be related simply by chance than in populations of more dispersive organisms (Hamilton, 1964; Gardner, 2010). This would mean that altruistic acts to conspecific neighbours would garner greater benefits to inclusive fitness, and make the evolution of indiscriminate helping of others more likely (Lion & Gandon, 2010). However, altruism is not expected to arise if the resulting increase in survival would create negative density dependant regulation on the population (Lion & Gandon, 2010). Due to the factors outlined above, a core prediction of kin selection and IFT is that relatedness should influence the level of altruism between individuals (Anthony, 2003).

### Siblicide

A trait to which this is directly relevant is siblicide, which occurs in many species (Mock & Parker, 1998) and in some cases even appears to be obligate behaviour (e.g., Anderson, 1990). The destruction of such close relatives as siblings has direct consequences for the inclusive fitness of the actor, so the benefits of such behaviour must outweigh this cost if it is to be selected for (West & Gardner, 2010). This has been well studied in avian taxa, but data from other groups are needed to fully understand its evolution (Ento, *et al.*, 2010). In cases where siblicide is beneficial to the attacker, refraining from committing it can be considered an altruistic behaviour in the context of kin selection: the actor forgoes the benefit (at a cost to individual fitness) for the better of the recipient (and thus the actor's inclusive fitness). A special form of siblicide is presented by those organisms which prey upon members of their own species and thus potentially their own relatives, raising questions about whether kin selection may influence the evolution of this trait.

### Cannibalism

The predation of conspecific individuals occurs across a broad array of animal taxa (Agarwala & Dixon, 1992), including the arthropoda (Duarte, *et al.*, 2010), mollusca (Nicolai, *et al.*, 2010) and chordata (Myint, *et al.*, 2010). Cannibalism of the egg stage is especially common, with intraspecific oophagy occurring in most groups of egg laying animals (Polis, 1981). It is especially common in insects, with most predatory species regularly consuming conspecifics (Fagan & Odell, 1996). The behaviour is acknowledged to improve survival of the actor, to occur more frequently when alternative prey are scarce and to act as a population regulatory mechanism (Polis, 1981;

Agarwala & Dixon, 1992; Getto, *et al.*, 2005). Cannibalism can also account for a large proportion of total mortality, sometimes as much as 90% (Polis, 1981), clearly making it a powerful force in shaping population structure for certain species. Occasionally this includes filial cannibalism (the consumption of one's own offspring (FitzGerald, 1992)), which occurs in many animals (Mehlis, *et al.*, 2010), especially the teleost fishes (Manica, 2002) and in some cases can occur more commonly than heterospecific predation (e.g., Agarwala & Dixon, 1992). This is germane to kin selection because of the obvious relevance of consuming offspring to reproductive success, and of consuming siblings to inclusive fitness. This is especially so in cases where the consumed siblings are genetically identical, as in the cannibalistic bacterium *Bacillus subtilis* (González-Pastor, *et al.*, 2003). Indeed, research suggests that parents eat their young only when it contributes to their overall fitness in the long term (FitzGerald, 1992) and in some cases cannibalism of siblings is only displayed as a last resort in times of resource stress (e.g., González-Pastor, *et al.*, 2003).

However, although its occurrence is widespread, the propensity for cannibalism varies widely both intra- and interspecifically (Rudolf, *et al.*, 2010). One reason that some species are less cannibalistic than others may be the risk involved in attacking similar individuals (Getto, *et al.*, 2005), however this does not explain why some species do not cannibalise immature life stages when the risk of injury is small (Rudolf, *et al.*, 2010).

Another limit on the prevalence of cannibalism may be differential risk of pathogen transmission, if pathogens are selected for optimal virulence in hosts of a certain genotype (Getto, *et al.*, 2005). Under these conditions, infection may be minimized if the species in question can avoid feeding on close relatives, which would be more likely to carry strains of microbe which are adapted to the immune environment created by their own genotype (Pfennig, 1997). However there is little evidence that this actually occurs (Rudolf & Antonovics, 2007) and may be unlikely because cannibals actively remove one or more infected individuals from the population, but on average only result in one new infection (Rudolf, *et al.*, 2010). This leaves kin selection as the probable limiting factor on the prevalence of cannibalism, meaning that cannibalistic species offer a convenient opportunity to study the role of kin selection (Mock & Parker, 1998). In this context, cannibalism is expected to become more common as genetic relatedness is reduced (Fox, 1975). Passing up the opportunity to cannibalise another individual can be regarded as an altruistic act since it involves a cost (loss of a meal) that benefits the spared victim (Anthony, 2003). This is supported by the observation that cannibalism generally increases the survival of the attacker (Dobler & Kölliker, 2010). In other words, the actor confers a survival gift *sensu* Lion & Gandon (2010).



In regards to siblicidal cannibalism, it should be noted that the fitness cost to a cannibalized sibling is not quite 100%, because its sacrifice is nourishing a close relative which is expected to carry some identical genes. Likewise, cannibalism of a sibling or other close relative does not represent a 100% positive effect on fitness because of the loss of inclusive fitness due to removing copies of shared genes from the population. In order for the effect of cannibalism on fitness to be positive and the causative genes to be selected for, the gain in individual fitness must outweigh loss of inclusive fitness (Dobler & Kölliker, 2010). This is likely in many cases however, as conspecifics usually represent a high quality food source, meaning that the energetic payoff can be lucrative (Gray, *et al.*, 2009; Rudolf, *et al.*, 2010).

Another reason for the persistence of cannibalism is that it may represent a form of density dependent population self-regulation through negative feedback on survival rates when individuals are numerous (Prete, 1999). In any case, it is more likely to arise if close relatives can be avoided because this allows reduction of the cost to inclusive fitness (Sherratt, *et al.*, 1999). Such behaviour has been identified in many cannibalistic amphibian species, such as the anuran *Spea multiplicata* (Pfennig & Frankino, 1997) and the salamander *Hynobius retardatus* (Wakahara, 1997), so it is conceivable that other species also have mechanisms of discriminating against attacking kin. Accordingly, because the study species in this case (*M. caffra*) is highly cannibalistic (Ramsay, 1990), we might expect some degree of kin discrimination to be displayed, as has arisen in several otherwise cannibalistic taxa because of the inclusive fitness loss involved in consuming one's own close relatives (Anthony, 2003; Dobler & Kölliker, 2010).

#### *Miomantis caffra* nymphs

*M. caffra* displays a phasic style of egg hatching, with small groups of nymphs emerging over a period of months (Ramsay, 1990). Newly eclosed *M. caffra* nymphs are usually 5 - 5.5 mm in length and immediately aggressive, quick moving and capable of capturing prey of a size equal to or smaller than themselves, including other nymphs (Ramsay, 1990). If this cannibalism is not kin-discriminated, it may suggest that the extended hatch phenology shown by *M. caffra* is an adaptation to protect nymphs from each other. If cannibalism is less likely between siblings (as in the spider *Stegodyphus lineatus* (Bilde & Lubin, 2001)), then the hatch phenology may have evolved to best overcome environmental stochasticity (Ramsay, 1990). However data from a species with different phenology (such as *Orthodera novaezealandiae*) would be necessary in order to examine this.

*M. caffra* nymphs hatch as orphans because of the univoltine life history of their parents (Ramsay, 1990), making their siblings the only relatives they have with an expected genetic relatedness of 0.5. For the same reason, they will never encounter their own offspring in the wild. This means that

if they do show discrimination in their cannibalistic tendencies, it should be in favour of their siblings as these are the closest relatives they will ever come across. Sharell (1971) observed *M. caffra* nymphs cannibalising one another before dispersing, so they are known to do so as long as they remain within proximity of each other. However, the likelihood of an encounter between nymphs depends largely on their dispersal propensity; if they do not move rapidly away from the ootheca after hatching, then their density will be high, increasing the risk of siblicidal cannibalism (Polis, 1981). In this case, kin recognition and discrimination is expected to arise to counteract it (Rudolf, *et al.*, 2010). Because of this, the dispersal of nymphs from their hatching location is pertinent to our predictions about kin selection and cannibalism in this species. However, the usual density of nymphs around their parent oothecae is probably high for several reasons. Up to 100 nymphs can hatch from each egg case (Ramsay, 1990), often in batches of 5 to 20 at a time (pers. obs.). The ootheca is fixed in position, unlike some insects which carry or periodically move them about (e.g., *Blattodea* sp. (Bell, *et al.*, 2007)), so all the nymphs hatch into the same area. They are unable to fly until reaching adulthood, which is not usually for around 5 months and even then only in males (Ramsay, 1990). In addition, they are cryptic, ambush style hunters and as such, spend a large proportion of their time awaiting prey while stationary. However, in order to confirm this, the typical density of nymphs after emergence is estimated and their hatching and dispersal rate are also examined.

#### Influence of body mass

Relative body mass can affect the occurrence of siblicidal and cannibalistic behaviour (Polis, 1981; Hvam, *et al.*, 2005) and a size difference reduces the inherent risk in attacking a conspecific for the larger individual (Rudolf, *et al.*, 2010). Therefore, we should expect cannibalism to be more prevalent in groups of nymphs within which there is some variation in size (Crumrine, 2010). A corollary of this is that if siblings avoid attacking each other even when there is a size difference (and risk is consequently lower for the larger nymph) then it would add weight to the conclusion that they display discrimination against attacking kin. Therefore cannibalism rates are examined here in groups of siblings and non-siblings comprised of both similarly sized and differently sized individuals. It could be possible for the size difference to confound a test of relatedness discrimination if nymphs use size to assess kinship, however size is not a good indicator of relatedness in this species because the nymphs hatch over a long period of time (Ramsay, 1990), allowing some siblings to outgrow others. As a result there should be mixtures of sizes within related broods of *M. caffra* nymphs in the wild.

### Predictions

Some previous studies have found evidence of kin discrimination in cannibalistic insects and others have found none (Sherratt, *et al.*, 1999; DeWoody, *et al.*, 2001; Gray, *et al.*, 2009). However, many studies on siblicide have focused on species with parental provisioning (e.g., Dobler & Kölliker, 2010; Ento, *et al.*, 2010), where individuals stand to gain resources by outcompeting or killing their siblings. In the case of *M. caffra* there is no such influence, and the evolution of behaviour towards siblings is based entirely on interactions within one generation. Consequently and according to kin selection theory, discrimination of kin is likely and siblings should attack each other less often than non-siblings. Alternatively, if selection on indiscriminate aggression is strong, as suggested via aggressive spill-over, siblings will be attacked as often as non-siblings.

Because of the factors discussed above it is predicted that cannibalism will be highest in differently sized unrelated groups, intermediate in differently sized siblings and unrelated but equally sized groups and lowest in groups of equally sized siblings.

## **3.2 Methods**

### Specimens

Oothecae were produced in the lab by captive *M. caffra* females over the period of March to June 2010. These females were kept on a plentiful diet of *Galleria melonella* larvae (Lepidoptera), *Tenebrio molitor* larvae (Coleoptera), *Locusta migratoria* juveniles (Orthoptera), *Drosophila melanogaster* adults (Diptera, flightless morph), *Sitophilus oryzae* adults (Coleoptera), *Exaireta spinigera* larvae (Diptera) and *Plodia interpunctella* larvae (Lepidoptera). The lab-laid oothecae were supplemented by 20 wild gathered egg cases to increase the availability of nymphs. When clutches began to hatch (in September 2010) they were split into fed and non-fed groups of siblings to create a within-brood size difference. Nymphs of the fed groups were allowed to prey *ad libitum* on *D. melanogaster* (flightless morph), those of unfed groups were not given any alternative prey but some cannibalism occurred. Both fed and un-fed nymphs were misted with water daily.

### In situ density and dispersal experiment

In order to estimate the natural density of nymphs that occurs near the oothecae in the wild the following procedures were carried out. A 1.8 m tall Kowhai (*Sophora microphylla*) sapling was cleared of any spider webs and wild mantis nymphs or oothecae. To simulate a hatching event, 10 newly hatched, sibling nymphs from lab-produced oothecae were placed at the plant's centre and the site of release was marked with a pencil. The sample size of 10 was chosen because most emergences of *M. caffra* nymphs observed in the lab consisted of 5 to 20 individuals. Once each day

over the following 5 days the number of nymphs remaining on the sapling was re-sampled with a thorough 10 minute search and the distance of each nymph found from the point of release was measured. This was repeated 7 times, but one 5-day set was excluded from analysis because it fell within a period of stormy weather conditions and winds were uncharacteristically high. During sampling it was noted that many nymphs remained in the same position from day to day, so the number of nymphs to remain on the same compound leaf for  $\geq 3$  consecutive days was counted. Although possible, it is not considered likely that nymphs would have swapped position perfectly and interfered with this count.

### Cannibalism experiments

Using lab-produced nymphs, treatment enclosures were set up in the following combinations. Sibling enclosures contained 10 nymphs from the same brood, non-sibling enclosures contained 5 nymphs from one brood and 5 from another. Different size nymph enclosures contained 5 nymphs from a fed group and 5 from a non-fed group. A sub sample of these different sized nymphs had a mean pronotum length of  $2.218 \text{ mm} \pm 0.18 \text{ SE}$  ( $N = 16$ ) in “large” nymphs and  $1.288 \text{ mm} \pm 0.06 \text{ SE}$  ( $N = 16$ ) in small nymphs. First or second instar nymphs were used for all enclosures, however some moulting occurred during the experimental period, so enclosures generally contained a mixture of first to third instar nymphs.

Table 3.1 Combinations of nymph size and relatedness used in experiments, each having 10 nymphs.

| Group          | Sibling  | Non-sibling |
|----------------|----------|-------------|
| Equal size     | $N = 15$ | $N = 16$    |
| Different size | $N = 15$ | $N = 16$    |

Each set of 10 nymphs was placed into an approximately  $30 \text{ cm}^3$  enclosure made of fine mesh screen, with a polyurethane window. These were misted with water daily. The number of surviving and dead nymphs was counted each day for 10 days. Any dead nymphs were inspected under a Leica MZ6 dissecting microscope for signs of cannibalism. If they were dismembered, had puncture wounds or were missing parts of the abdomen, thorax or head then they were counted as cannibalized, otherwise as having died of other causes. Loss of one limb or antennae was considered possible through problems with ecdysis so only those with more than one missing appendage were counted as cannibalised. Any moulted cuticle was removed from the enclosures daily. Nymphs were counted before and after opening the enclosures to ensure no escapes occurred; none were unaccounted for so any missing (i.e., not counted as dead or surviving) were presumed to

have been completely cannibalized. One enclosure had an unusually high natural mortality level within the first few days. This was excluded from analysis as an outlier because the density of nymphs was altered relative to the other enclosures, which could easily affect the cannibalism rate. This, as well as the availability of nymphs resulted in the number of treatments in each group given in Table 3.1.

### Statistics

All tests were carried out using the statistics package PAST© version 2.08 (Hammer, *et al.*, 2001).

#### Dispersal:

To estimate the natural density of nymphs after hatching, the mean number of nymphs to be re-sampled on each day and the mean distance of all nymphs from their release point on each day were calculated. The starting and ending number and distances of nymphs were both found to be non-normally distributed using the Jarque-Bera normality test. Therefore, the difference in number between first and last day was compared using the Mann-Whitney test, as was the difference in distances.

#### Cannibalism:

The mean number of nymphs to be cannibalised on each day was calculated for each treatment type. Normality of distributions was not found using Jarque-Bera tests, so the Kruskal-Wallis non-parametric ANOVA was used, to test the null hypothesis that the samples were taken from populations with equal medians. This included pair-wise two tailed Mann-Whitney tests made between each group.

Critical alpha levels were 0.05 for all statistical tests.

Means are reported with their standard error ( $\bar{x} \pm \text{SE}$ ).

## **3.3 Results**

### In situ density and dispersal experiment

Upon release onto the plant, nymphs typically moved several cm upwards on the main stem until they reached the underside of a leaf. During this initial dispersal, nymphs often encountered one another, sometimes clambering over their siblings to proceed up the branch. Nymphs were successfully recounted on every sample made, often being found in the same location on each day. On average, several nymphs could be found remaining on the plant on each of the following five days, with a slight reduction in their number over that period (see Figure 3.1). At the end of five

days, there were still  $3.2 \pm 0.6$  nymphs remaining on average, with a maximum of five and a minimum of one. Of the 30 nymphs released for this trial, 18 remained on the same compound leaf for  $\geq 3$  consecutive days. The nymphs that were re-sampled did not move far after the first day, with mean distance from the release site staying nearly constant over the observational period (see Figure 3.2). There was no significant difference between the number of nymphs present on the first and last day of the trial ( $U = 7.5$   $P = 0.102$ ) or their distance from the starting location ( $U = 328.5$   $P = 0.628$ ).

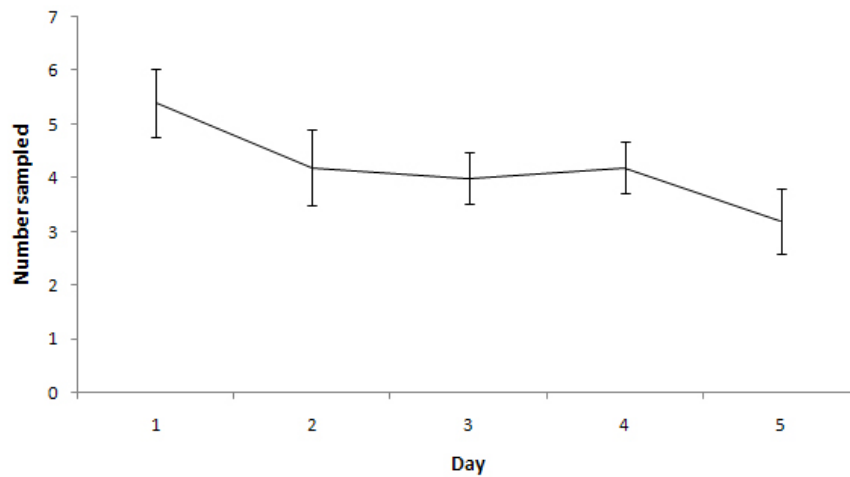


Figure 3.1 Mean  $\pm$  SE number of nymphs re-sampled each day.  
Initial release  $N = 10$ .

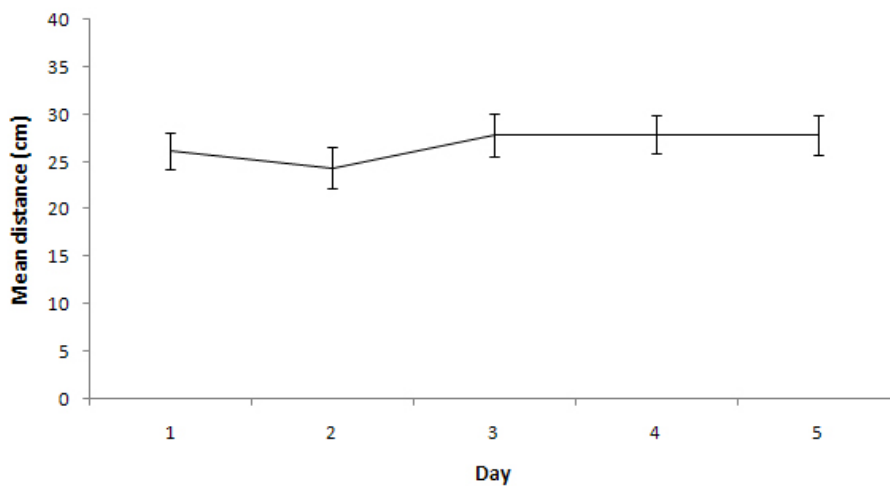


Figure 3.2 Mean  $\pm$  SE distance of re-sampled nymphs from the release point.

Note that because the nymphs are small and cryptic in colouration and behaviour, the actual number remaining was probably higher than that recorded by the researcher. This is also suggested by higher counts occasionally being made on subsequent days, indicating that some nymphs were missed on preceding counts. Therefore these represent conservative estimates of nymph density. Using the estimates of Ramsay (1990) of approximately 100 nymphs emerging from each ootheca over a 4 month hatching period, we could expect a mean of 4.1 further nymphs to hatch during 5 days. As this is greater than the loss of nymphs from the plant observed in this case, their density should tend to increase throughout the hatching period, with several nymphs within 30 cm from the ootheca on any given day during that time.

### Cannibalism experiments

Cannibalism was commonly observed in both sibling and non-sibling enclosures, accounting for greater loss of nymphs than natural mortality in all treatments with the exception of the equal sized non-siblings (see Table 3.2).

Table 3.2 Mortality across different treatments at the end of 10 days. Initial group size  $N = 10$ .

| Group                       | Mean final number<br>cannibalised $\pm$ SE | Mean number of natural<br>deaths $\pm$ SE |
|-----------------------------|--|---|
| Equal size siblings         | $3.40 \pm 0.50$                            | $2.93 \pm 0.59$                           |
| Different size siblings     | $5.07 \pm 0.45$                            | $2.43 \pm 0.52$                           |
| Equal size non-siblings     | $2.68 \pm 0.45$                            | $4.81 \pm 0.72$                           |
| Different size non-siblings | $5.63 \pm 0.61$                            | $2.13 \pm 0.51$                           |

Kruskall-Wallis ANOVA indicated a significant difference between groups ( $H = 17.5$   $P < 0.0001$ ). The final number of nymphs cannibalised at the end of 10 days was not significantly different between same sized sibling and non-sibling enclosures ( $U = 94.5$   $P = 0.311$  and see Figure 3.5). In addition, the mean number of nymphs to be cannibalised remained similar between relatedness groups throughout the ten day period (see Figure 3.3). In fact, the mean final number cannibalised was higher in sibling ( $3.4 \pm 0.5$ ) than non sibling ( $2.6 \pm 0.45$ ) enclosures when size was equal, although not significantly so ( $U = 94.5$   $P = 0.312$ ).

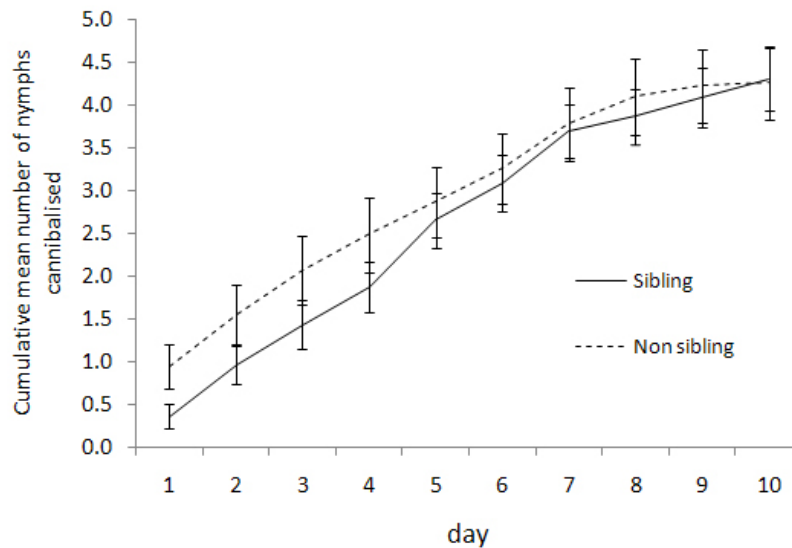


Figure 3.3 Cannibalism ( $\pm$  SE) over time in enclosures containing sibling or non-sibling groups, regardless of size class.

There was a difference between final number cannibalised in same-size and different-size nymphs when relatedness was combined, with enclosures that had a size difference showing a significantly higher rate of cannibalism ( $U = 189.5$   $P < 0.0001$  and see Figure 3.4). Despite this however, there was still no significant difference in final number cannibalised between sibling and non-sibling groups when there was a size difference between nymphs ( $U = 97.5$   $P = 0.378$ ), although cannibalism was slightly higher in non-siblings (See Table 3.2).

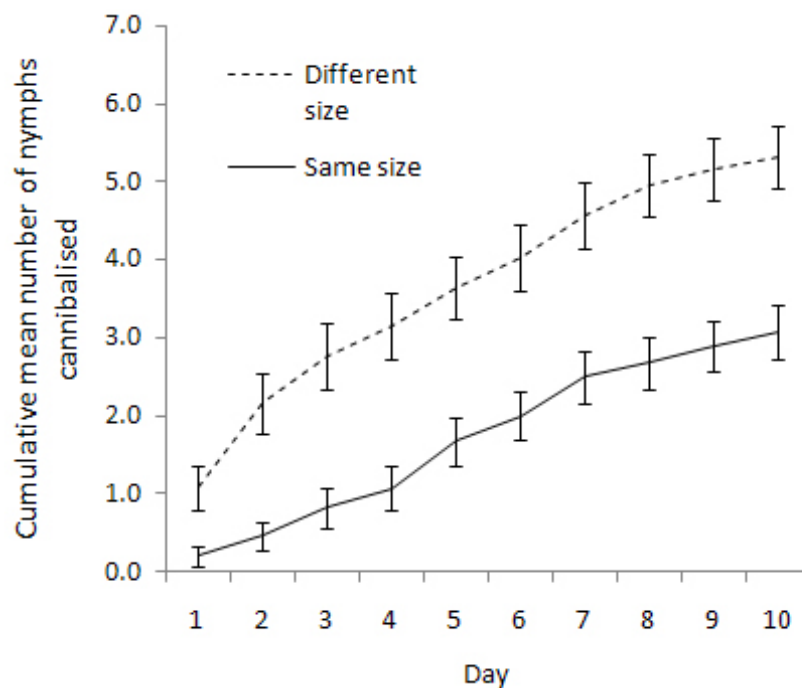


Figure 3.4 Cannibalism ( $\pm$  SE) over time in enclosures containing same or different sized groups, regardless of relatedness.



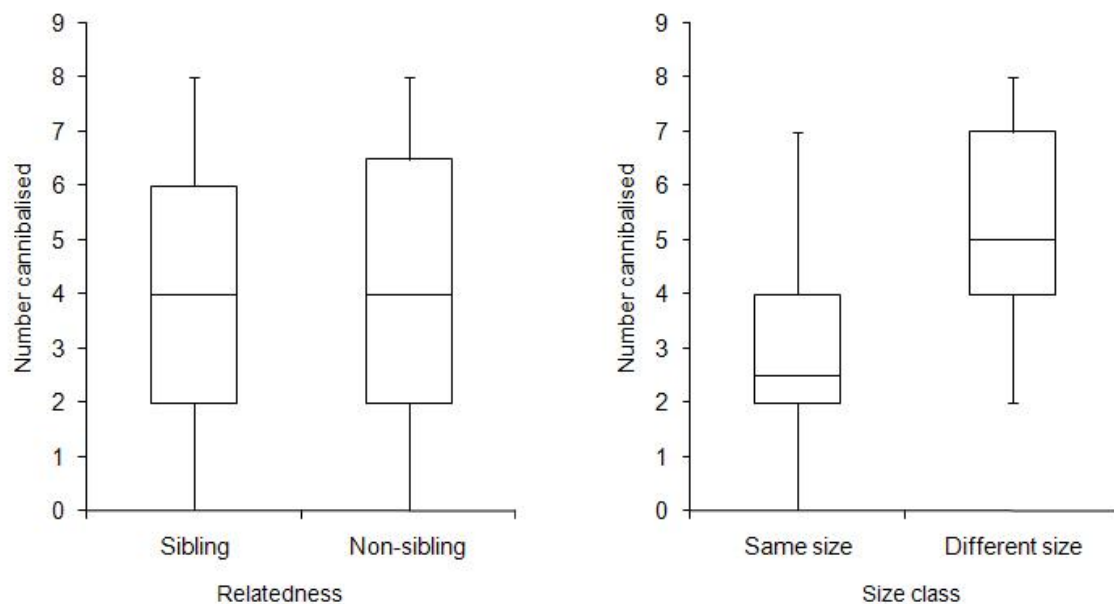


Figure 3.5 Number of nymphs to be cannibalised by the end of 10 days in sibling and non sibling groups with size categories combined (left hand plot) and in same and different sized groups, with relatedness combined (right hand plot). Horizontal bars represent the median number cannibalised, the upper and lower edges of boxes represent the third and first quartiles respectively and whiskers represent the maximum and minimum number cannibalised.

### 3.4 Discussion

#### Density

The slow reduction in nymph abundance on the test plant suggests that they tend to remain numerous near the ootheca after hatching. The lack of movement observed for many nymphs as well as their unchanging average distance from the release point over time indicate that they are not naturally dispersive and that the reduction in numbers was more likely to be due to mortality. This local density of nymphs around hatching oothecae makes encounters between early-instar juveniles likely, thus providing the opportunity for aggression between siblings. Since the nymphs remained on average within a 30 cm radius sphere centred on the release point, and over 100 nymphs can hatch from each ootheca (Ramsay, 1990), the probability of encounters between siblings is expected to be high over the hatching period.

#### Cannibalism

These results suggest that the nymphs of *M. caffra* do not show kin-biased discrimination in their

cannibalistic behaviour, despite the seemingly high likelihood of encounters between them after hatching. This is in contrast to studies which have found that discrimination does occur in other species of insect (e.g., Agarwala & Dixon, 1992). The nymphs did not cannibalise non siblings any more than siblings, even when there was a size difference between them and cannibalism should have been easy, thus supporting the suggestion that they do not bias their intraspecific predation efforts away from relatives. This is interesting because cannibals should be more likely to encounter relatives than arbitrary individuals due to their hatching proximity, which should cause cannibalism to result in more mortality of relatives on average unless a mechanism arises to prevent it, suppressing the appearance of cannibalism (Getto, *et al.*, 2005).

It is conceivable that the low food conditions of the enclosure forced siblings to cannibalise at a rate higher than they normally would simply in order to survive, thus masking any difference between the treatments. However, this does not appear to be the case because many ( $N = 14$ ) of the enclosures had low levels of cannibalism (i.e.,  $\leq 2$  nymphs missing) and yet several survivors, indicating that starvation was not severely affecting the groups. This is supported by the observation of a difference in cannibalism rate between size classes, as this shows that the nymphs were able to alter the rate of cannibalism and weren't forced to cannibalise at a certain level by the laboratory conditions i.e., to avoid starvation. Furthermore, mantids are generally adapted to withstand starvation, which is likely to occur during their development in the wild (Ramsay, 1990). For example Matsura (1981) found that the mantis *Paratenodera angustipennis* was able to live for up to 37 days without food.

The increased prevalence of cannibalism in enclosures with size variation supports the findings of studies which have shown within-cohort body mass differences to influence cannibalism in other juvenile insects (e.g., Lounibos, *et al.*, 1996; Crumrine, 2010) including a praying mantis (Fagan & Odell, 1996). This is important in regards to the influence of cannibalism on size structure in natural populations because that in turn impacts upon intraguild predation and competition in the community (Crumrine, 2005; Armsby & Tisch, 2006; Rudolf, 2007). For example, Wahlstrom *et al* (2000) found that size dependent cannibalism in lake perch created body mass structure within the population which influenced zooplankton density and mean size, which in turn altered phytoplankton abundance cycles. This is also interesting because various life history, developmental and ecological factors combine to promote size variation within cohorts of most mantid species (Fagan & Odell, 1996), suggesting that selection does not often suppress high levels of cannibalism in these species.

### Lack of kin discrimination

There are three mechanisms for reducing intra-brood cannibalism which might be employed by a species such as *M. caffra*: recognition and avoidance of kin, rapid dispersal from the oothecae and asynchronous hatch phenology. *M. caffra* nymphs do not appear to show any tendency to avoid their siblings, so kin recognition appears unlikely. Rapid dispersal also does not seem to be used by this species to reduce siblicide, since their movement away from the oothecae was very limited here. The extended hatching phenology could be a mechanism to allow nymphs to escape each other, except that since they don't seem to quickly disperse this is unlikely to function in that manner. This is especially so since it serves to create a size difference within the brood (Fagan & Odell, 1996), which appears to increase the rate of cannibalism (Huss, *et al.*, 2010). Therefore it appears that *M.caffra* lacks traits to reduce within-brood cannibalism. Since IFT clearly predicts that cannibalism of siblings should be avoided if possible (Hamilton, 1964; Anthony, 2003), the lack of any discrimination in the juveniles of this species raises questions as to why. This siblicidal predation might arise from a lack of recognition ability or a lack of avoidance behaviour. However *M. caffra* nymphs have ample opportunity to employ phenotype matching to recognise their siblings because they develop together in the same ootheca for several months , as well as having acute visual and chemosensory faculties (Ramsay, 1990). Because of this, a lack of ability to recognise kin is probably not responsible for the indiscriminate cannibalism they display. There are however several possible reasons why (which each generate further hypotheses) and two general aspects which might cause this behaviour to be retained: the predation of siblings is actually adaptive, or it is maladaptive but nevertheless persists for other reasons. Quantification of the fitness effects of sibling cannibalism in *M. caffra* nymphs would be highly useful in illuminating the reasons for its persistence in the population.

An adaptive explanation is that parents often produce more offspring than they or the environment can provide for, necessitating a negative regulation on the population during development (Mock & Parker, 1998), termed brood reduction (O'Connor, 1978). This seemingly wasteful oversupply may actually be beneficial, as it allows exploitation of stochastic increases in resource availability (e.g., Sergio, *et al.*, 2010), the ability of some offspring to provide essential nutrients to their siblings through cannibalism and for killed or injured members of the brood to be replaced, so that optimal density is maintained (Mock & Parker, 1998). This bet-hedging strategy equates to having some offspring on standby, in case conditions happen to support greater than usual density or mortality is unusually high (Simons, 2007). Thus the parallel brood characteristics of high nymph numbers and intra-brood cannibalism may serve to allow *M. caffra* to exploit temporary abundances of food resources, while allowing the energetic costs of high egg production to be recouped through cannibalism at other times.

In cases where kin cannibalism occurs, siblings can be thought of as resource caches that autonomously gather more food for their clutch, returning it in the form of their own biomass (Polis, 1981; Sherratt, *et al.*, 1999). This is an extension of the trophic egg concept which refers to the parental provisioning of offspring with un-hatched siblings (Kim & Roland, 2000). In some species this can represent a major component of the diet, for example in black widow spiders (*Latrodectus* sp.), individuals are able to develop to within 1 moult of adulthood solely on the sustenance given by their un-hatched sibling eggs (Kaston, 1968). This may be especially beneficial if younger nymphs are capable of accessing prey items which become unavailable to larger instars as they grow, such that they can be exploited by the mantis throughout its development via cannibalism (Polis, 1981; Getto, *et al.*, 2005). In some cases (e.g., Nikolskii, 1969) this is the only source of nutrition in adults for whom alternative food is no longer available, thus it is the juvenile's feeding which sustains the reproductive population (Polis, 1981). Therefore, siblicidal cannibalism may arise as a way for the mother to provide more of the energy she has available for the brood to a portion of the offspring, if the amount she is able to allocate to each is limited, for example by a maximum possible individual egg mass. Female *M. caffra* cannot provision for their offspring directly because of their non-overlapping generations, but in this manner may nevertheless be able to feed them by providing extra siblings as a living food source. Hatching asynchrony, as occurs in *M. caffra*, is conducive to within-brood cannibalism (Crumrine, 2010) and as such is expected to arise in species which use the trophic egg or resource cache strategy of parental investment (Polis, 1981). This strategy may be more likely to arise in species with a sit-and-wait hunting strategy (such as *M. caffra*), in order to increase the efficiency of foraging, thus it is possible that this is the case here.

However, it is not necessarily the case that because a trait persists it must be adaptive. For example, it may be an evolutionary relic (e.g., Rothstein, 2001) or a maladaptive trait that is linked (as by pleiotropy) to another beneficial one which is under strong positive selection (e.g. Krüger, *et al.*, 2001). Consequently, the possibility that the observed siblicide may simply be maladaptive must be considered and adaptive explanations remain speculative in the absence of empirical evidence (Andrews, *et al.*, 2002). With that caveat, there are a number of additional explanations for this behaviour which could be tested with *M. caffra*.

It has been suggested that kin biased discrimination should not be expected to arise in situations where competition among relatives is high (Queller, 1994). In such situations, the nutritive benefit of consuming a relative is likely to be high, as is the competitive benefit of eliminating another predator from the system (Sherratt, *et al.*, 1999). Therefore under those conditions, indiscriminate cannibalism may be adaptive despite the genetic cost incurred to inclusive fitness (Rudolf, *et al.*,

2010). Queller (1994) demonstrated mathematically that altruism towards kin should not be expected to occur in these cases where relatives compete heavily for resources. Since *M. caffra* nymphs occur at high densities and have a somewhat restricted diet (i.e., only living invertebrate prey of an appropriate size for their current instar (Ramsay, 1990)), there may indeed be high competition for food during their development. Under these conditions, the energetic and nutritional payoff of cannibalism is likely to be high and may exceed the genetic cost of consuming a relative, especially as the meal comes with the indirect benefit of eliminating a competitor (Tóth, *et al.*, 2010). In addition, if competition for resources is high and juveniles stand to gain by removing conspecifics, then siblicide may arise as a by-product of the species recognition system they use (Grafen, 1990). Since siblings tend to be more similar to each other than non-siblings, then they should recognise them as conspecifics more easily if this is carried out by a self-referential phenotype matching process (e.g., Le Vin, *et al.*, 2010). If coupled with a drive to remove conspecifics from the habitat (due to their potential for competition), this could result in an apparent preference for aggression toward kin (Gray, *et al.*, 2009).

An alternative reason for high rates of cannibalism in some species is aggressive spill over, or the selection for aggression levels which are necessary to ensure successful foraging but which are also displayed in other behavioural contexts where they may not be adaptive (Johnson & Sih, 2005). This is especially likely when aggression is beneficial during certain life stages but then retained into adulthood (Morse, 2004; Johnson & Sih, 2005). This hypothesis has been supported by research on the fishing spider *Dolomedes triton* in which propensity for pre-copulatory sexual cannibalism is correlated with aggression levels displayed throughout development (Johnson, 2001; Johnson & Sih, 2005). This may apply to *M. caffra* if it is necessary for nymphs to display aggression of a certain level in order to gather enough food to reach adulthood, regardless of whether it means killing siblings in the process, as found in the ladybirds *Propylea dissecta* and *Coccinella transversalis* (Pervez, *et al.*, 2005). Accordingly, it could be that cannibalism of siblings is a purely maladaptive trait that exists in the population due to selection for high foraging aggression, the benefit of which outweighs the cost of lost siblings. This is a behavioural syndrome *sensu* Sih *et al* (2004), in that there is a correlation in the behaviour shown by the organism between contexts, in this case foraging and interacting with siblings. This lack of plasticity in behaviour can help explain several interesting and seemingly detrimental traits, such as inappropriately high levels of pre-copulatory cannibalism (Arnqvist & Henriksson, 1997) or activity in the presence of predators (Maurer & Sih, 1996). Therefore if sibling cannibalism is detrimental in this species, this is a possible reason for its retention. This is an example of the ecological factors which may mean that kin discrimination regarding predation might simply be too costly to individual fitness to arise (Gray, *et al.*, 2009).

Damagingly high levels of cannibalism might also evolve simply because genes for high cannibalism should tend to remove genes for low cannibalism from the population, thus increasing their relative fitness. This process would tend to move genes for cannibalism towards fixation over time, and thus create situations where species exhibit siblicide even if it reduces their fitness. This is especially likely in a population where a certain level of cannibalism persists, such that the optimal strategy for reaching maturity is to be more cannibalistic than cohort members, particularly where outgrowing one's peers has a protective effect due to the size dependence of cannibalism probability (Fagan & Odell, 1996). If nymphs which refrain from cannibalism have relatively slowed development or reduced mass as shown in the caddis fly *Asynarchus nigriculus* (Wissinger, *et al.*, 2004), then that phenotype will inevitably be destroyed by the larger nymphs that do cannibalise, making it impossible for kin avoidance to arise. Determining whether or not the cannibalism observed in *M. caffra* nymphs results from a lack of recognition ability or a lack of restraint would also be informative in revealing whether the behaviour is selected for or simply a side effect of another trait. Estimation of the proportion of nymphs per oothecae that die due to cannibalism rather than other causes, as well as the number which generally survive to adulthood in the wild would also be useful in order to better understand the consequences of siblicide in this and other species.

Clearly, the effects of cannibalism and siblicide in particular on the evolution of kin recognition and discrimination are still not well quantified (Dobler & Kölliker, 2010), so elucidation of these possibilities is important in order to further our understanding of these behaviours (Rudolf, *et al.*, 2010). This is especially so since the importance of IFT in the evolution of sociality has recently been called into question (Nowak, *et al.*, 2010).

There is probably some bias in the literature towards reporting those cases where discrimination is demonstrated (Sherratt, *et al.*, 1999). However, studies which find little or no discrimination are informative because they provide other contexts to which kin selection and IFT are relevant, as well as being important to other behaviour such as oviposition site selection, clutch size determination and levels of parental provisioning (Sherratt, *et al.*, 1999). Studying this is also important because we still have a limited understanding of the evolutionary effects of cannibalism on other biological traits and interspecific interactions (Rudolf, 2008; Rudolf, *et al.*, 2010). The absence of kin biased discrimination in a certain species therefore opens further questions about their ecology and behaviour. Whether this occurs in other species of mantid is unknown and hence it is an interesting topic for future investigation.

### Limitations

The conclusions which can be drawn from the current study about the rate of cannibalism in *M. caffra* siblings are limited by the narrow age group used in the experiments. Only early instar nymphs were used, so the results are limited to describing their behaviour. Whether older juveniles or adults show the same trend would be interesting to discover, but could not be assessed here as priority was given to boosting sample sizes in the first and second instars rather than retaining nymphs to examine in later moults. However, due to the high mortality experienced by the nymphs, their density is likely to be highest during the early stages soon after hatching, so this is where kin-biased discrimination might be expected to be most important and most strongly expressed, if present.

### Conclusions

Cannibalism in the nymphs of *M. caffra* is not influenced by their relatedness in the early instars, despite a high probability of encounters between siblings soon after hatching.

The cannibalism rate does seem to be increased by size variance within cohorts however, an interesting feature because of the asynchronous hatching phenology of the species, which ensures that groups of siblings will differ in size.

Nymphs of *M. caffra* do not appear to undertake rapid dispersal away from their ootheca after hatching, suggesting that this is also not a mechanism of reducing intra-clutch cannibalism which they utilise. As a result it appears that this species lacks ways of decreasing siblicide, a feature which may be advantageous for reasons such as brood reduction or resource cache strategies, or a side effect of selection on other traits.

## 4. Fatal Attraction: Reproductive Interference by *Miomantis caffra* on *Orthodera novaezealandiae*

### 4.1 Introduction

Invasive insects pose a great threat to biodiversity, but despite this they have received little research relative to other invasive organisms (Kenis, *et al.*, 2009). Especially few studies of invasive insects use experimentation to identify the specific mechanisms by which the negative effects occur, instead relying primarily on comparison between invaded and non-invaded sites or times to infer impact (Kenis, *et al.*, 2009). This is also true even of invasive predatory insects where the mode of impact might be expected to be more straight-forward, but nevertheless lacks empirical assessment of the impact pathway (Reitz & Trumble, 2002; Kenis, *et al.*, 2009). Understandably there is also a strong bias towards studying invasive species which might impact human infrastructure, health or economy (Kenis, *et al.*, 2009), however the value of biodiversity to human economy and wellbeing through provision of ecosystem services is now becoming more apparent (Mack, *et al.*, 2000; Barlow, 2002; Hein, *et al.*, 2006).

#### Invasive insects in New Zealand

New Zealand is very familiar with the impacts of invasive species, due to the number of damaging examples which have arrived there since human settlement (Allen, *et al.*, 2006). These include over 2000 species of invertebrate (Brockerhoff, *et al.*, 2010) and hundreds of introduced insects which impact upon native species, such as the braconid *Microctonus aethiopoides*, which attacks native curculionoid beetles, particularly species of *Nicaeana* (Barratt, *et al.*, 2007). Another example is provided by the tachinid *Trigonospila brevifacies* which attacks native moths (Munro, 1998; Munro & Henderson, 2002). Together the exotic insect species established in New Zealand are responsible for vectoring disease of plants (Gadgil, *et al.*, 2000), feeding on plants (Suckling & Brockerhoff, 2010), hybridising with natives (Sullivan, *et al.*, 2008), competition for resources (Beggs & Wardle, 2006), predation and parasitisation of native species (Harris, 2001; Barron, *et al.*, 2003) and numerous other less overt forms of impact (Brockerhoff, *et al.*, 2010). Despite these examples, the invasive insect fauna of New Zealand has received little attention relative to its mammalian and plant counterparts (Brockerhoff, *et al.*, 2010). This is regrettable because insects are prolific invaders with diverse and severe impacts worldwide (Snyder & Evans, 2006) and furthering our



understanding of their dynamics upon introduction therefore holds great potential for preventing future loss of biodiversity (Kenis, *et al.*, 2009).

#### New Zealand mantids and displacement

The South African praying mantis *M. caffra* has been present in New Zealand since at least 1978 when it was discovered in Auckland (Ramsay, 1990) and it is widely believed that this species is displacing *O. novaezealandiae* as it expands its range south (Ramsay, 1990). However, although anecdotal evidence for this supposition is abundant, it appears to be based largely on a correlation between the spread of *M. caffra* and the apparent concomitant disappearance of *O. novaezealandiae* from invaded areas. As yet there has been no empirical examination of whether or not this is the case, or whether the presence of *M. caffra* causes any disruption of *O. novaezealandiae* populations (Brockerhoff, *et al.*, 2010). This is not surprising, since although the damage that invasive species can cause is well known, it can be difficult to demonstrate specific mechanisms by which impact occurs (Forrest & Taylor, 2002; Park, 2004).

Because of the complexity of ecosystems as they exist in nature and the timing of research relative to invasion progress, it is very challenging to isolate changes to native biota in the wild and demonstrate whether or not a newly introduced species is causing harm before extinctions occur (Mack, *et al.*, 2000; Forrest & Taylor, 2002). This is especially true of interactions occurring at the same trophic level, as in this case, due to the often indirect nature of the displacement (Kenis, *et al.*, 2009). In addition, the kinds of change which biotic introductions cause can be extremely hard to observe during the early part of the invasion process and are often only apparent once extinctions have resulted or the exotic organism has expanded to realize much of its potential range (Mack, *et al.*, 2000). This is exacerbated by the occurrence of a lag phase, which is displayed by some species (e.g., Lachmuth, *et al.*, 2010) before they become invasive (Mack, *et al.*, 2000; Marsico, *et al.*, 2010). In these cases the introduced population remains very small for a variable period of time, often going unnoticed, before undergoing a rapid growth and expansion phase and becoming invasive (Mack, *et al.*, 2000). The introduction of *M. caffra* to New Zealand provides an excellent opportunity to study the process of invasion, because it represents a case of displacement that is in progress (i.e., the native species is not yet extinct) and between only two similar organisms. This is a valuable study system as most biological invasions have progressed either to the extinction of the new species' main competitors and prey, or to a point where the early events of the introduction are not observable in retrospect (Reitz & Trumble, 2002). In other cases, there are simultaneous, multi-species invasions into the same habitat, complicating attempts to demonstrate impact (Pearson & Goater, 2009). However in this situation, the introduced species has just one native counterpart and has not yet driven it to such rarity that study of their interaction is not feasible (Ramsay, 1990).

Examination of whether *M. caffra* does influence *O. novaezealandiae* is certainly warranted, because if the anecdotal reports are true then it would seem to be the leading cause of decline in the native species (Brockerhoff, *et al.*, 2010). Indeed, predatory insects are one of the greatest threats posed to rare insects in many systems (Wagner & Van Driesche, 2010), so it is not unlikely that the spread of *M. caffra* is the cause. This is significant because *O. novaezealandiae* represents the entire native New Zealand Mantodea fauna (Ramsay, 1990). However, so far no specific mechanism of impact has been identified.

### Competition

It is plausible that competition is occurring between the species, because they are so physiologically similar and now share much of their range in New Zealand (Ramsay, 1990). This raises the possibility of competitive exclusion, which is the displacement of a species from its range due to monopolisation of resources or interference with its behaviour (Reitz & Trumble, 2002). This is responsible for the decline of an endemic New Zealand spider *Latrodectus katipo* by the South African import *Steatoda capensis*, which appears to outcompete the native and cause its displacement from coastal habitat (Hann, 1990). In that case the introduced species seems to compete through superior reproductive output and monopolisation of refugial and prey resources (Hann, 1990; Costall & Death, 2009). This type of impact is often the outcome of high levels of interspecific competition, when resources are driven too low to support one of the species in question (Crowder & Snyder, 2010) and is recorded from many pairs of invertebrate species, including several insects (Van Riel, *et al.*, 2007; Crowder & Snyder, 2010).

Because of this, the outcome of the introduction of an AGP such as *M. caffra* is often the extinction of similar native species (Snyder & Evans, 2006; Laparie, *et al.*, 2010), especially when the native and invasive species are similar (Parker, *et al.*, 1999). For example, the displacement of North American native coccinellid species from Maine was driven by the exotic beetles *Coccinella septempunctata*, *Harmonia axyridis* and *Propylea quatuordecimpunctata*, all lady bugs introduced for biocontrol of aphids (Alyokhin & Sewell, 2004; Kajita & Evans, 2009). The primary species responsible for this displacement appears to be *C. septempunctata*, which is now widespread in the United States and Canada (Hodek & Michaud, 2008). Since arriving in its introduced range, this species has increased its extent and abundance greatly, while population densities of natives have decreased (Kajita & Evans, 2009). It appears that reduction of aphid populations by predation from *C. septempunctata* impairs reproductive output of native coccinellid beetles through lowered food availability, leading to their replacement (Evans, 2004). This is especially common of impacts occurring between species of the same trophic level, for obvious reasons (Parker, *et al.*, 1999). However, in this particular case it is unlikely that the invader could be lowering prey resources to a

level which would impact the native mantis, as similar species have been shown to have weak effects on prey abundance (Fagan, *et al.*, 2002) and because they both occur at low density (for insects) in the wild and prey upon a broad range of numerous invertebrate species (Ramsay, 1990). For the same reasons it is also unlikely that direct predation of *O. novaezealandiae* by the exotic mantis could be responsible for its decline. This raises the question of how *M. caffra* is displacing *O. novaezealandiae* as current distribution suggests. In some cases, competition can be manifested as changes to behaviour caused by the mere presence of another species, such that one is impaired with no aggression between individuals, or any affect on mutual resources.

### Reproductive interference

There are a number of cases in which species of arthropod display attraction towards heterospecific individuals. For example, Lelito & Brown (2008) found that male *Mantis religiosa* were attracted to the female sex pheromones of the heterospecific mantid *Tenodera sinensis*, interfering with ordinary behaviour. Another example in which this occurs is provided by the reptile tick species *Aponomma hydrosauri*, *Amblyomma albolimbatus* and *Amblyomma limbatum* (Andrews, *et al.*, 1982). In that case the males are attracted to females of the other species by a non-species specific pheromonal signal, resulting in wasted mate searching effort and interference with reproduction by mate guarding (Andrews, *et al.*, 1982).

Attraction of mate-searching males to heterospecific females has also been demonstrated in other species of arthropod (e.g., Kasumovic & Andrade, 2004), which raises the possibility that a similar heterospecific attraction effect could operate in this case, with the exotic species causing reproductive competition with the native. As in the scenario of *T. sinensis* attracting *M. religiosa*, the species in question here are not closely related and originate on separate continents (Ramsay, 1990; Lelito & Brown, 2008), so it is plausible that *O. novaezealandiae* and *M. caffra* recognise each other as potential mates. In most insects and species of mantid for which this has been examined, mate searching is carried out by males using airborne sex pheromones produced by females as cues (Bailey, 1991; Hurd, *et al.*, 2004; Lelito & Brown, 2008), with some exceptions (e.g., Holwell, *et al.*, 2007). Males of many species have been shown to be able to locate females over long distances in this manner (Gemeno, *et al.*, 2005; Perez, 2005; Lelito & Brown, 2008) and it is likely that both study species here use airborne pheromones for mate location, because they show sexual dimorphism in antennal length (Ramsay, 1990), a hallmark of species which do so (Keil, 1999).

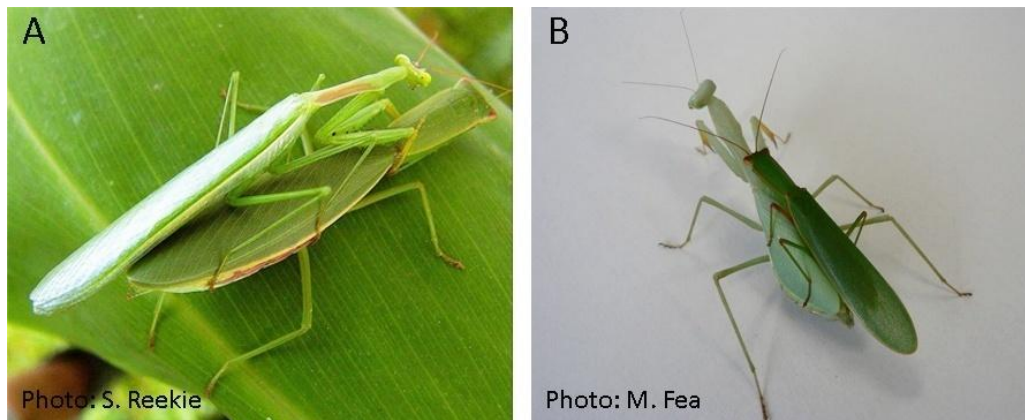


Figure 4.1 Males of *M. caffra* (A) and *O. novaezealandiae* (B) with females of the other species.

This raises the possibility of heterospecific, pheromone-based attraction in this case, especially because males of both species have been seen attempting to mate with females of the other (Ramsay, 1990 and see Figure 1), however the cause and frequency of this attraction has not been examined experimentally. The drive to react to female pheromone is likely to be high, because competition for mates in both species is essentially limited to finding females (scramble competition (Łomnicki, 2009)) since there is no aggressive male competition (Ramsay, 1990). Thus sexual selection on this character has probably strongly promoted the ability to detect and respond to extremely small quantities of the target compound, which may result in male recruitment to signals which are only slightly similar to that actually given by conspecific females. Other insect species have been shown to recognise heterospecific pheromone signals (e.g., Félix, *et al.*, 2011; Lichtenberg, *et al.*, 2011) so it is plausible that the specificity of these cues is low. Whether this occurs commonly in this species pair is unknown but there are several potential consequences if so (Hochkirch, *et al.*, 2007).

Hybridisation with natives is an impact which some invasive species, including insects can have (Kenis, *et al.*, 2009), sometimes resulting in contamination of the entire native gene pool and the genetic extinction of the species (Rhymer & Simberloff, 1996; Brockhoff, *et al.*, 2010). For example, the Lycaenid butterfly *Zizina labradus* which is native to Australia has ousted the New Zealand endemic *Zizina oxleyi* in this manner (Gibbs, 1981; Barlow, 2002). However, in this case the species in question are only very distantly related and no hybrids have been recorded, so this is unlikely to be the cause of displacement (Ramsay, 1990). However, heterospecific mate attraction has also been demonstrated to play a role in the displacement of native insects by invasives in the absence of hybridisation, in the case of the European bumble bee *Bombus terrestris*' introduction to

Japan (Kondo, *et al.*, 2009). Thus hybridisation is not necessarily the only way in which interspecific mate attraction can be deleterious to native species (Hochkirch, *et al.*, 2007).

*M. caffra* are aggressive foragers, quickly attacking anything nearby that moves (Ramsay, 1990). In encounters between arthropod predators and especially within feeding guilds (Snyder & Hurd, 1995), the larger species usually dominates (and often eats) the lesser (Polis, *et al.*, 1989) and in this case the larger species (by body length) is the South African (Ramsay, 1990). Thus if native males recruit to female *M. caffra*, they will almost certainly be caught and eaten. This is especially so if they are attempting to copulate, not only because of the prolonged amount of time spent near the female, but also because their approach is unlikely to be well adapted to avoid capture. This is because *O. novaezealandiae*, unlike *M. caffra* are not commonly sexually cannibalistic (Ramsay, 1990) and thus probably lack the courtship behaviour used by *M. caffra* males, which includes a very slow, cautious approach and thanatosis if attacked by the female (pers. obs.).

Sexual cannibalism is a significant source of male mortality in *M. caffra* (Ramsay, 1990) and other species of mantis (Lawrence, 1992; Gemenio & Claramunt, 2006), so if *O. novaezealandiae* recruit to heterospecific females, the same is likely to be true for them. This is especially so because any courtship behaviour they display is likely to be inappropriate for heterospecific females and thus also likely to increase rather than reduce their chances of being attacked. Indeed, variation in approach speed and distance, time of approach, mounting distance and orientation as well as antennal drumming on the female have been shown to alter the likelihood of cannibalism in other sexually cannibalistic arthropods, including other species of mantid (Kynaston, *et al.*, 1994; Elgar & Fahey, 1996; Moya-Lorano, *et al.*, 2004; Lelito & Brown, 2006; Maxwell, *et al.*, 2010). As a result, the mere presence of female *M. caffra* could result in raised mortality for *O. novaezealandiae* males. This may have the corollary effect of increasing the occurrence of unmated *O. novaezealandiae* females, hence impairing population-wide fecundity (Rhainds, 2010). This is especially likely since *M. caffra* tend to occur in larger numbers (Ramsay, 1990), meaning that searching male *O. novaezealandiae* may have difficulty finding conspecific females in an area filled with interfering signals, as has been demonstrated in the laboratory with other insects (Lelito, *et al.*, 2008).

The potential for this effect is further increased by the earlier appearance of adult *M. caffra* in the wild relative to *O. novaezealandiae*, with mature stages appearing 1-2 months before them (Ramsay, 1990), so that by the time female natives are present, any males may have already visited and been eaten by female *M. caffra*. This impact may be added to if *O. novaezealandiae* males eclose earlier in the season than females, as has been noted for other cannibalistic insects (e.g.,

Lounibos, *et al.*, 1996) including the mantis *Tenodera sinensis* (Hurd, *et al.*, 1994; Moran & Hurd, 1994), so that when they first arrive the only females that are present are heterospecific.

Another factor which may contribute to this impact is the observation that sexual cannibalism can be a lucrative female foraging strategy (Hurd, *et al.*, 1994), meaning that species which display this behaviour may be under selection to utilise an effective long range signalling mechanism. If this is the case, then *M. caffra* females are likely to have a more powerful and longer range signal than *O. novaezealandiae*, as the latter rarely cannibalise their mates (Ramsay, 1990). This is especially likely because *M. caffra* females are much less dispersive than those of the native species (Ramsay, 1990), suggesting a greater reliance on long range mate attraction. This could then result in a pre-emptive advantage in attracting heterospecific males as their signal is likely to be detected first, as well as a greater masking effect per female of the *O. novaezealandiae* signal. Even if *M. caffra* females did not attack native males, the combination of time spent attempting to copulate with them, the energetic cost of misdirected long distance flights and the number of introduced females in a given area might prevent male *O. novaezealandiae* from finding actual conspecific mates (Gröning & Hochkirch, 2008).

Therefore, mating experiments are carried out here to assess how common sexual cannibalism is in adult *M. caffra* and Y-choice experiments are used to determine whether heterospecific attraction occurs or not. To this end the hypothesis that males go to heterospecific females more often than expected is tested.

Additionally, in order to investigate whether the *M. caffra* females are more attractive to *O. novaezealandiae* males than conspecifics, Y-choice experiments are carried out using females of both species as simultaneously alternative options in the same apparatus. The date of eclosion in male and female *O. novaezealandiae* raised in the lab is also recorded in order to estimate whether or not males tend to mature earlier. Finally, heterospecific mating experiments are carried out to determine the rate of cannibalism in the case of *O. novaezealandiae* males recruiting to *M. caffra* females.

## 4.2 Methods

### Specimens

For the following experiments, specimens of both species were wild caught as 3<sup>rd</sup>-5<sup>th</sup> instar juveniles and raised to adulthood in the laboratory. *M. caffra* were housed in inverted, 400 ml, transparent plastic cups and raised on a diet of *Galleria melonella* larvae (Lepidoptera), *Tenebrio molitor* larvae (Coleoptera), *Locusta migratoria* juveniles (Orthoptera), *Drosophila melanogaster* adults (Diptera, flightless morph), *Exaireta spinigera* larvae (Diptera), *Lucilia sericata* adults (Diptera) and *Plodia interpunctella* larvae (Lepidoptera). These were fed out at a rate of 2-3 food items per individual per week. All *M. caffra* were captured in suburban Auckland.

*O. novaezealandiae* were housed individually in 30 cm<sup>3</sup> cubic mesh screen insect rearing enclosures and raised on an *ad libitum* diet of *Drosophila melanogaster* adults (Diptera, flightless morph), *Tenebrio molitor* larvae (Coleoptera), *Musca domestica* adults (Diptera) and *Lucilia sericata* adults (Diptera). All *O. novaezealandiae* were caught at Lake Karapiro, Waipa. All specimens were misted with water daily. The date of eclosion and the sex of each mantis were recorded as they reached maturity.

### Copulatory cannibalism

In order to assess mortality associated with cannibalism in *M. caffra*, mating observations were carried out in the laboratory. An approximately 40 cm tall, freshly cut, leafy branch was placed upright in a plastic jar. One lab raised, virgin female *M. caffra* was introduced onto the top of each piece of vegetation and allowed 30 minutes to orientate herself naturally. One lab raised, virgin male was then added to the branch at least 15 cm in a random direction away from the female. These were left for 16 hours beginning in the evening under natural light conditions. At the end of this period the survival or otherwise of the male was recorded. This was repeated with 23 pairs of separate individuals. Because the specimens were not observed for the duration each trial, it cannot be confirmed that all cannibalism was associated with courtship or copulation. However, the focus of this test was to determine the likelihood of cannibalism in males recruiting to females, rather than sexual cannibalism *per se*. Females which subsequently produced viable oothecae were recorded as having mated during this trial.

To estimate the mortality rate associated with cannibalism in heterospecific pairings, this approach was repeated with mixed-species pairs and the following differences. The branch and jar were placed inside a 1 × 0.5 × 0.5 m mesh enclosure, to prevent loss of the *O. novaezealandiae* specimens due to their greater propensity to run and fly about. This enclosure was large enough to allow males the choice of avoiding females should they be behaviourally adapted to do so.

Secondly, the pairs were placed together for only 7 hours and observed continuously so that any courtship or copulation attempts could be recorded. These trials comprised  $N = 16$  *O. novaezealandiae* male and *M. caffra* female pairs and  $N = 12$  *M. caffra* male and *O. novaezealandiae* female pairs.

### Y-maze experiments

In order to test whether males of either species respond to female olfactory cues, Y-choice experiments were undertaken. These took place using a glass and Perspex Y-maze, with a tube diameter of 4.5 cm and length of 60 cm.

The upper inside surface of the glass tube was lined with a strip of masking tape to provide a surface for the specimens to grip more easily. In order to match the study species' predilection for moving upwards, the tube was assembled at a 70 degree angle to the bench and supported by a cubic frame of white polyurethane tube, with the common chamber at the bottom and the target chambers at the top (see Figure 4.2).

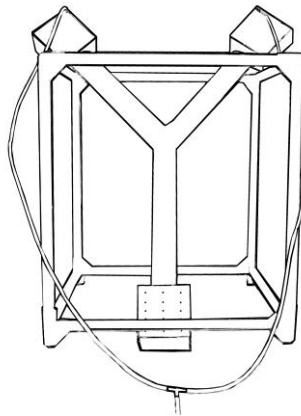


Figure 4.2 Set up of Y-maze and frame.

The apparatus and frame were stabilised in this position with white masking tape, and placed against a blank white wall. The entrance to each terminal chamber of the maze was blocked by a sheet of nylon gauze screen, to keep females in the appropriate chamber, prevent specimens from interacting and to disallow males from using visual cues to locate the female. A blank, white sheet of paper was hung from either side of the frame to provide identical visual input to each side of the tube. Air flow was provided by an Aqua One 7500 precision air pump, which was left running for at least one hour between each set of tests to cycle fresh air through the apparatus and ensure that no airborne traces of previous specimens remained inside. The pump was placed 2 m away from the apparatus to prevent it from recycling any air back through the control chamber, potentially confounding the tests.



The apparatus was air tight except for perforations in the common chamber, so that air flow had to move through the whole system from top to bottom to exit. Both target chambers and Y tube were cleaned with a 100% ethanol soaked tissue, rinsed with water and air dried between all tests. Lab raised, virgin females were placed into a randomly selected terminal chamber and the chamber was randomly assigned to the left or right-hand tube. Lab raised, virgin males were removed from their enclosures with a plastic vial and introduced to the common tube. Males which moved half way or further into either terminal tube were considered to have made a choice. Specimens which failed to move at least half way into either terminal tube within 40 minutes were recorded as having made no choice and were removed. Initial tests suggested that male *O. novaezealandiae* were strongly influenced by ambient light direction, so all subsequent tests were carried out under dim, diffuse lighting. In order to confirm that males would respond to potential mates using non-visual cues, conspecific tests (*O. novaezealandiae*  $N = 14$ , *M. caffra*  $N = 13$ ) were carried out prior to assessing heterospecific attraction.

Sixteen tests were carried out using *O. novaezealandiae* males and *M. caffra* females, and 13 tests with *M. caffra* males and *O. novaezealandiae* females. In order to examine whether female *M. caffra* had a stronger or more attractive signal than *O. novaezealandiae*, 18 further tests were carried out using one female of each species as simultaneous options, with male *O. novaezealandiae* able to choose which they would move to. Initial tests with *M. caffra* suggested that males were reluctant to move within the 40 minute timeframe, both during daylight or darkness and with either conspecific or heterospecific females. Replacing the air pump with a quieter model (Aqua One 2500) in case the loud sound of the larger pump was stressing the specimens did little to alter this. Therefore longer term trials were carried out with the time extended to 10 hours.

### Statistics

The mean number of days to adult eclosion (since the date of the first adult to moult in the lab) was compared between *O. novaezealandiae* males and females by an unpaired t-test.

Cannibalism and predation rates are reported as proportions and 95% CI.

Preference for treatment over control in Y-choice experiments was tested for by a binomial sign test, with the null hypothesis that the median number of males to go to control and treatment chamber was the same.

## 4.3 Results

### Eclosion phenology

Lab-raised, male *O. novaezealandiae* eclosed a mean of 5.33 days earlier than females, a non-significant difference ( $t = 1.582$   $P = 0.133$ ).

### Conspecific mating and cannibalism tests

0.3913 (95% CI  $> 0.2210 < 0.5927$ ) of the male *M. caffra* were killed and eaten during the 16 hour period they were left on a branch with a conspecific female. No males left the branch over night (i.e., they were either still present after 16 hours or had been cannibalised). Consequently, this figure would likely be higher if the trials were not ended artificially and males were allowed to stay until they were either eaten, achieved and survived copulation or left voluntarily. This represents a significant source of mortality for males, making it unlikely that they could survive more than one attempt at mating. Notably, cannibalism was more frequent than successful copulation, which occurred in 0.30 of the pairings. No females were cannibalised by males during the experiment.

In all cases where mating was observed ( $N = 5$ ) the female vigorously attacked the male. Males that were attacked but not killed ( $N = 2$ ) displayed thanatosis.

### Heterospecific mating and predation tests

None of the 12 *M. caffra* males interacted at all with the *O. novaezealandiae* females during 7 hours on the branch. Neither mantis approached the other at any point.

In contrast, most (0.6875, 95% CI  $> 0.4425 < 0.8609$ ) of the male *O. novaezealandiae* were killed and eaten by the *M. caffra* females. In all of these pairs, either the male approached the female, or the female spotted the male moving and climbed along the foliage to attack him. 2 of the males managed to mount the female and attempt copulation without being cannibalised, remaining on her back for 4 hours 38 minutes and 3 hours 12 minutes respectively, until the end of the trial. Only 1 of the 12 males which were attacked survived, although with the loss of a forewing. All pairs with surviving males were within close proximity to each other ( $\leq 4$  cm) at the end of the 7 hour observational period, with the specimens facing each other, thus it is likely that several more instances of predation would have occurred if the pairs weren't separated at this point.

### Y-choice tests

The females of both species usually found a perch on the gauze screen and remained motionless there, with the exception of occasional cleaning behaviour, indicating that she was not under increased stress due to the transfer to the apparatus. In the conspecific treatments, male *O. novaezealandiae* rapidly moved up the common tube of the Y choice apparatus as soon as they

found the entrance. Approximately half ( $N = 6$ ) paused at the junction, while the others continued without stopping until they reached the terminal chamber and were halted by the gauze screen. Of those which reached the positive chamber, very few ( $N = 2$ ) moved back down the tube, while the majority stayed on the gauze. The difference between the number of male *O. novaezealandiae* moving to the positive and control chambers was marginally non-significant (binomial:  $P = 0.0898$   $N = 14$ ), although males did move to the positive chamber more often than the control.

Heterospecific females however elicited a greater bias towards the treatment chamber, with *O. novaezealandiae* males choosing it significantly (binomial:  $P = 0.0384$   $N = 16$ ) more often than the control. Other than this no differences in the behaviour of the males was observed between the heterospecific and the conspecific treatment.

When given a choice between conspecific and heterospecific females, the male *O. novaezealandiae* moved to the exotic female significantly (binomial:  $P = 0.0112$   $N = 13$ ) more often than to the native, with 11 of the 13 specimens that made a choice doing so. Therefore the null hypothesis of no preference can be rejected for both sets of tests that used exotic females and native males.

Male *M. caffra* were reluctant to move at all in the Y-maze regardless of the species of female, with only 6 out of 26 total trials resulting in a choice. Neither changing the timing of trials to night, using a quieter pump or increasing the length of time improved this outcome, with none of the 10 hour or night time trials producing a decision. Because of this, the *M. caffra* male data was not analysed further. However, of the 2 which made a decision when presented with heterospecific females, both chose the treatment over control.

## 4.4 Discussion

### Eclosion phenology

Male *O. novaezealandiae* seem to mature earlier than females, although this could not be confirmed with the sample size used here. However, even a small precedence of male eclosion could be important because adult *M. caffra* tend to emerge 1-2 months earlier (Ramsay, 1990), meaning that adult exotic females will be present as soon as the first male *O. novaezealandiae* arrive, immediately exposing them to the risk of predation. In addition to this factor is the prolonged survival of adult *M. caffra* relative to the natives (Ramsay, 1990), such that they are present throughout the period during which native adults occur. *O. novaezealandiae* only have a narrow window of time (maximum of February to May each year) during which to find mates and produce

oothecae. Since *M. caffra* are at large throughout this period (Ramsay, 1990), their impact to the reproductive efforts of the native mantids may be severe.

#### Copulatory cannibalism and predation

The observed rate of cannibalism in conspecific pairs of *M. caffra* indicates that this is probably a significant source of mortality for males in the wild. This supports the remark of Ramsay (1990) that males seem to disappear quickly from wild populations. It also suggests that males may provide an abundant nutritive supplement for those females which can attract them over long distances, supporting the suggestion that females could be under strong positive selection for potent pheromone use (Hurd, *et al.*, 1994). Adding to this the mass of a *M. caffra* male (mean 0.178 g  $\pm$  0.005 SE in the specimens used here) relative to other prey which are available strengthens this possibility. In addition, the observation that more males were cannibalised than managed to mate with the female suggests that females may consume several males for every one which succeeds in copulating with her.



Figure 4.3 A male *O. novaezealandiae* attempts to establish genital contact with a female *M. caffra* during a heterospecific mating trial.

The very high rate of predation suffered by *O. novaezealandiae* males in heterospecific pairings indicates that their arrival at female *M. caffra* *in situ* is likely to be fatal. The attempts at copulation which were observed when males reached them (see Figure 4.3) suggest that mate attraction is the reason they tended to approach the females in both the enclosures and Y-maze. This may serve to increase the associated level of mortality if their courtship behaviour is inappropriate for interacting with *M. caffra* females, especially as though it would cause them to move into contact with the female and remain there for a long period of time. However, the observation that female *M. caffra*

often moved towards the male to capture him suggests that it is not necessary for *O. novaezealandiae* to reach the female in order to be attacked and thus they may suffer predation simply by landing nearby. This level of predation experienced by the male *O. novaezealandiae* is not surprising since they are effectively naive to the risk of approaching a cannibalistic female. This is consistent with the bold behaviour they displayed in the laboratory when approaching the females, which they did quickly and directly in both the mating observations and the Y-maze tests. In addition, none of the native males which were attacked displayed thanatosis to escape the female as the *M. caffra* males commonly did, indicating a lack of defensive behaviour appropriate to this predator.

### Y-choice

The results of the Y-maze tests show that *O. novaezealandiae* probably use a non-visual airborne cue to detect females, although this could not be confirmed with certainty by the present study. This ambiguity could arise from a lack of detection ability or a lack of responsiveness by males. Which is the causal factor cannot be determined by the present methodology, however it would appear more likely to be the latter since the males seemed quite able to locate exotic females. Alternatively, the *O. novaezealandiae* females may have been more idiosyncratic in their production of pheromone, such that some of the males were not presented with any cue to follow.

The results of the heterospecific tests indicate that *O. novaezealandiae* males are able to detect *M. caffra* females using non-visual cues and tend to approach them when they do so. In addition, the stronger response towards *M. caffra* suggests that the exotic females have a more compelling signal than conspecifics, a possibility that is supported further by the results of tests using both females simultaneously. In those iterations of the test, the male *O. novaezealandiae* chose to move to the heterospecific female even more often than when given the control chamber as an alternative, indicating a great advantage to *M. caffra* females relative to conspecifics in competing for male *O. novaezealandiae*. This result may be due to the combination of two female's pheromone eliciting a greater proportion of the males to make a decision, but with a preference for *M. caffra* causing nearly all the males to choose the heterospecific female once the tube junction was reached. This superiority of the exotic attraction cue may be the result of selection on *M. caffra* females to attract males as a foraging tactic (Hurd, *et al.*, 1994), whereas *O. novaezealandiae* females are less likely to be under similar selection since they are less commonly cannibalistic (Ramsay, 1990; Newman & Elgar, 1991). This is an extension of the observation that spermatophore-feeding female Orthoptera can increase their fitness by attracting more males than are necessary to achieve optimal fertilisation in order to acquire more nutrients (Gwynne, 1984). Since *M. caffra* males are a large prey item relative to other species which the female might encounter and since they must go to the female in

order to attempt copulation, it is expected that they should provide an abundant nutrition source and mate attraction as a foraging tactic should be favoured in this species (Newman & Elgar, 1991; Hurd, *et al.*, 1994).

Alternatively, the greater attractiveness of *M. caffra* females to *O. novaezealandiae* may be a side effect of a preference for heterogeneity in mate selection by the natives, in order to maximise outbreeding, as has been demonstrated to occur in other insects (e.g., Lewis & Wedell, 2009; Lihoreau & Rivault, 2010). Such a preference would be beneficial in *O. novaezealandiae* since all siblings emerge simultaneously from their ootheca (Ramsay, 1990) and thus develop to adulthood synchronously, suggesting a benefit from kin recognition in avoidance of inbreeding, as found in other species with the same life history characteristic (e.g., Lihoreau, *et al.*, 2007). Consequently, if *O. novaezealandiae* are more strongly attracted to dissimilar signals, the heterospecific cue might be especially alluring and easily outcompete that of the native females, resulting in the observed preference for the exotic females.

An additional factor may be that *O. novaezealandiae* have lost precautions against the costly behaviour of responding to heterospecific pheromones, because of their isolation as the only mantid species in New Zealand. In this singular state the optimal male condition is expected to be minimum discrimination and maximum responsiveness to female cues in order to optimise detection of females.

Regardless of the possible reasons why, these observations suggest that in the wild, native males will seek out exotic females from beyond their range of vision. This is likely to be the case even when there are competing airborne signals from each species, with *M. caffra* not only attracting some native males, but possibly more than *O. novaezealandiae* females. The non-visual nature of the attraction suggests that it could operate over a long distance, potentially allowing one *M. caffra* female to interfere with native mate searching over a large area and to capture males from distant populations. Such long range mate attraction occurs in other species of mantid (Gemeno, *et al.*, 2005; Perez, 2005) so it is likely that the same is true in this case. This is compounded by the greater abundance of *M. caffra* than *O. novaezealandiae*, which will serve to reduce the ability of native males to find conspecific females.

The lack of response from *M. caffra* males prevented assessment of their mate searching tendencies, but their failure to approach conspecific females in the Y-maze suggests that this was due to the laboratory conditions rather than inability of females to attract them. Thus the present study neither confirms nor rejects the possibility that they recruit to heterospecific females in the wild. The reluctance of *M. caffra* to advance towards females may be an adaptation to help them avoid

capture by their visually hunting, cannibalistic mates. Conversely, *O. novaezealandiae* which are less cannibalistic (Ramsay, 1990), appear to lack this precaution. When *M. caffra* were observed approaching a female during the tests of cannibalism rate, they did so at extremely reduced speed relative to their usual movement, sometimes taking hours to precede several cm closer to the female. The *O. novaezealandiae* males however moved quickly regardless of their proximity to females, both in enclosures and the Y-maze. This supports the suggestion that *O. novaezealandiae* males are likely to suffer a greater level of mortality due to recruitment to *M. caffra* females in the wild than *M. caffra* males do. This is especially likely if *M. caffra* females do not recognise them as potential mates and refrain from attacking them, as they presumably must do in regards to conspecific males at least some of the time in order for the species to persist.

The lack of participation by *M. caffra* males in the laboratory prevented analysis of their behaviour for the current study, but field experiments may yield improved results in the future. It is possible that they have developed extreme cautiousness in approaching females as a self preservation behaviour which prevented them from responding under all but the most suitable conditions, resulting in the lack of movement in the laboratory. The fact that male *M. caffra* failed to respond to the presence of females in the Y-maze even though they clearly must be able to find mates in the wild suggests that the laboratory conditions or methods used were to blame. Because of this, their disinterest in heterospecific females is not necessarily an indication that they do not recruit to them in natural conditions, especially as though they have been observed attempting to mate with *O. novaezealandiae* females in the wild (see Figure 4.1 A). Therefore the risk of impact to *O. novaezealandiae* through attraction of heterospecific males remains possible, although it could not be demonstrated presently.

### Consequence

The combination of superior attractiveness and earlier adult emergence in *M. caffra* females give them a clear advantage in recruiting *O. novaezealandiae* males. Adding to this the high level of predation experienced by the native males when approaching them suggests that this may be a significant cause of mortality for *O. novaezealandiae*. If male *O. novaezealandiae* do emerge sooner than their female counterparts as is weakly suggested here, this effect may be considerably stronger due to the removal of males from the population before native females appear to compete with the exotics.

This heterospecific attraction could impair *O. novaezealandiae* fitness even in the absence of cannibalism, due to the large numbers of exotic females, their apparently greater attractiveness to *O. novaezealandiae* males and the length of time males spend at the female during copulation attempts (Gröning & Hochkirch, 2008). The effectiveness of competing pheromone signals in

disrupting the reproduction of insects is attested to by the development of pest control methods which successfully use pheromones for this very purpose (e.g., Mafra-Neto & Baker, 1996; Singh & Chandrasekharai, 1996). The occurrence of predation by females worsens this situation significantly, ensuring an impact to *O. novaezealandiae* abundance and sex ratio.

In addition, the potential penalty incurred to *O. novaezealandiae* fitness is mirrored by a benefit to *M. caffra*; females of the latter are essentially given meals for which they need not expend much energy in finding, without the costs of eating potential mates which are usually associated with the behaviour (Johnson, 2005). The same is not true of *O. novaezealandiae* as they are not as commonly cannibalistic (Ramsay, 1990) and won't usually attack another insect unless it is significantly smaller than themselves (pers. obs.). As a result, the native species suffers the consequences of this heterospecific mate attraction while the exotic is at worst unaffected. Estimation of the range over which *M. caffra* females can recruit native males (such as by mark and recapture methodology using a female *M. caffra* as an attractant) would be helpful in determining the probable severity of impact due to this effect.

Models of the interactions between species have shown that extinction due to heterospecific mating is possible, even without the effects of competition for common resources (Ribeiro & Spielman, 1986). Furthermore, simulated population viability analyses show increased risks of extinction when sex ratios are altered (Brook, *et al.*, 2000), a pattern which still applies when males are the limiting sex, as long as their mating capacity is reduced (Hatcher, *et al.*, 1999). Since the mating capacity of males is completely reduced when they are killed, such an impact is therefore probable in this case, especially because of the greater density of exotic females (Ramsay, 1990) and their apparently superior ability to attract *O. novaezealandiae* males. Whether or not sex ratios in *O. novaezealandiae* populations are unusually female-biased where they co-occur with *M. caffra* would be an interesting question to address in regard to this.

The impact of *M. caffra* through this heterospecific attraction is multifaceted, including several related consequences for the native insects:

1. Native males are removed from the population, skewing the sex ratio.
2. Exotic females are fed additional high quality prey items, increasing their fitness.
3. Native females' mate attraction efforts are likely to be masked by the exotics' superior cues.

This potential reduction of male *O. novaezealandiae* numbers and masking of female mate attraction cues (signal jamming) may combine to impair fecundity for the native species if it causes a significant number of females to remain unmated by the end of the adult season (Hatcher, *et al.*, 1999). Certainly it seems that female *M. caffra* sometimes remain unmated due to their cannibalism



of potential mates (Ramsay, 1990), so they may cause the same problem in the *O. novaezealandiae* population. Even if male *O. novaezealandiae* numbers are not reduced enough to cause some females to go unmated, there may nevertheless be an impact through reduced outbreeding in the population due to the lessened number of males contributing to fertilisations (Lee, *et al.*, 2011; Yamauchi & Kobayashi, 2011).

There is also the potential for this removal of recruiting males from the population to provide strong selection pressure against responsiveness to female pheromones, an effect that is consequential in its own right but which would also feed back into the impairment of native mate attraction (Gröning & Hochkirch, 2008). This could be especially significant since it would be expected to drive responsiveness below the threshold required to allow location of native females before that of exotic females, due to the differing strength of their mate attraction cues. Such an effect has the potential to cause a lasting detriment to the viability of *O. novaezealandiae* populations even if *M. caffra* subsequently disappear from the area, making it a potentially serious side-effect of male mortality due to heterospecific mate attraction.

The consequences of possible male *M. caffra* attraction to heterospecific females include both the potential for predation of the female and the prevention of access by *O. novaezealandiae* males, due to the duration of copulation in mantis species (e.g., Lawrence, 1992). Mate guarding, the protection of females against male competitors (Alcock, 1994) is not specifically recorded in these species (Ramsay, 1990), however, the matings which were observed presently lasted for many hours and this duration may serve to prevent further males from reaching the female. This is especially likely to be detrimental to the reproduction of the natives in a situation where males are rare and female's mate attraction efforts are already impaired, combining to severely reduce the chances of successful egg laying before the onset of winter and the associated senescence of the adult population.

Whether or not male *M. caffra* are attracted to female *O. novaezealandiae* from beyond visual range could not be examined here due to the reluctance of the males to move in the laboratory, however the observations of them attempting copulation *in situ* suggest that this is a possibility. Investigation of this in the wild may answer whether or not it is a likely source of additional impact on *O. novaezealandiae*.

This form of competition blurs the line between reproductive interference and intraguild predation, both of which have been shown to cause displacement between insects during biological invasions when acting in isolation (Snyder & Evans, 2006; Kondo, *et al.*, 2009). Acting together, these mechanisms consequently have great potential to impair the *O. novaezealandiae* population in New Zealand. This impact may become more severe as *O. novaezealandiae* numbers are reduced and the *M. caffra* population continues to increase, since the relative strength of each effect on the native

will be greater in small populations where *M. caffra* outnumber natives (Gregory & Courchamp, 2010). Thus the displacement of *O. novaezealandiae* may follow a positive feedback pattern and accelerate over time. Furthermore, if the abundance of *O. novaezealandiae* is reduced enough, the population may be exposed to Allee effects (Allee, *et al.*, 1949; Lee, *et al.*, 2011). These are factors (such as difficulty in finding mates) which reduce individual fitness at low population sizes (Allee, *et al.*, 1949). This can lead to extinction independently of external pressures such as predation or competition (Labrum, 2011), so in combination with interference from another species, disappearance of a reduced population can occur rapidly (Gregory & Courchamp, 2010; Kramer & Drake, 2010).

The finding of non-visual, heterospecific attraction and predation of *O. novaezealandiae* males by *M. caffra* females therefore suggests that this may be the mechanism of impact on the native species which is causing their displacement where *M. caffra* occur. The specificity of this impact to one species may seem to suggest that the Mantodea are not a broadly threatening group as invasive species, however several aspects of their life history and ecology give them potential for more widespread impact. They are common in many ecosystems, highly fecund and have little dietary limitation as well as having been demonstrated to play a significant role in natural arthropod community structure (Fagan, *et al.*, 2002). In addition to these factors, their overwintering as an oothecae stage containing hundreds of eggs, which is also small, highly resistant and often hidden on human objects give them great propensity for accidental translocation in large numbers. Their charismatic appeal to many people also makes them popular as live items of trade in their own right. Therefore determination of the specificity of mantis pheromones from a number of species would reveal whether introduced mantids are likely to threaten native species through this mechanism in other locations.

### Limitations

Low availability of *O. novaezealandiae* specimens meant sample sizes smaller than preferable were used for all the experiments in this chapter. Hence, the results could be greatly improved by further tests with new specimens. The laboratory methodology used was also unable to address the likelihood of attraction *in situ* and transferability of the results to the field is only assumed so far. The Y-maze and mating observation experiments were also unable to assess the possibility of male *M. caffra* recruitment to *O. novaezealandiae* females, a drawback which might also be remedied by examination of this factor in the field. Another important variable which could also be assessed by field experiments is the range at which *M. caffra* females are able to attract males, as this has relevance to the potential for impact on the native species.

## Conclusion

The combined effects of male *O. novaezealandiae* recruitment to sexually cannibalistic exotic females, their possibly earlier maturity than their female counterparts, more potent pheromone use in *M. caffra* females, native naivety to larger, more aggressive and cannibalistic mates, earlier arrival of adult exotics and the greater abundance of exotic mantids mean that there is great potential for impact to *O. novaezealandiae* populations due to heterospecific mate attraction. Because of this, it could be plausible to infer impact merely from the observations of heterospecific copulation attempts (Ramsay, 1990), however these could simply be the result of short-range, visual misidentification made when a male and female of each species happened to come across one another. In order for the impact to be significant enough to cause the widespread decline of *O. novaezealandiae* that has been suggested, active recruitment of males to heterospecific females over long distances is probably required (Gröning & Hochkirch, 2008). Therefore, the most important factor in this case is the use of an airborne, non-visual cue that is recognised by male *O. novaezealandiae*.

As a cause of displacement of native species by exotics, such interspecific reproductive interference has been largely overlooked, despite the number of invasion scenarios to which it may be relevant (Valero, 2010). It seems that heterospecific mate attraction to *M. caffra* is a contributing factor in the apparent disappearance of *O. novaezealandiae* from much of its range. To date this is the only suggestion of a specific displacement mechanism for this pair that the author is aware of. Anecdotal reports that *M. caffra* possibly out-competes the native appear to be based largely on a general correlation between the spread of the exotic and diminishment of the native, however no causal mechanism had been suggested. This is significant because it implicates *M. caffra* in the decline of *O. novaezealandiae*, the only native New Zealand mantid. As a result, if *M. caffra* continues to expand its distribution in New Zealand as it appears to be doing (Ramsay, 1990; Chapter 2), the native species may be completely extirpated. This also suggests that reproductive interference is yet another form of impact which invasive species may commonly inflict in their introduced ranges.

The impact of heterospecific matings that do not result in hybrids has rarely been investigated (Kondo, *et al.*, 2009), including as a mechanism of the displacement of native species by exotics (Valero, 2010). Although this species pair exhibit high potential for this to occur because of the occurrence of sexual cannibalism in *M. caffra*, other species may also be affected by interspecific mate attraction through mate guarding (e.g., Viljanen, 2009), waste of mate searching effort, injury of mates (e.g., Harris, *et al.*, 2010), production of inviable eggs and the masking of native mate attraction cues (Kondo, *et al.*, 2009). Reviews by Ord & Stamps (2009) and Gröning & Hochkirch (2008) revealed that weak pre-copulatory species barriers may exist in many animals, suggesting

that heterospecific mate attraction may be a common factor in the impact of numerous invasive species. This is especially likely in groups which have fitness costs associated with copulation even in conspecific pairs, which is common in many insects (e.g., McLain & Pratt, 1999; Rolff & Siva-Jothy, 2002; Rönn, *et al.*, 2007). Because of this, the potential for reproductive interference by introduced organisms is not limited to those which show cannibalistic behaviour and should be considered in other cases where invasive species have similar native counterparts.

## 5. General Discussion

### 5.1 Synthesis

The aim of this thesis was to investigate aspects of the invasiveness and behaviour of two largely unstudied insect species in New Zealand. This is a contribution to the knowledge of New Zealand's mantis fauna, as well as the understanding of invasive insects in general, which have a relatively small body of literature describing their pathways and impacts, especially outside of the social hymenoptera (Kenis, *et al.*, 2009). This provides the first evaluation of the role of *M. caffra* in displacing *O. novaezealandiae* as well as estimating the potential for further decline of the latter species.

The results of Chapter 2 describe a potential future scenario of the expansion of *M. caffra* into the eastern areas of the South Island and highlight the highest risk areas for establishment of this species there. This is valuable not only for the above result but also as use of an SDM package with a new species and region, a process which needs to be ongoing to provide continual refinement of modelling techniques. That pursuit is especially important to the field of invasion biology, where SDMs show great promise for allowing pre-emptive management of problem species, but which also require low levels of omission to be attained from poor data sets (Mack, *et al.*, 2000; Simberloff, 2008). The consistency achieved by the Maxent software under varying input conditions and without any tuning of model parameters to fit the study organism's biology is impressive and supports the value of that technique to examining invasive species, as well as other applications where locality data may be sparse (such as conservation of rare species).

The results of the field test using *M. caffra* oothecae were equivocal due to a lack of resolution in the sample size, or a lack of influence of climate on the hatching success of the developing nymphs. It may also be the case that the juvenile stages of *M. caffra* are more vulnerable to climatic factors than the oothecae, potentially making them a better predictor of limitation to the spread of this species. In either case the results of the field test show that the oothecae can remain viable under a variety of climatic extremes, including the often sub-freezing, alpine environment of Twizel, which suggests little hindrance to the dispersal of this species in New Zealand. Therefore it is predicted that *M. caffra* should eventually reach all the areas predicted as suitable by the digital approach, making them all potential habitat for the species. The lack of pattern in the ootheca data made evaluation of the Maxent output against it less meaningful, however it does show that there are factors outside of the features typically used by SDMs which influence spatial distribution. This highlights the simplification of natural systems inherent in modelling approaches and restates the

importance of interpreting their projections in light of that. It also reiterates the importance of independent field data to assess model outputs, however, tests of *in situ* survivability of species and SDMs is largely un-utilised (Stankowski & Parker, 2010) and the current attempt is the only simultaneous use of field and simulated approaches that the author is aware of.

The results of Chapter 3 elucidate a previously un-described trait of the South African species, revealing a lack of kin-discrimination in a cannibalistic insect and highlighting interesting questions regarding the evolution of negative behavioural interactions between relatives. Furthermore, the occurrence of indiscriminate cannibalism in *M. caffra* juveniles is surely an important factor in shaping their adult population structure (Polis, 1981), which is in turn significant to their role as generalist predators of the arthropod assemblage in natural communities (Rudolf, 2007). This trait is thus relevant to their importance as a new predator in the New Zealand fauna, because it influences their abundance, size distribution and recruitment of cohorts, all of which may be determinants of their establishment success in new areas (Polis, 1981). Indeed, it may well have been the propensity for cannibalism which allowed so many nymphs to survive inside the vials used for the ootheca test, despite a lack of alternative prey over the several months for which they were deployed. This suggests that even an ootheca transported within a sealed container could not only hatch but produce propagules that can sustain themselves in isolation for a long period by cannibalising their siblings. This adds another level of resilience to a translocated ootheca, suggesting a level of dispersal ability for *M. caffra* which might not otherwise be expected due to their sedentary adult females.

The results of Chapter 3 are also of interest regarding the evolution of cannibalism itself because they contrast with the predictions of theory on how relatives should interact to maximise indirect fitness benefits (Sherratt, *et al.*, 1999). The apparent lack of other traits in *M. caffra* to reduce siblicide also raises further questions about the reasons for the non-existence of a mechanism to prevent the killing of full siblings and the adaptiveness or otherwise of cannibalism within broods. There are multiple hypotheses (aggressive overflow, resource cache, brood reduction, competition) which could explain the observed state in *M. caffra* and further testing may be successful in narrowing down this selection and illuminating the underlying processes at work.

The cannibalism displayed by *M. caffra* also provides some insight into the possible cause of displacement of *O. novaezealandiae* as outlined in Chapter 4, a topic which has previously remained in the realm of speculation. While there are certainly other possible mechanisms behind this apparent impact, the attraction and predation of *O. novaezealandiae* males by *M. caffra* females seems sufficient to have caused the reported withdrawal of *O. novaezealandiae* from the invaded range of *M. caffra*. Because of the non-gregarious, dispersed nature of the adult insects,

conventional predation of adult *O. novaezealandiae* by *M. caffra* is unlikely to be a major cause of mortality for the natives, however, this may not be the same of nymphs which hatch in large numbers into the same vicinity and consequently occur in greater densities. The finding of increased cannibalism among *M. caffra* nymphs of varying size is also relevant in regards to *O. novaezealandiae*, because of the fact that *M. caffra* nymphs emerge asynchronously, possibly giving some a head-start over those of *O. novaezealandiae* and creating a size difference between the developing cohorts of each species. These two observations together suggest that *M. caffra* juveniles may find any native nymphs which hatch in the same area to be easy prey, meaning that this could be a large source of mortality in juveniles and a possible cause of cohort failure for *O. novaezealandiae*. The probability of this occurring will be greater if both species tend to lay their oothecae in similar locations, a possibility because many mantid species tend to aggregate their oothecae into clumps (Eisenberg & Hurd, 1990), suggesting active choice of optimal oviposition sites, which may be based on criteria common to both species.

The results of Chapter 4 are also significant because they identify a feature which we rarely have the opportunity to examine; the causal details of competition in an invasion scenario (Park, 2004). The greater our understanding of this topic, the better equipped we are to evaluate the potential invasiveness of imported organisms, protect the species they threaten and argue the case for prevention of introduction (Park, 2004). The results of that chapter also highlight a pathway of impact through which other arthropods, especially cannibalistic species, may impair native fauna. This heterospecific attraction has been recognised as a cause of impact in the past, but mainly in regard to the problems associated with hybridisation (Kondo, *et al.*, 2009; Valero, 2010) and (to the author's knowledge) has rarely been considered for other cases. Also highlighted is the value of experimental investigation of invasive species' impacts, an approach which is not used often (perhaps due to the difficulty of bringing threatened species into the lab) but which nevertheless has significant potential to further our appreciation of impact mechanisms (Parker, *et al.*, 1999; Park, 2004; Kenis, *et al.*, 2009).

The results of chapters 2 and 4 together suggest that *M. caffra* may be the cause of *O. novaezealandiae*'s decline and that the former will continue its incursion into the range of the latter. This is consequential because of the large overlap between the currently known distribution of *O. novaezealandiae* and that projected for *M. caffra* in the South Island, suggesting that most populations of the native will become threatened by the introduced species in the coming years. If the ability of *M. caffra* females to attract *O. novaezealandiae* males does prove to be a significant source of prey for the exotics, it may also mean that they have an especially easy task invading areas where there are populations of the native species. This may result in a preferential or

accelerated rate of expansion into those locations, increasing the likelihood of impact there and creating strong populations of *M. caffra* from which further spread could take place. It will be interesting to see whether *M. caffra* are more successful in invading areas with or without pre-existing populations of *O. novaezealandiae*, because if so it may suggest that foraging through heterospecific mate attraction is a beneficial factor to the establishment success of the introduced species.

The findings of this study contribute to the science of predicting invasiveness in introduced AGPs, by addressing the potential distribution of an exotic organism, identifying cannibalism as a life history trait that might increase invasive potential, and addressing the potential impact on native species. Additionally, the finding of non kin-biased cannibalism in juvenile *M. caffra* contrasts with the majority of studies which could be found on this topic, thus contributing to a more holistic understanding of this behaviour in an evolutionary context. It also provides an example of an organism to which comparison with more discriminating species may be made, in order to approach the underlying ecological factors which determine whether or not kin-recognition is likely to arise. As an important factor in the mortality level experienced by developing *M. caffra*, this trait may also be limiting to population growth in areas of sub-optimal habitat. Hence, this makes it relevant to the viability of newly established populations beyond the current range of the species. The combination of inter- and intraspecific behavioural interactions described here, together with the information generated regarding potential distribution, improves our understanding of the role of *M. caffra* in New Zealand.

## 5.2 Concluding remarks

This thesis investigated behaviour in two species which are otherwise unstudied beyond their early description by Ramsay (1990) and Suckling (1984). The interesting trait of unrestrained siblicide is identified in *M. caffra*, which may make this species a good model for further investigation of kin selection in cannibalistic arthropods. Some evidence is found to substantiate the common claim that *M. caffra* is displacing populations of *O. novaezealandiae* and a probable mechanism is identified. This implicates heterospecific attraction as a possible form of impact for other invasive insects, especially those which have fitness costs associated with copulation. An estimate of *M. caffra*'s potential for range expansion within New Zealand is also made, which together with the possibility of impact outlined above suggests that this species will threaten *O. novaezealandiae* throughout most of the country. This provides another example of an invasive organism causing impairment to native species in its introduced range and elucidates some of the relevant factors in this interaction, as well as the potential for future impact. While these provide basic steps in examining these species, there are many other questions raised which identify opportunities for further investigation.



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## 7. Appendices

### Appendix 1. Specific locations of oothecae used in Chapter 2.

| Location       | Vial | Degrees East | Degrees South |
|----------------|------|--------------|---------------|
| Christchurch   | 1 a  | 172° 38.540' | 43° 24.492'   |
|                | 1 b  | 172° 38.543' | 43° 24.493'   |
| Hanmer Springs | 2 a  | 172° 48.802' | 42° 30.575'   |
|                | 2 b  | 172° 48.810' | 42° 30.552'   |
| Kaikoura       | 3 a  | 173° 42.486' | 42° 19.833'   |
|                | 3 b  | 173° 42.487' | 42° 19.834'   |
| Blenheim       | 4 a  | 173° 50.275' | 41° 30.807'   |
|                | 4 b  | 173° 50.278' | 41° 30.805'   |
| Nelson         | 5 a  | 173° 14.248' | 41° 16.839'   |
|                | 5 b  | 173° 14.247' | 41° 16.842'   |
| Murchison      | 6 a  | 172° 18.870' | 41° 48.007'   |
|                | 6 b  | 172° 18.864' | 41° 48.002'   |
| Reefton        | 7 a  | 171° 55.380' | 42° 09.612'   |
|                | 7 b  | 171° 55.393' | 42° 09.625'   |
| Westport       | 8 a  | 171° 35.837' | 41° 45.592'   |
|                | 8 b  | 171° 35.873' | 41° 45.593'   |
| Otira          | 9 a  | 171° 37.462' | 42° 46.225'   |
|                | 9 b  | 171° 37.454' | 42° 46.193'   |
| Hokitika       | 10 a | 170° 54.418' | 42° 49.157'   |
|                | 10 b | 170° 54.430' | 42° 49.146'   |
| Franz Joseph   | 11 a | 170° 09.642' | 43° 23.017'   |
|                | 11 b | 170° 09.642' | 43° 23.018'   |

|              |      |              |             |
|--------------|------|--------------|-------------|
| Haast        | 12 a | 169° 02.670' | 43° 52.890' |
|              | 12 b | 169° 02.662' | 43° 52.886' |
| Makarora     | 13 a | 169° 13.105' | 44° 15.096' |
|              | 13 b | 169° 13.097' | 44° 15.097' |
| Wanaka       | 14 a | 169° 09.069' | 44° 41.599' |
|              | 14 b | 169° 09.071' | 44° 41.599' |
| Kingston     | 15 a | 168° 40.569' | 45° 25.204' |
|              | 15 b | 168° 40.579' | 45° 25.239' |
| Te Anau      | 16 a | 167° 46.641' | 45° 19.217' |
|              | 16 b | 167° 46.636' | 45° 19.219' |
| Invercargill | 17 a | 168° 24.013' | 46° 24.237' |
|              | 17 b | 168° 24.010' | 46° 24.232' |
| Tapanui      | 18 a | 169° 19.378' | 45° 53.174' |
|              | 18 b | 169° 19.377' | 45° 53.174' |
| Dunedin      | 19 a | 170° 33.135' | 45° 45.821' |
|              | 19 b | 170° 33.139' | 45° 45.814' |
| Oamaru       | 20 a | 170° 59.897' | 45° 00.255' |
|              | 20 b | 170° 59.893' | 45° 00.253' |
| Kurow        | 21 a | 170° 20.922' | 44° 39.464' |
|              | 21 b | 170° 20.900' | 44° 39.464' |
| Twizel       | 22 a | 170° 05.215' | 44° 15.875' |
|              | 22 b | 170° 05.224' | 44° 15.873' |
| Geraldine    | 23 a | 171° 04.860' | 44° 07.426' |
|              | 23 b | 171° 04.851' | 44° 07.425' |
| Oxford       | 24 a | 172° 13.089' | 43° 14.464' |
|              | 24 b | 172° 13.087' | 43° 14.469' |

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