Intraspecific and interspecific interactions between *Argyrodes antipodianus,* a kleptoparasitic spider, and its New Zealand hosts

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General Abstract

Kleptoparasitism is a common foraging strategy in which one animal steals resources from another. Kleptoparasitism is therefore an important but often overlooked aspect of ecosystem dynamics. Ecosystem processes can be impacted by the interactions between invertebrate kleptoparasites and their hosts. One such interaction is that of the kleptoparasitic spider, *Argyrodes antipodianus*, common name “The Dew Drop spider” is native to Australia and introduced to New Zealand, which kleptoparasitises several species of web-building spiders. In my thesis, I test how *A. antipodianus* interacts with its New Zealand hosts and conspecifics. Firstly, I conducted a natural history survey to determine which hosts *A. antipodianus* commonly kleptoparasitise and how many *A. antipodianus* can kleptoparasitise a single host. I also tested whether the presence of *A. antipodianus* influenced the likelihood of a host abandoning its web and identified factors that influence kleptoparasitism by *A. antipodianus* (Chapter Two). I then investigated whether *A. antipodianus* can detect, recognise and are attracted to chemical cues from potential hosts and conspecifics (Chapter Three). Finally, I investigated the effects of kleptoparasitism by *A. antipodianus* on the fitness of their hosts and conspecifics (Chapter Four). I found that *A. antipodianus* kleptoparasitises the knobbled orb weaver *Socca pustulosa* more often than the New Zealand sheet web spider *Cambridgea foliata*. I also found that *A. antipodianus* tended to kleptoparasitise hosts alone, rather than in groups. Large host webs and host site fidelity both positively correlated with the presence of *A. antipodianus* in host webs. I did not find evidence that *A. antipodianus* responded to airborne chemical cues released by potential hosts or conspecifics. My results indicate that while *A. antipodianus* do not kleptoparasitise *C. foliata* well under lab conditions, there is little evidence to date that the presence of *A. antipodianus* negatively affect the foraging success of *C. foliata*. This suggests that interactions between *A. antipodianus* and its hosts differ with host species. I suggest that further research is needed to determine whether the relationship between *A. antipodianus* and *C. foliata* is kleptoparasitic, kleptobiotic or commensal.

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Chapter 1

General Introduction

1.1 Kleptoparasitism

Kleptoparasitism is an interaction between two organisms in which one individual (the kleptoparasite) steals a resource from another individual (the host) (Faust et al., 2012; Garay et al., 2020; Iyengar, 2008). In most cases that resource is food that has already been acquired but has yet to be consumed by the host, though it can also be nest building materials or nesting sites (Gaglio et al., 2018; Iyengar, 2008; Tso & Severinghaus, 1998). For the relationship to be considered kleptoparasitism the relationship must negatively affect the host. Situations where a host is stolen from but doesn't incur a negative cost are termed kleptobiosis and the thieves kleptobionts (Iyengar, 2008). Hosts are more likely to be kleptoparasited when they have long food handling times, need to travel with food items or store them for later use as these provide windows of opportunity for kleptoparasites to steal from them (Drisya-Mohan et al., 2019; Gaglio et al., 2018; García et al., 2010; Iyengar, 2008).

Kleptoparasitism is common and has been reported in annelids, insects, arachnids, crustaceans, molluscs, echinoderms, fish, reptiles, birds, and mammals (Iyengar, 2008). Kleptoparasitism is not without risks for the kleptoparasite. In cases where the host is larger than the kleptoparasite, the kleptoparasite may be injured or preyed upon by the host (Rochette et al., 1995; Whitehouse, 1997). For this reason, for kleptoparasitism to be maintained in a system the benefits must outweigh the risks. For example, kleptoparasitic whelks, *Buccinum undatum* (Linnaeus & Salvius, 1758), usually avoid large starfish, *Leptasterias polaris* (Müller & Troschel, 1842), that are potential predators but will approach starfish to steal food (Rochette et al., 1995). Whelks can consume almost 22% of their body weight from a single starfish kill, suggesting that starfish prey are an important resource for the whelks that compensates for the risk of predation during kleptoparasitism (Rochette et al., 1995).

1.2 Population Density

Population density is the measure of the number of individuals of a species in an area. It is often used to describe how closely members of the same species live to one another (Gause, 1932; Lowe et al., 2017). The population density can influence intraspecific competition (Lowe et al., 2017; Lutscher & Iljon, 2013; Travis et al., 2013, 2023) and drives the evolution of different genotypes and phenotypes through density-dependent selection. In density-dependent selection, some phenotypes are selected for when the population density is low, and other phenotypes are selected for when the population density is high (Clarke, 1972; Travis et al., 2013).

There are intrinsic costs associated with living in a group, such as increased intraspecific competition for resources (Donahue, 2006). For this reason, some animals remain solitary and live at low densities. For organisms to form groups, the fitness benefits of being in a group must outweigh the costs of competition (Donahue, 2006; Lutscher & Iljon, 2013). There are two categories of benefits an organism may gain by being in a group, cooperation and conspecific cueing (Donahue, 2006). Cooperation is when animals work together to achieve a common goal (Dugatkin, 2002). This can be increase in food (e.g., cooperative hunting), a reduction in the likelihood of being predated, or an increase in mating opportunities from having readily available mates (Gascoigne & Lipcius, 2004;

Régnière et al., 2013; Teixeira Alves & Hilker, 2017). Conspecific cueing occurs when an individual seeks out members of its own species as an indication of habitat quality. The individual doesn't necessarily gain direct benefits from being near conspecifics, but the costs of intraspecific competition are outweighed by the quality of the habitat (Donahue, 2006).

1.3 The effects of population density on kleptoparasitism

The population density of both the host and kleptoparasite can directly and indirectly affect the relationship between the two organisms. Kleptoparasitism incurs a cost to the host and as such the host may be selected to develop anti-kleptoparasite defences (Ridley & Raihani, 2007). However, these defences may be costly and thus only deployed facultatively depending on kleptoparasite and host density. For example, the fork-tailed drongo (*Dicrurus adsimilis*) (Bechstein, 1793) is a kleptoparasite of the pied babbler (*Turdoides bicolor*) (Jardine et al., 1835) (Ridley & Raihani, 2007). Drongos give alarm calls when a predator approaches a group of pied babblers, however the drongo will also make false alarm calls when a babbler finds food in order to scare away the babbler and kleptoparasitise the meal (Ridley & Raihani, 2007). Small groups of pied babblers are more tolerant of drongos despite the risk of kleptoparasitism as the drongos warn them of approaching predators (Ridley & Raihani, 2007). Large groups of babblers are much less tolerant and mob drongos when they see them as larger groups have more individuals to share the costs of anti-predator vigilance (Ridley & Raihani, 2007).

Many gull species will engage in kleptoparasitism when their population density is high (Spencer et al., 2017). This may have helped gulls invade novel habitats such as urban environments as new gulls unfamiliar with what items were edible and which weren't could steal food from other, more experienced gulls (Spencer et al., 2017). A high population density facilitates facultative kleptoparasitism because a dense population means more individuals and therefore more opportunities to steal (Hamilton, 2002). Also, a high population density means more competition for resources so there is more incentive to steal from others than search for food oneself (Hamilton, 2002).

1.4 Spiders as hosts for kleptoparasites

Spiders make good hosts of kleptoparasites because they have long prey handling times and often store immobilised prey in their web (Drisya-Mohan et al., 2019; Iyengar, 2008). Both insects and other spiders exploit this to steal food. For example, scorpionflies of the genus *Panorpa* (Linnaeus & Salvius, 1758) invade the webs of spiders and aggressively force the spider away from captured prey (Thornhill, 1975). This is risky, as scorpionflies are also preyed on by large spiders (Thornhill, 1975). Fireflies of the genus *Photuris* (Dejean, 1833) feed on other species of fireflies that have been caught in the webs of araneid spiders (Alcock, 2018; Faust et al., 2012). Spiders may respond to these kleptoparasitic fireflies either by aggressively chasing them out of the web, cutting the prey item that the firefly is feeding from loose from the web, or by subduing and wrapping the kleptoparasitic invader in silk (Faust et al., 2012). Wasps and ants also invade the webs of spiders and steal prey, remembering the locations of webs and returning to them to forage (Drisya-Mohan et al., 2019; Rößler et al., 2019). Spiders are also frequent kleptoparasites of other spiders and are well suited to moving on silk webs. However, some spider kleptoparasites struggle to walk on certain silk types (Whitehouse, 1988). For example, the kleptoparasitic spider *Argyrodes antipodianus* (Cambridge, 1880) struggles to walk on cribellate silk, a type that achieves its adhesive properties though very fine silk strands (Whitehouse, 1988). However, *A. antipodianus* can walk on non-cribellate silk, which gains its adhesive properties through natural glue, with relative ease (Whitehouse, 1988). Nevertheless, kleptoparasitism by spiders of other spiders is such a successful strategy that some spider families have become specialised web invaders.

1.5 Kleptoparasitic spiders

1.5.1 Argyrodinae

The Argyrodinae are a subfamily of spiders within the Theridiidae. Argyrodinae are known for their exploitation of other spiders. Two hundred species have been described across six genera: *Argyrodes, Ariamnes, Faiditus, Neospintharus, Rhomphaea, and Spheropistha* (Agnarsson, 2004; Whitehouse, 2011). Many species within Argyrodinae demonstrate social and foraging behaviours that are atypical of spiders. The *Argyrodinae* are a sister group to true social theridiids, which may explain their high tolerance of conspecifics compared to many other theridiids (Agnarsson, 2002, 2004).

Six foraging strategies have been described in members of the Argyrodinae, consisting of: 1) consuming the silk of the host web (Tso & Severinghaus, 1998); 2) gleaning insects off the edge of the host web (Hénaut et al., 2005); 3) stealing food bundles wrapped by the host (Vollrath, 1979); 4) feeding with the host spider at the hub/center of the web (Whitehouse, 1997); 5) opportunistically attacking the host while it is moulting (Tanaka, 1984; Whitehouse, 1986), and; 6) preying on the host or its spiderlings either by lunging or throwing sticky silk to immobilise the spider (Larcher & Wise, 1985; Trail, 1980; Whitehouse, 1986).

There has been a lot of debate about how the foraging strategies of the Argyrodinae evolved and whether one strategy is derived from another. Smith & Trail (1980) first put forward the hypothesis that the adaptations of kleptoparasitic Argyrodinae that allowed to them to sneak unnoticed into the webs of their hosts to steal prey preadapted them to prey on the hosts themselves. Other hypotheses suggest that araneophagy evolved first and Argyrodinae evolved kleptoparasitism later (Vollrath 1984). Yet others have suggested that the kleptoparasitic and araneophagic strategies evolved separately along different evolutionary paths as kleptoparasitic species use biting and lunging strategies, while araneophagic species use sticky silk to capture their spider prey (Whitehouse et al., 2002). It is now generally accepted that kleptoparasite specialists and araneophagic specialists evolved from a generalist ancestor that used basal forms of both strategies. The biting methods of kleptoparasitic species is probably a basal trait, while the silk slinging methods of the pure araneophages is a derived trait (Agnarsson, 2004).

1.5.2 Social behaviours of Argyrodinae

Members of the Argyrodinae form aggregations in the webs of other spiders. While the number of Argyrodinae that inhabit a host web varies greatly depending on species and host web size, as many as 45 conspecific Argyrodinae have been observed in the web of a single host (Grostal & Walter, 1999; Kerr & Quenga, 2004; Miyashita, 2001, 2002; Vollrath, 1987). However, very little research has been done on the social dynamics of Argyrodinae. Whitehouse & Jackson (1993) investigated the movement and time budgets of *Argyrodes* *antipodianus* (Cambridge, 1880) an Australasian species of Argyrodinae which employs a mostly kleptoparasitic lifestyle. *Argyrodes antipodianus* has a fluid social structure that is similar to the fission-fusion dynamics of some social vertebrates (Aureli et al., 2008) rather than the more permanent social fixtures of other social spiders (Christenson, 1984; Uetz & Cangialosi, 1986; Ward & Enders, 1985).

Members of the Argyrodinae demonstrate varying levels of intraspecific tolerance. Intraspecific interactions take up very little time for *A. antipodianus* or *A. argentatus* (Cambridge, 1880) (Whitehouse & Jackson 1993; Kerr 2005). An increase in the density of *A. argentatus* on the webs of host spiders did not result in a proportional increase in intraspecific aggression despite a suspected increase in competition for food (Kerr 2005). However, this is in contrast to *A. flavipes* (Rainbow, 1916) which has frequent aggressive interactions with conspecifics (Whitehouse & Jackson, 1998). It is unclear what drives differences in intraspecific tolerance. Some species of *Argyrodes* will be less aggressive to conspecifics when they are feeding at the hub with their host, which may reduce the risk of being detected and attacked by the host (Whitehouse, 1997).

It was previously believed that kleptoparasitic species of *Argyrodes* also lacked complex mating displays that are often employed by males to supress female aggression (Cangialosi, 1990; Wignall & Herberstein, 2022). This led some to believe that reduced aggression as the species evolved kleptoparasitism also allowed them to better tolerate conspecifics (Cangialosi, 1990). However, more recent observations have found that kleptoparasitic species that are usually group living and non-predatory actually do have complex courtship displays (Whitehouse, 2011). Courtship displays in this context may be a product of sexual selection and competition for mates rather than a way to prevent cannibalism during mating attempts (Whitehouse, 2011).

1.5.3 *Argyrodes*

The genus *Argyrodes* are kleptoparasitic spiders. They are found throughout the world, typically kleptoparasitising the webs of orb weaving spiders (Whitehouse et al., 2002). There are two common foraging tactics that *Argyrodes* spiders use (Whitehouse, 1986, 1997). Many *Argyrodes* feed with their host, removing the need for *Argyrodes* to produce the necessary digestive enzymes to break down prey themselves (Whitehouse, 1986, 1997). Alternatively, *Argyrodes* glean insects from the edge of the webs of their hosts (Hénaut et al., 2005; Whitehouse, 1986). *Argyrodes* may also occasionally prey on their hosts (when hosts are moulting) and the host's spiderlings (Whitehouse, 1986).

1.5.4 *Argyrodes antipodianus*

Argyrodes antipodianus (formerly known as *Argyrodes antipodiana*) is found in Australia and New Zealand and is the focus of my thesis research. Like other species of *Argyrodes*, *A. antipodianus* both steal prey off the web and feed directly with the host. In Australia, *A. antipodianus* prefers to kleptoparasitise the webs of *Trichonephila plumipes* (formerly *Nephila plumipes*) (Latreille et al., 1804) however *Trichonephila* are largely absent in New Zealand (Whitehouse, 2011). In New Zealand, *A. antipodianus* typically kleptoparasitises *Socca pustulosa* (formerly *Eriophora pustulosa*) (Walckenaer et al., 1841) (Whitehouse, 2011). Interestingly, *S. pustulosa* are also present in Australia but few *A. antipodianus* are found in their webs in Australian ecosystems (Whitehouse, 2011).

Argyrodes antipodianus typically live in groups on the webs of their hosts (Grostal & Walter, 1997; Whitehouse & Jackson, 1993). The ability of *A. antipodianus* to gain food is reliant on the host not detecting them (Whitehouse, 1986). The presence of multiple *A. antipodianus* may distract the host during feeding events, allowing some individuals to steal food while the host is distracted (Agnarsson, 2002; Whitehouse et al., 2002). There is also evidence that the colouration of *Argyrodes* attracts prey into the webs of their hosts (Peng et al., 2013; Zhang et al., 2022). Multiple *Argyrodes* in a web may be able to lure prey more effectively than individual *Argyrodes*, which would potentially benefit both the *Argyrodes* and host because there is more food (Zhang et al., 2022). However, hosts of *A. antipodianus* may abandon their webs when there are too many *A. antipodianus* kleptoparasitising them (Grostal & Walter, 1997). This generates several questions: Is the formation of groups by *A. antipodianus* in host webs the result of cooperation or is it conspecific cueing? How does the number of kleptoparasites in a web affect the fitness of *A. antipodianus*? Do *A. antipodianus* regulate their numbers in a host's web? And what factors influence the decision of the host spider to abandon its web?

1.6 Thesis structure

In my thesis, I test how *A. antipodianus* interacts with its hosts and conspecifics, exploring how group size affects the fitness of *A. antipodianus* and their hosts. *Argyrodes antipodianus* are an excellent model species to test hypotheses about kleptoparasitic relationships due to their abundance, as well as the abundance of their hosts. My research will add to our understanding of how the interactions between a kleptoparasitic organism and its hosts and conspecifics can affect the fitness of both. Firstly, in Chapter Two I conducted a natural history survey to quantify group sizes and host use in *A. antipodianus*. I also investigated host site fidelity in the presence of kleptoparasitism in the field. My results identify factors that may drive the kleptoparasitic relationship between *A. antipodianus* and its hosts.

In Chapter Three, I tested whether *A. antipodianus* can detect, recognise and are attracted to the airborne chemical cues of potential hosts and conspecifics. This chapter adds to our understanding of host selection and conspecific interactions by *A. antipodianus*.

In Chapter Four, I tested how the number of *A. antipodianus* in a host web influences the fitness of *A. antipodianus* and its hosts*,* using weight change as a proxy for fitness. This chapter helps our understanding of the population dynamics of *A. antipodianus* and why they may gather in aggregations on host webs.

In my final chapter, I discuss the potential advantages to web invasion by *A. antipodianus*, the dynamics of living in a group on a host web and the relationship between *A. antipodianus* and its sheet web host *Cambridgea foliata*. I also discuss avenues for future research.

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Chapter 2:

Natural history and host choice by *Argyrodes antipodianus*

2.1 Abstract

Kleptoparasitism is an interaction between two animals in which one steals from another. Kleptoparasitism can have large effects on the functioning of an ecosystem, but we still have a poor understanding of the ecological and evolutionary dynamics of kleptoparasitic relationships. I investigated the relationship between *Argyrodes antipodianus*, a kleptoparasitic spider introduced to New Zealand, and its hosts *Socca pustulosa* and *Cambridgea foliata*. I used field surveys to determine which of the two host species' webs *A. antipodianus* is found in more often, quantify how many *A. antipodianus* typically kleptoparasitise a host, investigate the relationship between the presence of *A. antipodianus* and host site fidelity, and what factors correlate with kleptoparasitism by *A. antipodianus*. I found that *A. antipodianus* are found in the webs of *S. pustulosa* more often than the webs of *C. foliata*. Only one *A. antipodianus* was usually found in a host web, which differs to their grouping behaviour in host webs in their Australian range. The presence of *A. antipodianus* correlated with longer host site fidelity, perhaps because *A. antipodianus* tended to be found in larger host webs which host spiders may be less likely to abandon due to their investment in them. My results suggest that the relationship between *A. antipodianus* and its hosts differ with host species.

2.2 Introduction

Kleptoparasitic relationships are defined by a kleptoparasite (thief) stealing resources from a host (Garay et al., 2020; Hamilton, 2002; Hamilton & Dill, 2003; Iyengar, 2008). Kleptoparasitic relationships are predominantly based on the theft of food resources, but the theft of nesting materials or sites are also forms of kleptoparasitism (Iyengar, 2008; Tso & Severinghaus, 1998; Whitehouse, 1986). Kleptoparasitism can be very risky (Rochette et al., 1995; Rößler et al., 2019; Whitehouse, 1997). Some hosts will defend their resources, attacking, killing and in some cases even predating the kleptoparasite (Rochette et al., 1995; Rößler et al., 2019; Whitehouse, 1997). Some kleptoparasitic animals work in groups in order to overwhelm the host's defenses (Hamilton & Dill, 2003). A vital part of the kleptoparasite-host relationship is a period of handling time between the host acquiring and using the resource, particularly in kleptoparasitic relationships where food is being taken (Gaglio et al., 2018; Iyengar, 2008). If a host consumes a food item immediately, there is no time for a kleptoparasite to steal it (Iyengar, 2008). For this reason, web-building spiders are often hosts to kleptoparasites as they handle and store food in their webs (Drisya-Mohan et al., 2019; Thornhill, 1975; Whitehouse et al., 2002).

Argyrodes (Theridiidae: Argyrodinae) are a genus of spiders that kleptoparasitise other spiders by entering their webs and consuming the prey caught by the host (Whitehouse et al., 2002). *Argyrodes* are found in the Americas, Australasia and Asia (Dash & Sivaperuman, 2023; Grostal & Walter, 1997, 1999; Hénaut et al., 2005; Miyashita, 2001; Smith Trail, 1980; Tanaka, 1984; Whitehouse et al., 2002). In most regions, *Argyrodes* kleptoparasitise orb weaving spiders which may provide them with more diverse foraging opportunities (Whitehouse et al., 2002). For example, *A. kumadai* (Bösenberg & Strand,

1906) have more foraging options when kleptoparasiting the orbweaver *Cyrtophora moluccensis* (Doleschall, 1857) than the funnel web spider *Agelena silvatica* (Bösenberg, W & Strand, E, 1906) (Baba et al., 2007). *Argyrodes* have diverse foraging strategies, including stealing and eating the silk of host webs (Tso & Severinghaus, 1998), gleaning insects from the host web that are too small for the host to eat (Hénaut et al., 2005), and entering the web while the host is distracted handling prey to feed simultaneously with the host (Whitehouse, 1986). *Argyrodes* may also prey on their host when they're moulting, or on the host's offspring (Whitehouse, 1986).

Hosts respond differently to *Argyrodes* depending on species, web type, prey preference, and body size (Grostal & Walter, 1999; Hénaut et al., 2005; Whitehouse, 1988). Host responses can in turn change *Argyrodes*' behaviour as *Argyrodes'* may retreat from webs and abandon feeding attempts when hosts react aggressively to detecting *Argyrodes* in their webs (Whitehouse, 1997b). For this reason, *Argyrodes* avoid actions that may draw the host's attention. For example, intraspecific competitions for food are conducted outside the host's web (Whitehouse, 1997a). Conflicts on the web could cause vibrations, attracting the host's attention to the *Argyrodes* making it harder for *Argyrodes* to effectively kleptoparasitise (Whitehouse, 1997b). Intraspecific conflict may also distract the *Argyrodes* from evading the host should the host attempt to take aggressive action against them (Whitehouse, 1997b). Hosts may also abandon their webs if the presence of *Argyrodes* exceeds what they will tolerate (Grostal & Walter, 1997). As web building is an energy expensive activity for a spider, a host with a large web is less likely to abandon its web than a host with a small web (Eberhard, 2020).

Argyrodes antipodianus (Figure 2.1A) (Cambridge, 1880) can be found in groups in the webs of their hosts in both New Zealand and Australia (Grostal & Walter, 1999; Whitehouse & Jackson, 1993). Studies have shown that *A. antipodianus* (and other species of *Argyrodes*) readily kleptoparasitise orb weavers (Hénaut et al., 2005; Miyashita, 2001; Tso & Severinghaus, 1998; Whitehouse, 1988, 1997). In New Zealand, *A. antipodianus* typically kleptoparasitises the orb weaver *Socca pustulosa* (Figure 2.1B) (Walckenaer et al., 1841) (Whitehouse & Jackson, 1993) as well as the native sheet web spider *Cambridgea foliata* (Figure 2.1C) (Cambridge, 1879) (Court, 1982; Forster, 1967). Both *A. antipodianus* and *S. pustulosa* are also found in Australia, where *A. antipodianus* more often kleptoparasitises another orb weaver, *Trichonephila plumipes* (Latreille et al., 1804) (Grostal & Walter, 1997, 1999). Although the relationship between *A. antipodianus* and *S. pustulosa* has been well documented (Whitehouse, 1988, 1997), there is little information about *A. antipodianus's* relationship with *C. foliata*.

Figure 2.1: (A) *Argyrodes antipodianus* (photo credit: pimelea / iNaturalist (*CC BY*) (B) *Socca pustulosa* (photo credit: Saryu Mae / iNaturalist (*CC BY*) (C) *Cambridgea foliata* (photo credit: Anne Wignall)

I tested whether *A. antipodianus* kleptoparasitises *S. pustulosa* more often than *C. foliata* in New Zealand. I also recorded if the presence of *A. antipodianus* caused the host spider to abandon their web more frequently than host spiders without *A. antipodianus* in their web. I tested whether host sex, web size, the presence of prey in the web or the presence of host egg sacs correlated with the presence of *A. antipodianus*. I predicted that *A. antipodianus* would be more likely to kleptoparasitise *S. pustulosa* over *C. foliata* as the literature suggests that other *Argyrodes* species prefer orb weavers when they are available to other species of web building spiders (Grostal & Walter, 1999; Miyashita, 2002; Whitehouse, 1988; Whitehouse et al., 2002). I also predicted that *S. pustulosa* are more likely to abandon webs with *A. antipodianus* than *C. foliata* as they build smaller, less complex webs and thus have less incentive to tolerate the presence of *A. antipodianus*.

2.3 Methods

2.3.1 *Study site*

My survey was conducted in a section of the Massey University bush on the Albany campus adjacent to the Fernhill Escarpment (Auckland, New Zealand). The section is dominated by kanuka trees (*Kunzea ericoides*) (Richard & d'Urville, 1832), with introduced and native trees and shrubs in the understory (e.g., gorse, ferns). The survey section was approximately 550m by 500m. Walking paths and mountain bike trails had been previously cleared through the bush, providing access throughout. North of the escarpment is a small, grassy field approximately 270m by 270m. To the east of the escarpment is Massey University campus and west and south of the escarpment is suburban development. A series of paths approximately 200m long on the eastern side of the escarpment served as the focus for my study. The surveys were conducted in September 2023 every Monday, Wednesday and Friday (9pm-11pm) for three weeks (nine surveys). A tenth survey was conducted on the 29th of October a month later to record long term host-kleptoparasite changes on webs.

2.3.2 *Survey methods*

I searched for the webs of *S. pustulosa* and *C. foliata* within my survey area. When a web was located, I recorded the resident spider species, sex and age (male, female, juvenile), the resident spider's location on the web, how many *A. antipodianus* were on the web, the approximate age of any *A. antipodianus* present (juvenile, adult), web size (length, width), if there were prey items caught in the web, if there were eggs sacs present on the web, if there were other spiders on the web (i.e., conspecifics or other spider kleptoparasites), how many other potential host webs were within a 1m proximity of the focal web, and how many other kleptoparasitised webs were within a 1m proximity of the focal web. Approximate web area was calculated by measuring the length and width in millimetres using a measuring tape, then multiplying the two measurements. *C. foliata* webs have three dimensions, however, only the area of the sheet was measured, with drop down threads ignored for simplicity.

I marked each focal web with flagging tape tied to a nearby branch. On subsequent surveys, I surveyed previously marked webs and noted whether the resident spider was still present. I did my best to disturb the spiders as little as possible throughout the survey. Measuring the webs occasionally caused disturbance to the web, resulting in some of the spiders running to their retreat. For this reason, web measurements were performed last.

2.3.3 *Data analysis*

All data analyses were performed using R version 4.4.0 (R Core Team, 2024). I used a chi-square test to test whether there is a difference in kleptoparasitism rates by *A. antipodianus* of the two host species in the field. I also tested if there was a difference in the number of *A. antipodianus* that inhabited the web of each host species using a generalised linear mixed model (GLMM) with a Poisson distribution in the lme4 package (Bates et al., 2015). I included the number of *A. antipodianus* present as the dependent variable, with host species as a fixed effect and web ID as a random effect. I tested for normality of residuals using a Shapiro-Wilks test of normality. As residuals were not normal, I calculated confidence intervals using bootstrapping methods to validate the results of the GLMM in the boot package (1000 samples) (Canty & Ripley, 2016). Webs with no kleptoparasitises comprised a large proportion of the dataset and so I also repeated this analysis excluding webs with no kleptoparasites.

I tested whether *A. antipodianus* influenced host site fidelity using a generalized estimating equation (GEE) model in the ‘geepack’ package (Højsgaard et al., 2006). I measured fidelity as how many consecutive survey’s a host remained in its web. I included the number of surveys a host was present as the dependent variable and the presence of *A. antipodianus* (yes/no) and host species as fixed effects and host web ID as a random effect (Bates et al., 2015). While there was no guarantee that spiders observed at the same site were in fact the same spider, as they were not marked, it is highly likely that it was the same individual. For this reason, a spider seen in the same site over consecutive surveys was considered the same individual. As the residuals were not normally distributed, I calculated confidence intervals using bootstrapping methods to validate the results of the GEE (1000 samples). To test what factors might influence kleptoparasitism, I used a GLMM with binomial distribution to explore whether the sex or age of the host, the size of the host web, or the presence of prey in the web were correlated with the presence of *A. antipodianus*. Host web size was scaled logarithmically in order to resolve problems of convergence within the model. I compared models using AIC values to determine the model with the best fit. All figures were created using the ggplot2 package (Wickham, 2016).

2.4 Results

I compared the number of *A. antipodianus* that kleptoparasitised the webs of *S. pustulosa* and *C. foliata*. First, I compared the number of observations of *A. antipodianus* found in the host webs across all the surveys. Some host webs were included more than once as they were observed across multiple surveys. I found that *A. antipodianus* kleptoparasitise *S. pustulosa* more than *C. foliata* ($\chi^2 = 32.75$, df = 1, *P*-value = <0.001; Figure 2.2A). 33% of *S. pustulosa* web observations included at least one *A. antipodianus* in the web, but only 12% of *C. foliata* web observations included at least one *A. antipodianus*. Secondly, I compared the number of observations of *A. antipodianus* found in host webs, this time counting each web only once. If a web had an *A. antipodianus* in any of the surveys, it was classified as kleptoparasitised. *Argyrodes antipodianus* again kleptoparasitised *Socca pustulosa* more than *Cambridgea foliata* ($\chi^2 = 5.00$, df = 1, *P*-value = 0.03; Figure 2.2B). 58% of *S. pustulosa* webs were found to have at least one *A. antipodianus* in them throughout the study, while 31% of *C. foliata* webs had at least one *A. antipodianus* in them.

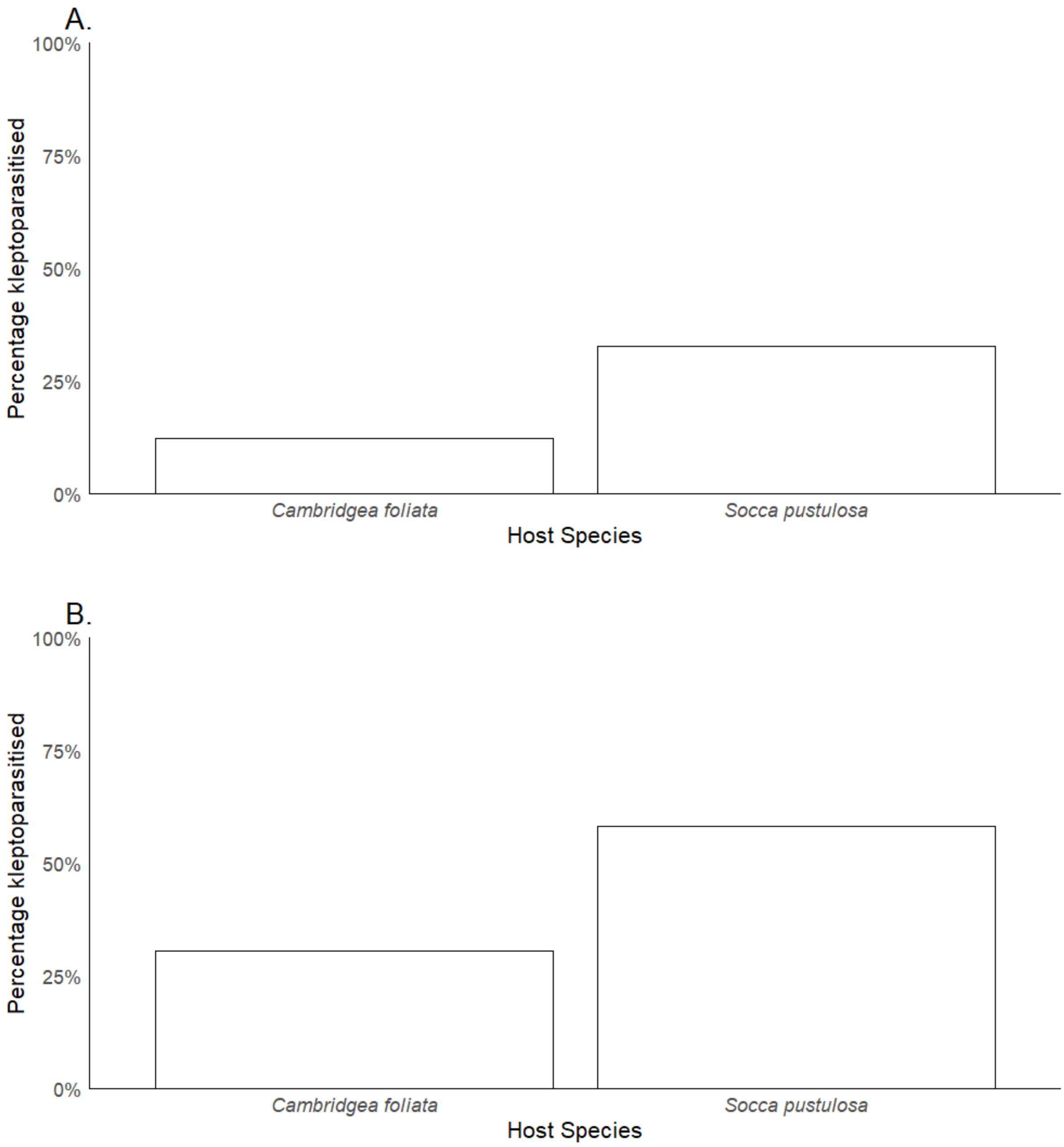

Figure 2.2: Percentage of webs kleptoparasitised by *A. antipodianus* when, (A) webs may be counted multiple times if they were observed in multiple surveys, and when (B) webs were only included once by pooling observations over the survey period (if a web had an *A. antipodianus* at any point in the field study it was considered kleptoparasitised).

Next, I compared the number of *A. antipodianus* found in the webs of *S. pustulosa* and *C. foliata*. Some webs were included more than once as they were assessed over multiple surveys. I found that *S. pustulosa* have more *A. antipodianus* in their webs compared to *C. foliata* (GLMM: Z-value = 3.29, *P*-value < 0.001; bootstrap 95% confidence intervals: -3.21, -1.79; Table 2.1). However, most *S. pustulosa* and *C. foliata* webs were not kleptoparasitised (67% and 89% respectively, Figure 2.3 A&B). As a result, I ran a second analysis removing webs with no kleptoparasites from the analysis. When these webs were removed from the dataset, *S. pustulosa* and *C. foliata* had a similar number of *A. antipodianus* in their webs (GLMM: Z-value = 0.28, *P*-value = 0.78; bootstrap 95% confidence intervals: 0.30, 0.64; Table 2.2). Most kleptoparasitised *S. pustulosa* and *C. foliata* webs only had a single *A. antipodianus* in them (43% and 48% respectively; Figure 2.3C&D).

Table 2.1: GLMM comparing the number of *A. antipodianus* found in the webs of the two host species. All survey observations were included.

	Estimate	Std Error	Z-value	*P*-value	Variance	Std Dev	CI Lower Bound	CI Upper Bound
Random effect (Web_ID)	-	-	-	-	2.86	1.69	-	-
Residual	-	-	-	-	0.50	0.70	-	-
(Intercept)	-3.23	0.45	-7.15	**<0.001**	-	-	-3.21	- 1.79
Host species	1.66	0.50	3.29	**<0.001**	-	-	-	-

P < 0.05 indicated in bold

Table 2.2: GLMM comparing the number of *A. antipodianus* found in the webs of the two host species. Only kleptoparasitised webs were included.

	Estimate	Std Error	Z-value	*P-value*	Variance	Std Dev	CI Lower Bound	CI Upper Bound
Random effect (Web_ID)	-	-	-	-	0.18	0.42	-	-
(Intercept)	0.50	0.22	2.25	**0.02**	-	-	0.30	0.64
Host species	0.07	0.25	0.28	0.78	-	-	-	-

P < 0.05 indicated in bold

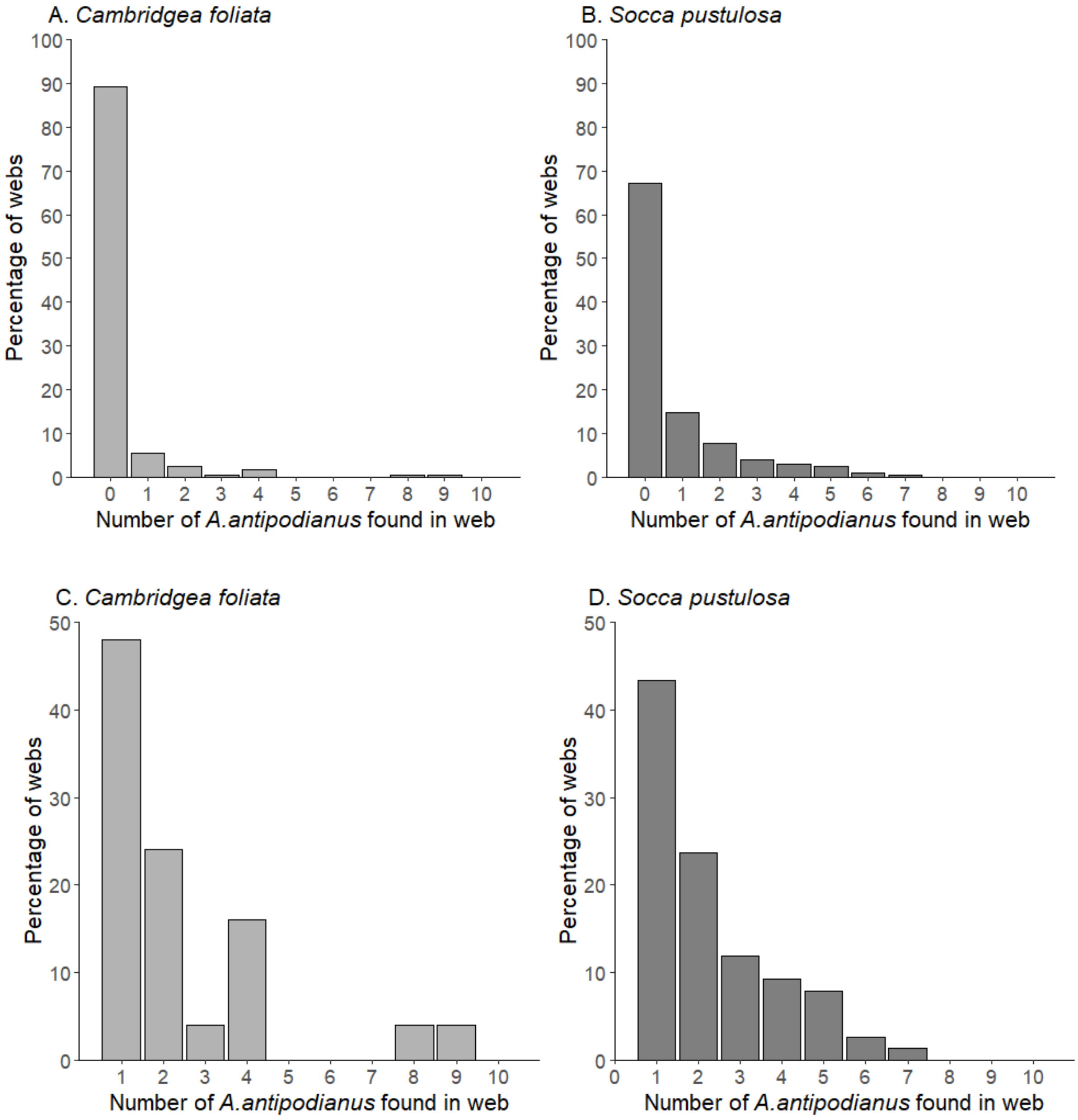

Figure 2.3: (A & B) Frequency distribution of number of *A. antipodianus* observed in *C. foliata and S. pustulosa* webs respectively. All observations were included regardless of kleptoparasite status, with some webs represented more than once if it was surveyed on multiple days. (C & D) Frequency distribution of number of *A. antipodianus* observed in *C. foliata and S. pustulosa* webs respectively. Only observations that had one or more *A. antipodianus* in their webs were included, with some webs included more than once if the web had kleptoparasited over multiple surveys.

I compared the web site fidelity of both kleptoparasitised and non-kleptoparasitised *S. pustulosa* and *C. foliata*. Kleptoparasitised host spiders showed more fidelity to a web site than non-kleptoparasitised spiders (GEE: Wald = 6.60, *P*-value = 0.01; bootstrap 95% confidence intervals: 1.45, 1.85; Table 2.3; Figure 2.4). There was no difference between host species on site fidelity (GEE: Wald = 0.00, *P*-value = 0.96; Table 2.3; Figure 2.4), or any evidence of an interaction between *A. antipodianus* presence and host species on site fidelity (GEE: Wald = 0.81, *P*-value = 0.37; Table 2.3; Figure 2.4).

Table 2.3: GEE model testing how the presence of *A. antipodianus* and the species of host affects host site fidelity.

	Estimate	Std Error	Wald	*P*-value	Variance	Std Dev	CI Lower Bound	CI Upper Bound
Random effect (Web_ID)	-	-	-	-	0.08	0.27	-	-
(Intercept)	1.59	0.11	192.14	**<0.001**	-	-	1.45	1.85
A. antipodianus present	0.39	0.15	6.60	**0.01**	-	-	-	-
Host species	-<0.01	0.18	0.00	0.96	-	-	-	-
A. antipodianus presence: host species	-0.20	0.23	0.81	0.37	-	-	-	-

P < 0.05 indicated in bold

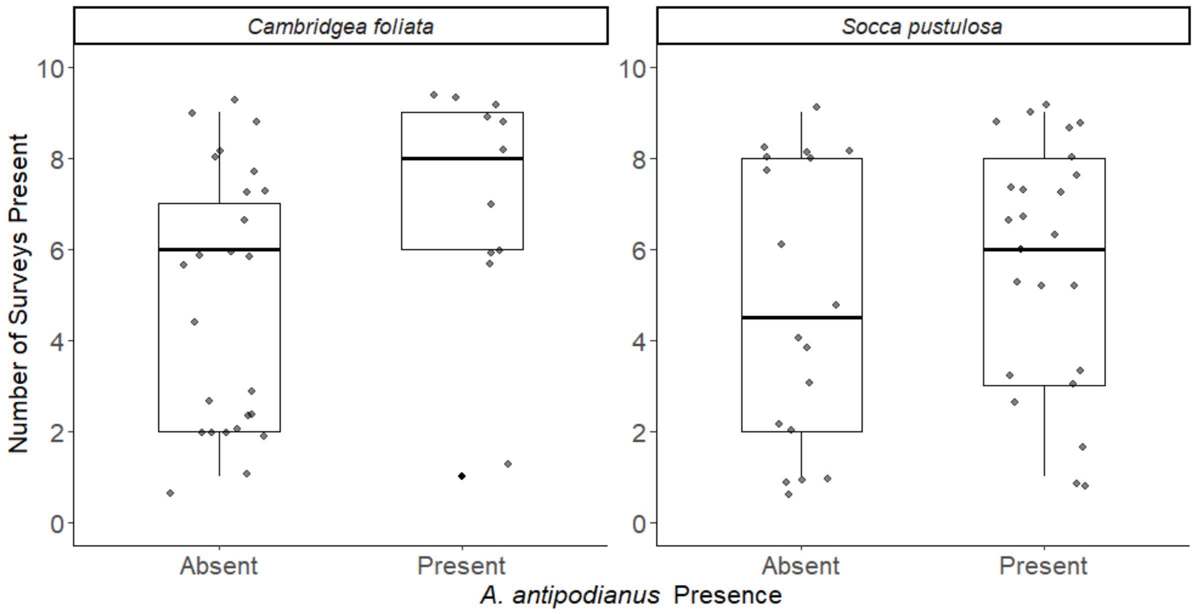

Figure 2.4: Number of consecutive surveys a spider was observed in the same web location (spiders found in the same location over consecutive surveys were assumed to be the same spider). I considered a web kleptoparasitised if at least one *A. antipodianus* was observed in the host web.

Argyrodes antipodianus tended to kleptoparasitise hosts with large webs (GLMM: Z-value = 3.43, *P*-value < 0.01; Table 2.4; Figure 2.5). There was no effect of prey presence or host sex on the probability of kleptoparasitism (Table 2.5). To further explore the effect of web area on the presence of *A. antipodianus,* I tested for an interaction between web area and host species in a simpler model. I found that while host species and web area influence the presence of *A. antipodianus* (host species: Z = 4.22, *P*-value < 0.001; web area: Z = 2.86, *P*-value < 0.001; Table 2.4), there was no interaction between host species and web size (Z = 1.08, *P*-value = 0.28; Table 2.5).

Table 2.4: GLMM model testing the effect of host species, web size, prey presence and host sex on the presence of *A. antipodianus*.

	Estimate	Std Error	Variance	Std Dev	Z value	*P*-value
Random effect (Web_ID)	-	-	4.25	2.06	-	-
(Intercept)	-3.72	0.84	-	-	-4.45	**<0.001**
Host species	3.04	0.75	-	-	4.08	**<0.001**
Web area (scaled)	0.93	0.27	-	-	3.43	**<0.001**
Prey items in web	-0.05	0.48	-	-	-0.11	0.91
Host sex	-0.44	0.62	-	-	-0.7	0.48

P < 0.05 indicated in bold

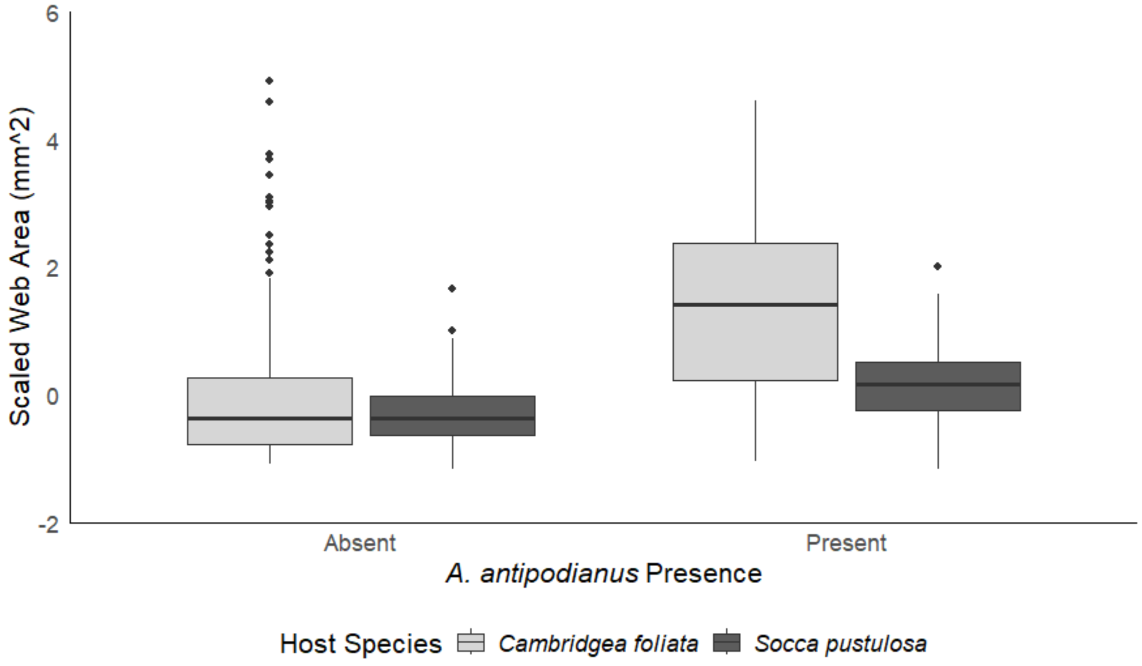

Figure 2.5: Comparison of host web size (scaled) between kleptoparasitised and non-kleptoparasitised webs. All survey observations were included as *S. pustulosa* rebuild their webs regularly, so their size can change often.

Table 2.5: GLMM model testing the effect of host species, web area and the interaction between host species and web area on the presence of *A. antipodianus.*

	Estimate	Std Error	Variance	Std Dev	Z value	*P*-value
Random effect (Web_ID)	-	-	4.11	2.03	-	-
(Intercept)	-3.90	0.62	-	-	-6.26	**<0.001**
Host species	2.92	0.69	-	-	4.22	**<0.001**
Web area	0.73	0.25	-	-	2.86	**<0.001**
Host Species:Web area	0.61	0.57	-	-	1.08	0.28

P < 0.05 indicated in bold

2.5 Discussion

I found that *A. antipodianus* kleptoparasitise the webs of *S. pustulosa* more often than the webs of *C. foliata*. This is not unexpected as *Argyrodes* worldwide kelptoparasitise the webs of orb weavers (Miyashita, 2001, 2002; Tso & Severinghaus, 1998; Vollrath, 1979; Whitehouse, 1988; Whitehouse et al., 2002). *Argyrodes antipodianus* only inhabit the webs of a relatively small percentage of their host population at any one time. However, I found that over half the webs of *S. pustulosa* had at least one *A. antipodianus* in their webs over the duration of my study. This suggests that *A. antipodianus* move between hosts often, a conclusion supported by Whitehouse & Jackson, (1993). I also found that the size of a web was an indicator of *A. antipodianus* presence, suggesting that *A. antipodianus* are more likely to kleptoparasitise a host with a large web. This finding was also supported by other studies of *A. antipodianus* conducted in Australia (Grostal & Walter, 1999).

Despite differences in how often they kleptoparasitise the webs of each host species, *A. antipodianus* appear in similar numbers within the webs of each host species. Usually, only one *A. antipodianus* was found in a host's web. It therefore seems unlikely that *A. antipodianus* that group together on the same host web have a fitness advantage over *A. antipodianus* that kleptoparasitise a host web alone, or else I would have expected more *A. antipodianus* to be found in groups. Determining the reasoning for why *A. antipodianus* enter host webs will be necessary to determine if group formations are beneficial. During my study I assumed that any *A. antipodianus* in a host web were there solely to kleptoparasitise the host. However, some individuals may have been seeking shelter in a web and were not intending on feeding. The effect of group kleptoparasitism on *A. antipodianus* and hosts still needs to be tested. Experiments on *Argyrodes* species in Japan have found that after removing *Argyrodes* kleptoparasites from the webs of their orb weaver hosts, the kleptoparasites returned to almost half their original density within two days (Miyashita, 2001). This suggests that either direct or indirect competition from the already established *Argyrodes* was preventing the others from entering the web. A closer look into how sex affects the potential benefit of grouping up should also be investigated. Male *A. antipodianus* disperse more widely in search of females and as such may have biased the results if female only groups were the norm (Whitehouse & Jackson, 1993; Whitehouse & Lubin, 2005). The reflective colouration of *A. antipodianus* in Australia can attract prey into the webs of their host, *Trichonephila plumipes* (Zhang et al., 2022). It would be interesting to test whether *A. antipodianus* can also attract prey in New Zealand.

The groups of *A. antipodianus* observed in my own and other studies may have formed due to those webs being particularly favourable, rather than the result of selection on group formation. *A. antipodianus* may seek out the cues of conspecifics as an indication that a host is good quality. The phenomenon of animals using conspecific cues as an indication of favourable circumstances is called conspecific cueing (Andrews et al., 2015; Buxton et al., 2020; Donahue, 2006; Freeberg et al., 2024). Interestingly, my results also suggest that there may be selection pressure on *A. antipodianus* to reduce negative effects on host spiders as only a small portion of the host population is kleptoparasitised at any one time. However, large proportions of the population appear likely to have at least one *A. antipodianus* at some stage in time – although this requires further testing. Further, it is rare for more than one individual *A. antipodianus* to kleptoparasitise a host at a time. Together, these behaviours may result in a reduced impact by *A. antipodianus* on the host spiders. Another possible explanation is that *A. antipodianus* cannot meet all their needs on single host web and have to move between host webs to satisfy their needs (Whitehouse & Jackson, 1993).

The presence of *A. antipodianus* correlated with greater host site fidelity. I also found that *A. antipodianus* in New Zealand commonly kleptoparasitise hosts with large webs. Other species of *Argyrodes* prefer to kleptoparasitise large and structurally complex webs (Dash & Sivaperuman, 2023), probably because these webs are a large investment of energy on the part of the host and therefore the hosts are less likely to abandon them. Alternatively larger webs may catch more prey making them able to support a larger kleptoparasite population. A preference in *A. antipodianus* for large webs that hosts are less likely to abandon make it difficult in the present study to test a causal relationship between *A. antipodianus* presence and site fidelity. Experimental studies in Australia with *A. antipodianus* have shown that the presence of *A. antipodianus* increased how often their hosts, *Trichonephila plumipes*, moved their webs (Grostal & Walter, 1997). Those experiments used the orb weaver host *T. plumipes*, whereas *C. foliata* is a sheetweb spider, so a recreation of Grostal and Walker's (1997) methods using *C. foliata* may yield an interesting comparison of site fidelity in different web types when kleptoparasites are present.

My study was conducted between September-October, prior to the reproductive season of *A. antipodianus*, *S. pustulosa* and *C. foliata*. For one this means that we mostly observed juveniles, which were probably over wintering and weren't prioritising feeding. The effects observed in my study may differ in the breeding season, when there are a larger percentage of adults in the population. The presence of host egg sacs may also increase the presence of *A. antipodianus,* as *A. antipodianus* also opportunistically prey on the spiderlings of their hosts (Whitehouse, 1986).

In conclusion, *Argyrodes antipodianus* kleptoparasitise webs of the orb weaver *S. pustulosa* more often than the sheet-web spider *C. foliata*. *Argyrodes antipodianus* appear to move between webs frequently, a conclusion supported by other studies (Whitehouse & Jackson, 1993). Further studies are needed to determine the reason for this frequent movement between webs. Kleptoparasitism by *A. antipodianus* correlates with increased host site fidelity, but this is likely to be due to *A. antipodianus* seeking out hosts with larger webs because hosts are less likely to abandon them. My results suggest that *A. antipodianus* does not gain a direct benefit foraging in groups, their frequent movement between webs suggests that a single web host web struggles to support *A. antipodianus* for long periods of time and as such they meet their needs by frequenting multiple webs with little need to live within a group.

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Chapter 3

Responses of *Argyrodes antipodianus* to airborne chemical cues of potential host and conspecific spiders

3.1 Abstract

Chemical cues are commonly used by animals to locate important resources and avoid dangers within their environment. *Argyrodes antipodianus* is a kleptoparasitic spider which feeds on prey caught in the webs of other spiders. However, we know very little about how *A. antipodianus* locate potential hosts. I used an olfactometer to determine if *A. antipodianus* can detect, recognise and are attracted to chemical cues released by two potential host species (*Socca pustulosa* and *Cambridgea foliata*). I also tested whether *A. antipodianus* responds to conspecific chemical cues. I found that *A. antipodianus* showed no preference for potential host or conspecific chemical cues when given a choice against an odourless control. My results suggest that *A. antipodianus* does not use airborne chemical cues produced by potential host spiders or conspecifics to locate hosts.

3.2 Introduction

Chemoreception plays an important role in finding nutrients, identifying conspecifics and avoiding dangers both biotic and abiotic (Pearce et al., 2002). Most organisms release chemical volatiles either during communication or as a side effect of their biological processes, providing an opportunity for other organisms to exploit the information as chemical cues (Ache & Young, 2005; Vlot & Rosenkranz, 2022). For example, chemical cues are often used in mediating social interactions, foraging behaviour and anti-predator behaviour (Ache & Young, 2005; Caspers et al., 2017; Fischer et al., 2017; Henkel & Setchell, 2018; Krieger & Breer, 1999). Chemical cues are also important for social species with complex social structures such as many species of birds and mammals who use olfactory cues to distinguish individuals within and outside their social group (Henkel & Setchell, 2018).

Chemoreception plays an important role in helping invertebrates locate food sources and appraise their quality over long distances (Zjacic & Scholz, 2022). Both terrestrial and aquatic invertebrates use chemical cues to locate food and prepare for ingestion (Kamio & Derby, 2017; Zjacic & Scholz, 2022). For example, snails and slugs have olfactory epithelia in their frontal tentacles and are strongly attracted to the odours of potential food sources such as apples or carrots (Kiss, 2017). In cnidarians such as jellyfish and anemones, the detection of food chemicals primes the cnidocytes, stinging cells in their tentacles, for mechanical stimulation (Kamio & Derby, 2017). Chemical cues prepare the gastrointestinal system and primes the motor feeding programs in the soil living, round worm *Caenorhabditis elegans* (Maupas, 1900) (Zjacic & Scholz, 2022). Priming optimises resource use and affects longevity and reproduction, thus increasing fitness (Zjacic & Scholz, 2022).

Spiders are excellent at detecting and responding to chemical stimuli from conspecifics (Fischer, 2019). Chemoreception occurs in the feet (tarsi) of a spider (Foelix, 1970), though recent studies have suggested that their pedipalps also contain chemoreceptors (Müller et al., 2020; Sentenská et al., 2017). Most literature about spider chemoreception focuses on the use of chemical cues in mate location and courtship (Cerveira & Jackson, 2013; Gaskett, 2007). For example, male *Cyrba algerina* (Lucas et al., 1844) and *Cyrba ocellata* (Kroneberg, 1875) jumping spiders are able to discern the difference between the pheromones of conspecific males and females, as well as the pheromones of conspecific and heterospecific females (Cerveira & Jackson, 2013).

Spiders are renowned for their acute mechanosensory abilities allowing them to detect prey and predators, however some spiders are also able to exploit chemical cues when hunting and avoiding predators (Barth, 1998, 2004; Robledo-Ospina & Rao, 2022; Zurek et al., 2010). Some web building spiders exploit the chemical cues of their prey in order to lure them into their webs (Fischer, 2019). The bolas spider, *Mastophora cornigera* (Hentz, 1844) use a common component in moth courtship pheromones to attract a wide variety of moth species (Fischer, 2019; Stowe et al., 1987). Spiders from the *Zodarion* genus intercept the chemical cues of their social ant prey (Cárdenas et al., 2012). However, *Zodarion* spp. are very specialised hunters and are only able to discern the pheromones from a few species of ants within the same genus (Cárdenas et al., 2012). The wolf spider *Tigrosa helluo* (formerly *Hogna helluo*) (Walckenaer et al., 1841) can act as both prey and predator to the sympatric wolf spider *Pardosa milvina* (Hentz, 1844) depending on their relative size to one another (Persons & Rypstra, 2001). *Pardosa milvina* avoid substrates saturated in the chemical cues of *T. helluo* larger than themselves, demonstrating an ability to detect, recognise and respond to chemical cues appropriately (Persons & Rypstra, 2001).

The *Argyrodes* are a cosmopolitan genus of kleptoparasitic theridiid spiders that enter the webs of other spiders (Whitehouse et al., 2002). There is a diversity of foraging strategies within the *Argyrodes* genus. Some *Argyrodes* glean small prey items caught at the edges of the host web that would usually go unnoticed by the host spider (Whitehouse, 1986). Another strategy some *Argyrodes* employ is to feed with the host, exploiting the digestive enzymes generated by the host to break the prey down and consuming the nutrient rich juices (Whitehouse, 1986). *Rhinoliparus lanyuensis* (formerly *Argyrodes lanyuensis*) (Yoshida & Severinghaus, 1998) steal and consume the silk of the host's web rather than the prey caught within it (Tso & Severinghaus, 1998).

Despite the diversity of foraging strategies within the *Argyrodes*, we do not know how *Argyrodes* locate hosts and the factors they consider when selecting a host. Kleptoparasitism is an inherently risky foraging strategy, as the animal being stolen from is often capable of injuring, killing and/or predating the kleptoparasite itself (Iyengar, 2008; Rochette et al., 1995; Whitehouse, 1997b). For this reason kleptoparasites may choose hosts which pose less of a risk to them, or a kleptoparasite may only engage in theft when the reward is of particular value or the risk is reduced by other factors (i.e, the host being distracted by feeding or mating) (Fretwell & Lucas, 1969; Grostal & Walter, 1999; Hénaut et al., 2005; Rochette et al., 1995; Rößler et al., 2019; Whitehouse, 1997b). It is still uncertain how *Argyrodes* determine this risk. *Faiditus globosus* (previously *Argyrodes globosus*) (Keyserling et al., 1884) more commonly kleptoparasitise the webs of the larger, slower *Trichonephila clavipes* (formerly *Nephila* clavipes) (Linnaeus & Salvius, 1758) than of *Leucauge venusta* (Walckenaer et al., 1841) which are faster and more alert to disturbances in their webs (Hénaut et al., 2005). Some *Argyrodes* species move between host webs frequently (Whitehouse & Jackson, 1993). *Argyrodes* do show preferences for some host species over others, but we do not know what cues they use to distinguish or locate preferred hosts (Grostal & Walter, 1999; Hénaut et al., 2005; Miyashita, 2002). Chemical cues from the host spiders or from their webs are both plausible possibilities. Hénaut et al. (2005) noted that *Trichonephila clavipes* ignores many of the smaller insects caught in their webs, allowing *Faiditus globosus* to exploit the insects instead. *Argyrodes* may also use the chemical cues of prey captured in the web to find their hosts, although other studies have found that *Argyrodes* typically use web vibrations to navigate through host webs and locate caught prey. The possibility that *Argyrodes* spp*.* may also use olfaction to locate prey can't be discounted (Vollrath, 1979b). The presence of conspecifics may also attract *Argyrodes* to a host web, as *Argyrodes* are tolerant of conspecifics and can cohabit in a host web in large groups (Agnarsson, 2002; Vollrath, 1979b; Whitehouse et al., 2002; Whitehouse & Lubin, 2005).

Argyrodes antipodianus (Cambridge, 1880) is native to Australia and introduced to New Zealand (Grostal & Walter, 1997; Whitehouse, 1986). In its New Zealand range, *A. antipodianus* primarily kleptoparasitises the webs of *Socca pustulosa* (formerly *Eriophora pustulosa*) (Walckenaer et al., 1841), another native Australian spider, but *A. antipodianus* has also been observed in the webs of the native New Zealand sheet web spider, *Cambridgea foliata* (Cambridge, 1879) (McCambridge et al., 2019; Whitehouse, 1988). *Argyrodes antipodianus* both gleans insect prey and feeds with the host in the webs of *S. pustulosa* (Whitehouse, 1986). *Argyrodes antipodianus* occasionally live together in groups in the webs of their hosts and probably have a fusion-fission social structure akin to social vertebrates where individuals move between different hosts webs in an area (Aureli et al., 2008; Whitehouse & Jackson, 1993). We do not know how *Argyrodes antipodianus* locate host webs and if the host spider or conspecifics play a role in host location. In this chapter, I tested whether *A. antipodianus* can detect, recognise and are attracted to the chemical cues of potential hosts and conspecifics. I predicted that *A. antipodianus* would move towards the chemical cues of potential hosts (*S. pustulosa* and *C. foliata*) and conspecifics.

3.3 Methods

3.3.1 *Study species*

I collected spiders from the bush on Massey University Albany campus adjacent to the Fernhill Escarpment, and suburban gardens in Auckland, New Zealand. Spiders were collected between 9pm-11pm between December 2023 – March 2024. Males and females were used in the study and ranged in age from juvenile to adult. All spiders were maintained in the lab in a reverse light cycle room. Lights were maintained on a 12:12 hour light:dark cycle, with a one hour dimming cycle at 6am to simulate dusk, with lights completely off by 7am. Lights ramped up at 7pm to simulate dawn and were fully on by 8pm. The room was kept at a 19.5˚C ± 0.5˚C and 60% ± 11% humidity. All spiders were weighed the day after they were caught. Spiders were tested between three and seven days after being caught to give individuals time to acclimatise to the lab and light cycle, but also minimise the effects of long-term laboratory conditions on behaviour as has been observed in studies on other spider species (Trabalon, 2022). *Argyrodes antipodianus* were maintained in transparent, cylindrical, polypropylene, screwcap vials (28ml, 26mm X 57mm (D x H)). The host spiders were maintained in transparent, cylindrical, polypropylene, screwcap vials (30ml, 27 x 87mm (D x H)). Maintenance vials had holes or mesh in their lids for ventilation. I returned spiders to the field at the end of the experiments.

3.3.2 *Experimental arenas*

I used two glass Y-tube olfactometers (1cm diameter, Figure 3.1) to test the responses of *A. antipodianus* to airborne chemical stimuli from potential host spiders and conspecifics. Air was pumped through the olfactometers using two Aqua One 1500 air pumps via Teflon tubing (500mL/min). Air was filtered with activated charcoal. The filtered air passed into two chambers, one containing the odour stimulus and the other an empty control, and then into the arms of the olfactometer. Exits to the stimulus chambers were covered using gauze to prevent stimulus spiders escaping. A Y-shaped piece of clean paper was placed into the olfactometer as a substrate for the test spiders to walk on. All trials ran between 10am-6pm (the middle of the simulated night in the laboratory). Tests were recorded with an infrared camera (Canon XA 11) placed above the apparatus.

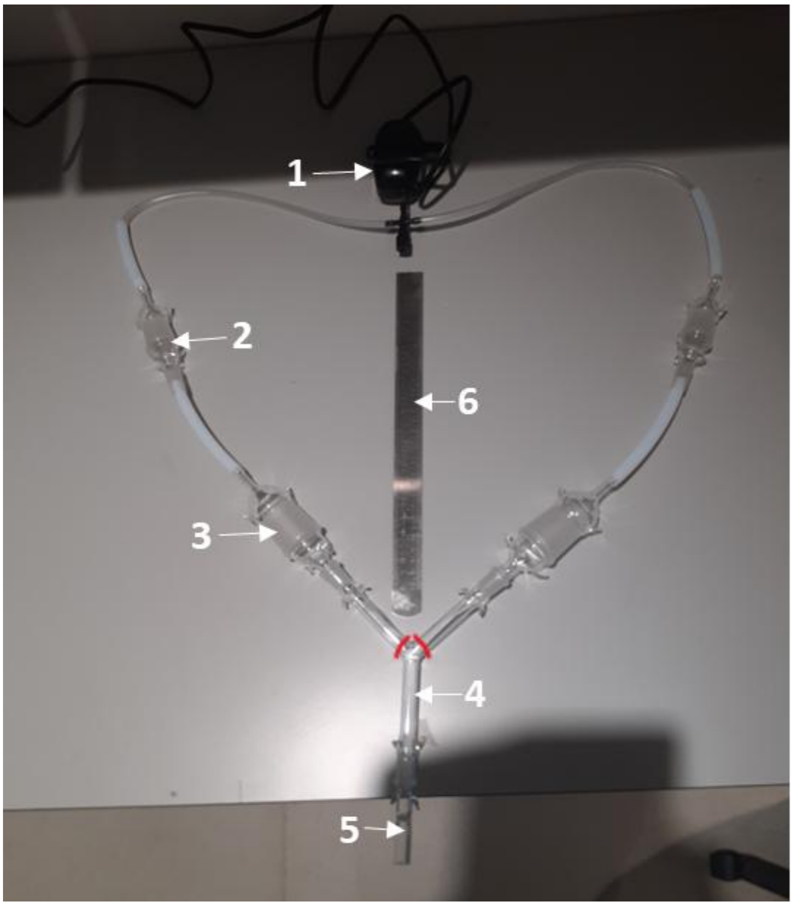

Figure 3.1: Y-tube olfactometer. (1) Aqua One 1500 air pump; (2) Activated charcoal chamber; (3) Left stimulus chamber; (4) Y- tube; (5) Glass stopper used to prevent *A. antipodianus* from exiting the arena; and (6) 30cm ruler for scale. If the test *A. antipodianus* crossed one of the red lines with their opisthosoma, it was considered to have made a choice for that side.

3.3.3 *Experimental procedure*

I tested the responses of *A. antipodianus* to the chemical cues of potential host spiders and conspecifics. I placed a randomly selected stimulus spider (one of either *A. antipodianus* (n = 20), *C. foliata* (n = 20) or *S. pustulosa* (n = 20),) into a randomly allocated left or right stimulus chamber of the olfactometer. A test spider (*A. antipodianus*) was then placed at the entrance of the olfactometer and given 90 minutes to make a choice. Adult male-female pairings of *A. antipodianus* were avoided due to the potential confounds of mate choice. A choice was defined by the opisthosoma of the test spider crossing into one of the olfactometers' arms leading to one of the stimulus chambers (Figure 3.1). Test spiders that did not move into one of the olfactometer arms after 90 minutes were considered to have made no choice.

I recorded the side of the olfactometer the stimulus spider was placed in, the stimulus choice (stimulus spider or control, if any) made by the test spider, and the side of the olfactometer (left or right, if any) the test spider chose. The olfactometer was washed in ethanol, rinsed with tap water, and dried with a hair dryer after each test. Where possible, test spiders were tested three times, once in each treatment (*A. antipodianus, C. foliata* and *S. pustulosa*, in random order) and given at least 30-minute rests between tests. However, due to constraints in capturing wild caught specimens and some deaths, not all the *A. antipodianus* were tested in all three treatments. Only eight *A. antipodianus* were tested in all three treatments (n = 8).

3.3.4 *Data analyses*

All data analyses were performed in R version 4.4.0 (R Core Team, 2024). To determine if *A. antipodianus* chose the olfactometer arm containing the chemical stimulus, I ran three chi-square tests (one for each treatment). I then tested whether *A. antipodianus* choices were biased toward one side of the olfactometer (left or right) using another three chi square tests (one for each treatment). I tested if the weight of *Argyrodes antipodianus* influenced their choices using multinomial regression (multinom function) in the *nnet* package

(Venables & Ripley, 2002). I used choice of stimulus treatment (i.e spider or no stimulus) as the dependent variable, weight as the fixed effect and individual ID as a random effect. This again was done individually for each treatment.

3.4 Results

In 47% trials, *A. antipodianus* made no choice. There was no significant preference in *A. antipodianus* for the stimulus (30%) or non-stimulus (23%) arms of the olfactometer in any of the treatments (*A. antipodianus*: $\chi^2 = 1.30$, df = 2.00, *P*-value = 0.52; *C. foliata*: $\chi^2 = 1.30$, df = 2.00, *P*-value = 0.52; *S. pustulosa*: $\chi^2 = 1.90$, df = 2.00, *P*-value = 0.39; Figure 3.2). *Argyrodes antipodianus* also showed no preference for the left or right olfactometer side (*A. antipodianus*: $\chi^2 = 2.27$, df = 1, *P*-value = 0.13; *C. foliata*: $\chi^2 = 3.60$, df = 1, *P*-value = 0.58; *S. pustulosa*: $\chi^2 = 0.09$, df = 1.00, *P*-value = 0.76; Figure 3.3). The weight of *A. antipodianus* did not affect their choice (all $P > 0.05$; Table 3.1).

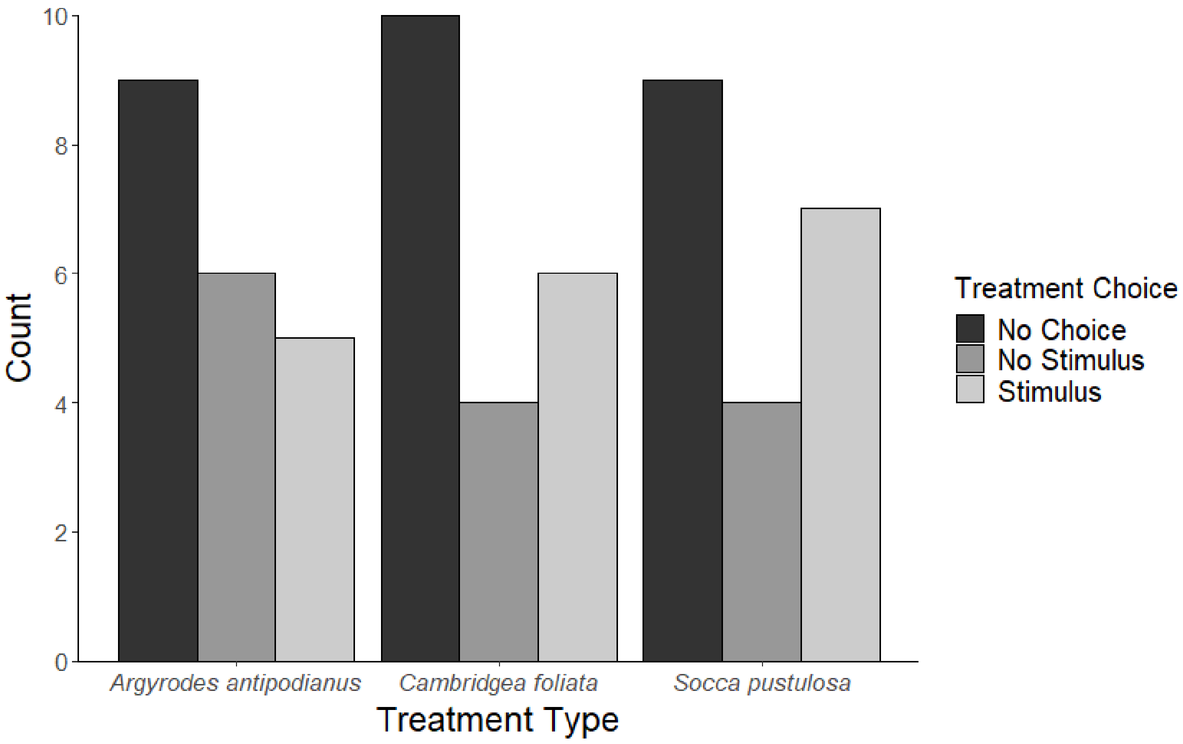

Figure 3.2: Stimulus choices made by *Argyrodes antipodianus*.

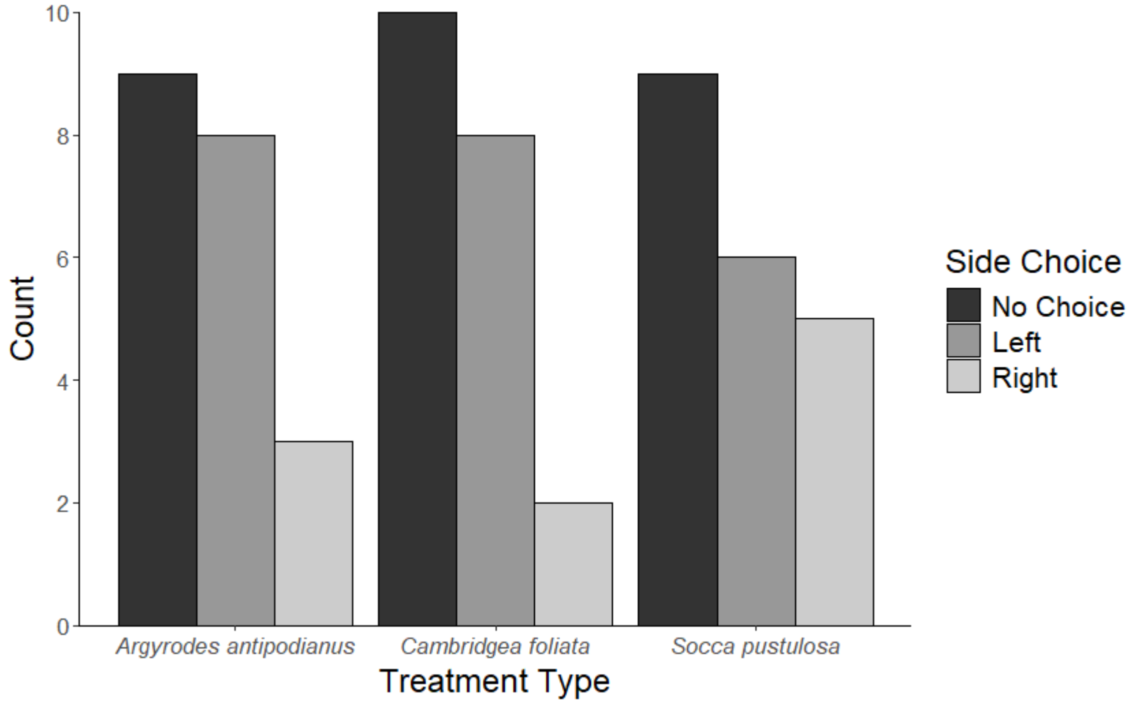

Figure 3.3: Olfactometer side choices made by *Argyrodes antipodianus*.

Table 3.1: Multinomial regression testing the effect of weight on *A. antipodianus* choices.

	Coefficients	Std Error	Z_value	*P*-value#
A. antipodianus treatment*				
No stimulus Intercept	-0.45	0.78	-0.57	0.57
No stimulus & weight	-1.05	0.90	-1.16	0.25
Argyrodes stimulus intercept	-5.06	151.11	-0.03	0.97
Argyrodes stimulus & weight	79.51	152.90	0.52	0.60
C. foliata treatment*				
No stimulus intercept	-0.58	0.89	-0.70	0.49
No stimulus & weight	-0.21	0.77	-0.27	0.79
Cambridgea stimulus intercept	-69.78	204.88	-0.34	0.73
Cambridgea stimulus & weight	-129.57	210.02	-0.62	0.54
S. pustulosa treatment*				
No stimulus intercept	-0.58	0.83	-0.70	0.49
No stimulus & weight	-0.21	0.77	-0.27	0.79
Socca stimulus intercept	-69.78	204.88	-0.34	0.73
Socca stimulus & weight	-129.57	210.02	-0.62	0.54

* No choice is the reference choice in each test.

\# *P* < 0.05 are indicated in bold

3.5 Discussion

My results indicate that *A. antipodianus* is not attracted to chemical cues released by potential host or conspecific spiders. Almost fifty percent of *A. antipodinaus* did not make a choice within the olfactometer. Of those spiders that did make a choice, there was no evidence of attraction to the chemical cues of potential hosts or conspecifics. There are three potential explanations for this. Firstly, *A. antipodianus* may not have the anatomical structures to detect and process chemical cues. This however is extremely unlikely as other spiders, including others within the Theridiidae, use chemical cues in their courtship (A. Fischer, 2019; Scott, Anderson, et al., 2018; Scott, Gerak, et al., 2018). Compounds assumed to be related to chemical communication have been found in *A. elevatus* (Taczanowski, 1873) and in *A. antipodianus* themselves (Chinta et al., 2016; Whitehouse, 1987). Male *A. antipodianus* show a behavioural response, shuddering, when they encounter the web silk of females indicating that they can detect chemical cues (Whitehouse, 1991, 1997a; Whitehouse & Jackson, 1994b). It would therefore seem likely that *A. antipodianus* is capable of olfaction. Alternatively, *A. antipodianus* may detect the chemical cues from host and conspecific spiders but do not recognise them and therefore don’t act on the information. Thirdly, *A. antipodianus* may detect and recognise the chemical cues, but choose not to respond to the information.

It seems unlikely that *A. antipodianus* would not recognise chemical cues released by conspecifics. Chemoreception plays an important role in spider courtship and other intraspecific interactions in many species, including in *Argyrodes antipodianus* (Cerveira & Jackson, 2013; A. Fischer, 2019; Gaskett, 2007; Scott, Gerak, et al., 2018; Stafstrom & Hebets, 2019; Whitehouse, 1991, 1997a; Whitehouse & Jackson, 1994b). While I cannot claim with certainty that *A. antipodianus* can recognise the chemical cues of potential hosts, many spiders use chemical cues when hunting prey and avoiding predation (Hostettler & Nentwig, 2006; Patt & Pfannenstiel, 2008; Persons & Rypstra, 2001). It therefore seems logical that for a spider whose ecology is closely tied to that of their host spiders that it too would be able to recognise their chemical cues

The possibility that *A. antipodianus* chose not to respond to the chemical cues in my experiment seems most plausible. However, this poses new questions such as why wouldn't *A. antipodianus* respond to the chemical cues produced by a potential host. One possible explanation is that *A. antipodianus* weren't stimulated enough to seek out the hosts. It's possible that the novel conditions of the olfactometer, stopped the *A. antipodianus* engaging in their usual host searching behaviours.

If *A. antipodianus* do not respond, do not recognise or do not detect the chemical cues from potential host spiders then my hypothesis that *A. antipodianus* use airborne chemical cues produced by host spiders to locate host webs is incorrect. Future experiments may test if *A. antipodianus* are attracted to chemical cues from host silk rather than the hosts themselves as silk is important in *A. antipodianus* mating events (Whitehouse & Jackson, 1994b). Chemical cues on silk are often an important mediator of reproductive behaviour in spiders and may be intercepted by *A. antipodianus* (Scott, Anderson, et al., 2018; Stafstrom & Hebets, 2019). Alternatively, *A. antipodianus* may use chemical cues from prey. I had earlier deemed it unlikely that *A. antipodianus* use chemical cues from prey caught in the host web to locate host webs. In my natural history survey (Chapter Two), only 28% of the webs that had *A. antipodianus* in them also had prey items caught in the web.

However, some species, such as the social spider *Mallos gregalis* (Simon, 1909)*,* adorn their webs with the carcasses of dead prey to attract new prey (Tietjen et al., 1987). For this reason, we can’t rule out that *A. antipodianus* use chemical cues from prey to locate hosts and as such this should also be investigated.

A. antipodianus move between host webs so there must be a cue they use to navigate between webs (Miyashita, 2001; Whitehouse & Jackson, 1993). I hypothesised that conspecifics played a role in locating and/or selecting a host. *Argyrodes antipodianus* may be attracted to host webs that already have conspecifics present, either as a form of conspecific cueing (as those hosts may be seen as higher quality and therefore worth kleptoparasitising), or because of a potential benefit from being together in a web (Donahue, 2006; Freeberg et al., 2024). Alternatively, *A. antipodianus* could be repelled by the presence of conspecific cues to avoid intraspecific competition, as in other arthropods (Byers, 1989; Castelo et al., 2003; Franks et al., 2007). My results indicate that *A. antipodianus* do not respond to conspecific chemical cues. Chemical cues are an important part of spider intraspecific interactions, often facilitating reproductive behaviour (Fischer, 2019). This suggests that *A. antipodianus* should be able to detect, recognise and respond to conspecific chemical cues. Molecular compounds in the exoskeleton of *Argyrodes antipodianus* may serve as sexual pheromones, though this hasn’t been tested yet (Chinta et al., 2016). Regardless, *A. antipodianus* not responding to airborne conspecific chemical cues in my experiment is evidence against my hypothesis that conspecific cues are used to find a host. Chemical communication may play a role in the intraspecific interactions of *A. antipodianus*, just not in the context of host location. Conspecific silk may play a role in host location, but this still requires further testing. Alternatively, *A. antipodianus* may respond to conspecific chemical cues when they are accompanied with host chemical cues. Further research is needed to determine if *A. antipodianus* is attracted to the combination of host and conspecific cues together and what cues these may be (Campos et al., 2017).

If *A. antipodianus* do not actively seek conspecifics, it suggests that *A. antipodianus* do not gain direct benefits from forming groups. Other well-known kleptoparasites, such as spotted hyenas (*Crocuta crocuta*) (Erxleben, 1777) form groups and work together to steal prey from hosts (Lehmann et al., 2017). It seems that *A. antipodianus* are unlike other social spiders, which work together to reduce the individual cost of capturing and processing prey (i.e., web silk and digestive enzymes)(Lubin & Bilde, 2007). This difference in behaviour is most likely because *A. antipodianus* already exploits its host for food resources and therefore doesn’t have to rely on conspecifics for foraging (Whitehouse & Lubin, 2005).

Argyrodes antipodianus may be ill-suited to the olfactometer, resulting in few individuals making choices in my experiments. Despite placing paper within the tube of the olfactometer for the test spiders to walk on, I observed many individuals attempted to walk upside down on the glass roof of the tube instead. Other methods such as placing a potential cue (either a live spider or silk) on blotting paper, allowing the chemical cue to be absorbed by the paper and having the *A. antipodianus* chose between the scented paper and an untouched control is a potential alternative.

In conclusion, my experiment has laid the groundwork for future studies testing how *A. antipodianus* locate their hosts and interact with conspecifics. My results suggest that *A. antipodianus* are unlikely to locate potential hosts using chemical cues from their hosts. I suggest future work confirm this by adjusting the experimental design. I also suggest two new avenues of research investigating the role of host silk and prey presence on host location by *A. antipodianus*.

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Chapter 4

How kleptoparasitism by *Argyrodes antipodianus* influences the fitness of host and conspecific spiders.

4.1 Abstract

The density of a population of animals can impact the effectiveness of foraging strategies. For this reason, animals may choose to forage alone or in groups depending on the foraging strategy they are using. Kleptoparasites are animals that steal resources, such as food or nesting materials, from another organism. Kleptoparasites reduce their hosts fitness, therefore a larger kleptoparasitic load would result in a larger reduction in host fitness and is therefore avoided by the host. However, there are few direct tests of the effects of kleptoparasite density on host fitness. I tested the effects of a kleptoparasitic spider, *Argyrodes antipodianus*, on their host, the sheet web spider *Cambridgea foliata*, using weight change as a proxy for fitness. I compared the effects of zero, one and two kleptoparasites on host and kleptoparasite fitness, as well as the fitness of kleptoparasites without a host. I found that the weight of host spiders was unaffected by the presence of kleptoparasites. However, all *A. antipodianus* lost weight over the experimental period regardless of whether they were alone, in a host web or in a host web with a conspecific. My results bring into question the nature of the relationship between *Argyrodes antipodianus* and *Cambridgea foliata.* Despite *Argyrodes* primarily being considered as a kleptoparasitic of their hosts, my research suggests they may have a kleptobiotic or commensal relationship with some host species.

4.2 Introduction

Animals have evolved diverse strategies to find and exploit the limited resources within their environment (Winterhalder, 1983). Questions such as when to forage, where to forage, what food types to exploit and what risks are worth taking in order to acquire food are fundamental challenges for individuals (Mobbs et al., 2018; Winterhalder, 1983). Optimal foraging theory states that animals only invest in acquiring a resource when the energy gained compensates for the energy spent in acquiring it (MacArthur & Pianka, 1966). Optimal foraging theory is closely linked with the marginal value theorem which claims that resources are distributed non-uniformly in patches (Charnov, 1976). As resources in a patch are used, the returns on energy intake diminish over time (Charnov, 1976). However, moving between patches also incurs costs in energy and time (Charnov, 1976). As such, animals that successfully find food (e.g., a predator catching prey), are more likely to remain in the same location to search for more food (Charnov, 1976). Similarly, some animals such as harbour seals (*Phoca vitulina*) (Linnaeus & Salvius, 1758) remember and return to locations where they have previously caught prey (Iorio-Merlo et al., 2022). In addition to returning to profitable patches, animals can also increase their foraging success through other means.

Hunting and living within social groups is a common strategy for maximizing foraging success (Ward & Webster, 2016). Social predators can take on different roles within the hunt, allowing predators to set up ambushes and gain access to prey much larger than what they would be able to hunt alone (Ward & Webster, 2016). However, there are intrinsic costs associated with living in groups, such as increased intraspecific competition (Donahue, 2006). For group-living organisms, the fitness benefits of being in a group must outweigh the costs of intraspecific competition (Donahue, 2006). There are two categories of benefits an organism may gain from grouping with conspecifics: cooperation and conspecific cueing (Donahue, 2006).

Cooperation is when individual’s form groups to work towards specific goals. Some groups can form permanent associations such as eusocial insects whereas other groups can be temporary and ever shifting such as fission-fusion groups in social vertebrates (Andersson, 1984; Aureli et al., 2008; Dugatkin, 2002). Benefits of forming groups can include predator avoidance, better hunting outcomes, and shared responsibilities in offspring rearing (Donahue, 2006). However, when group size becomes too large these benefits may be outweighed by intraspecific competition due to insufficient resources to support the group. Conspecific cueing occurs when individuals use the presence of conspecifics to determine the quality or safety of a habitat, resulting in aggregations that are a byproduct of favourable conditions (Buxton et al., 2020; Freeberg et al., 2024). The high quality habitat compensates for the costs of intraspecific competition (Buxton et al., 2020). Conspecific cueing is a common strategy in migratory and seasonally reproducing species allowing them to find or return to breeding sites (Andrews et al., 2015; Buxton et al., 2020). Animals can also form interspecific associations.

Commensalism is a type of interspecific relationship in which one member of the relationship gains a fitness benefit while the other remains unaffected (Leung & Poulin, 2008). One such relationship is Kleptobiosis (Iyengar, 2008). In this relationship the kleptobiont takes a resource from a host, that the host wasn’t going to use. For example, a scavenger feeding from a carcass that a predator had already discarded (Leung & Poulin, 2008). The kleptobiont gets to benefit from the predators kill but the predator is unaffected neither positively nor negatively. However, if a kleptobiont steals a resource the host still intended to use, for example a scavenger stealing the carcass before the predator had fed from it, the relationship became kleptoparasitism (Iyengar, 2008).

Kleptoparasitism occurs when one individual (the kleptoparasite) steals a resource from another individual (the host) (Iyengar, 2008). In most kleptoparasitic interactions the resource is food, but it can also be nesting materials or sites (Faust et al., 2012; Focardi et al., 2017; Iyengar, 2008; Matsui et al., 2010; Ridley & Raihani, 2007; Tso & Severinghaus, 1998; Whitehouse, 1986). A key characteristic of kleptoparasitic relationships is that the host incurs a fitness cost from the kleptoparasite stealing the resource (Focardi et al., 2017; Iyengar, 2008). An organism that steals a resource but does not impose a fitness cost on the host is a kleptobiont (Iyengar, 2008). Kleptoparasitism is advantageous for the kleptoparasite as it allows the kleptoparasite to benefit from the effort another individual used to acquire the food item, thus reducing the cost of foraging for the kleptoparasite and access food they otherwise wouldn’t have (Focardi et al., 2017; Rochette et al., 1995). However, kleptoparasitism is not without risks, as some hosts will defend their resources by attacking, killing and in some cases even consuming the kleptoparasite (Rochette et al., 1995; Whitehouse, 1997b). Some kleptoparasitic animals work in groups in order to overwhelm host defenses when stealing resources (Hamilton & Dill, 2003). Kleptoparasitic relationships are often characterized by the presence of a period of handling time between the host acquiring the resource and using it, particularly in kleptoparasitic relationships where food is being taken (Iyengar, 2008). If the host consumes the food item immediately, there is no time for the kleptoparasite to steal it (Iyengar, 2008). For this reason, spiders are common hosts for kleptoparasites as web-building spiders often store food in their webs (Drisya-Mohan et al., 2019; Thornhill, 1975; Whitehouse et al., 2002).

Web-building spiders spin a web of silk to ensnare prey insects. Webs can also function as defensive structures, as vibrations generated by predators in the web can indicate to the resident spider that they are under attack and give them warning to retreat, as well as impede the predator's ability to catch them (Herberstein, 2011). Web building is not without cost, if their web is destroyed due to harsh weather conditions or the activity of large animals, they will receive no return on their investment of energy (Foster et al., 2015). In environments or time periods of prey scarcity, active hunting spiders are more abundant than web building spiders as passive prey capture isn't as reliable as active predatory strategies (Ross & Winterhalder, 2015). Webs can also be exploited by other animals, including kleptoparasites. Kleptoparasitic individuals may lay in wait near, or sometimes on, a web in order to steal from the host spider (Drisya-Mohan et al., 2019; Thornhill, 1975; Whitehouse et al., 2002).

The *Argyrodes* are a genus of theridiid spiders which kleptoparasitise other spiders by entering their webs and consuming their prey (Whitehouse et al., 2002). *Argyrodes* are found in the Americas, Australasia and Asia (Dash & Sivaperuman, 2023; Grostal & Walter, 1997, 1999; Hénaut et al., 2005; Miyashita, 2001; Smith Trail, 1980; Tanaka, 1984; Whitehouse et al., 2002). In most regions, *Argyrodes* kleptoparasitise orb weavers (Whitehouse et al., 2002) and they engage in multiple foraging strategies including stealing and eating the silk of their host's webs (Tso & Severinghaus, 1998), gleaning smaller insects from the host web that are too small for the host to eat (Hénaut et al., 2005), and entering the web while the host is distracted handling prey and feeding simultaneously with the host (Whitehouse, 1986). *Argyrodes* also prey on their hosts when they're moulting, and on the spiderlings of their host (Whitehouse, 1986).

Argyrodes antipodianus (Cambridge, 1880), previously *A. antipodiana*, is native to Australia and introduced to New Zealand. In its New Zealand range, *A. antipodianus* typically kleptoparasitises the orb weaver *Socca pustulosa* (Walckenaer et al., 1841) but has been observed kleptoparasitising the webs of the sheet web spider *Cambridgea foliata* (Cambridge, 1879) (McCambridge et al., 2019; Whitehouse, 1986). *Argyrodes antipodianus* employs two strategies when kleptoparasitising its hosts: gleaning small insects from the edge of the web, or feeding with the host as it starts to process a prey item (Whitehouse, 1986). Aggregations of *A. antipodianus* are often found together within host webs, although it is unclear whether these aggregations have a purpose (Whitehouse, 1991; Whitehouse & Lubin, 2005).

I tested whether the presence of *Argyrodes antipodianus* influences the fitness of its native sheet web spider host, *Cambridgea foliata,* and whether these effects, if any, scale with the number of *A. antipodianus* present in the web. I also tested whether the fitness of *A. antipodianus* is influenced by access to a host, or the number of conspecifics kleptoparasites present in the host web. My results will contribute to an understanding of the factors driving *A. antipodianus* to aggregate in host webs and the eco-evolutionary dynamics of kleptoparasitism.

4.3 Methods

4.3.1 S*pecimens*

In preliminary trials, *S. pustulosa*, an introduced orb weaver, did not reliably construct complete orb webs in the laboratory. The alternate host, *C. foliata* is a native spider abundant in Auckland, New Zealand and readily constructed sheet webs in the laboratory. Therefore, I chose *C. foliata* as host spiders for this experiment. *Cambridgea foliata* (n = 60) and *A*. *antipodianus* (n = 80) were collected from the bush at Massey University, Albany campus adjacent to the Fernhill Escarpment, and from gardens on the North Shore and West suburbs of Auckland, New Zealand. During field collections of *A. antipodianus* I recorded the host species, and the number of other *A. antipodianus* in the host web. During field collections of *C. foliata* I recorded the number of *A. antipodianus* in the web. Male, female and juvenile *A. antipodianus* were included in the study. Male and female *C. foliata* were also included in the study.

Spiders were collected using transparent, cylindrical, polypropylene vials (30ml, 27 × 87mm (D × H) for *C. foliata*; and 28ml, 26mm × 57mm (D × H) for *A. antipodianus*). *Cambridgea foliata* were maintained in the lab in experimental arenas consisting of transparent, square, plastic containers (180mm × 180mm × 130mm) to allow spiders to construct webs (see Experimental Procedure). Small holes were poked into the lids of the arenas to allow air flow. Two strips of scotch tape were applied horizontally to the opposing walls of each arena to help the spiders attach their webs to the walls. *Argyrodes antipodianus* were kept in their vials for three days after being collected and weighed, then moved into the experimental arenas at the start of the experimental trials. All specimens were kept in a reverse light cycle room (12 hr : 12 hr night, day cycle) so they would be active when I fed them. Lights started to dim at 6am to simulate dusk and were completely off by 7am. Lights started to ramp on at 7pm to simulate dawn and were fully on by 8pm. The room was maintained at 19.5°C ± 0.5°C with 60% ± 11% relative humidity. Spiders were fed twice a week on mealworms (*Tenebrio molitor*) (Linnaeus & Salvius, 1758) and vinegar flies (*Drosophila melanogaster*) (Meigen, 1818). Food remaining from the previous feed was removed to ensure the spiders had access to fresh food and a clean experimental container. Water was provided using a spray bottle. After the experiments were completed, all spiders were released into the bush on Massey University, Albany campus.

4.3.2 *Experimental Procedure*

Each spider was weighed immediately after collection using an Ohaus Explorer Semi-Micro EX125D balance (0.01mg). *Arygrodes antipodianus* were photographed using a Motic SMZ 168 microscope and Canon EOS 700D camera. *Cambridgea foliata* were photographed using a Canon XA11 camera. Spiders were measured using the image processing program imageJ version 1.54i (Schneider et al., 2012). Each host spider was then placed into an experimental container. Host spiders were given three days to acclimatise and construct a web. *Argyrodes antipodianus* were maintained in plastic vials for these three days to acclimatise to the lab. After the three-day acclimatisation period, the hosts and *A. antipodianus* were randomly assigned to four groups: *Argyrodes* control, *Cambridgea* control, one kleptoparasite and two kleptoparasites. In the *Argyrodes* control group (n = 20), one *A. antipodianus* was placed inside an experimental container. In the *Cambridgea* control group (n = 20), one *C. foliata* was placed inside an experimental container. In the one kleptoparasite treatment (n = 20), one *C. foliata* and one *A. antipodianus* were placed in an experimental container. In the two kleptoparasites treatment (n = 20), one *C. foliata* and two *A. antipodianus* were placed in an experimental container. I weighed each spider every seven days for the duration of the experiment. I made note of any spiders that died and the condition of prey (i.e, live, dead, or consumed) on weighing days. I also recorded the presence of egg sacs or evidence of a moult (i.e, exoskeletons in the container). The experimental period lasted four weeks, after which I weighed spiders for the final time before releasing them.

4.3.3 *Data analyses*

All analyses were performed in R version 4.4.0 (R Core Team, 2024). I calculated the residuals from a linear regression between size and weight for each species separately (*C. foliata*: t = 8.41, df = 41, *P*-value = <0.001; *A. antipodianus*: t = 3.27, df = 50, *P*-value = <0.01). The residuals provide an estimate of recent feeding history, and are currently used as a measure of body condition, although I also note previous discussions debating whether residuals are a reliable measure of body condition and interpret them with caution (Jakob et al., 1996; Wilder et al., 2016; Wolters, 2019). I tested whether the number of kleptoparasites (*A. antipodianus*) in host webs in the field influenced the condition of spiders (both *A. antipodianus* and *C. foliata*) using linear models. The residuals were used as the dependent variable, the number of kleptoparasites in the host web as the fixed effect.

I calculated the percentage change in weight over the four-week experimental duration for each spider. Containers (n = 30) which had one or more spider deaths were removed from this analysis as deaths changed the proportion of hosts to kleptoparasites. I tested if there was a difference between treatments in percentage weight change over the duration of the experiment using a linear mixed effects model (LMM) in the lme4 package (Bates et al. 2015). A linear mixed effects model was used rather than a GLMM as weight change was calculated as a percentage that went beyond the 0-100 range, and so behaved more like a continuous variable. Treatment, species and the interaction between treatment and species were included as fixed effects, and container ID was included as a random effect.

I also tested whether treatment influenced the number of deaths. I constructed a GLMM with a binomial distribution in the lme4 package, using the ratio of spiders: number of deaths per container as the dependent variable. I included treatment as a fixed effect, and container ID as the random effect.

4.4 Results

In the field, the number of kleptoparasites in the host web did not correlate with the body condition of *C. foliata* or *A. antipodianus* (*C. foliata,* t = 0.11, *P*-value = 0.91; *A. antipodianus,* t = 1.03, *P*-value = 0.31; Table 4.1; Figure 4.1). In the laboratory, the number of kleptoparasites in the web had no effect on percentage weight change of either the host spider, or the other kleptoparasites (Table 4.2; Figure 4.2). However, percentage weight change differed by species (t = 2.57, *P*-value = 0.02; Table 4.2; Figure 4.2). *Cambridgea foliata* gained weight over the duration of the experiment, regardless of treatment, whereas *A. antipodianus* lost weight, regardless of treatment. There was no interaction between treatment and species in percentage weight change (t = 1.67, *P*-value = 0.11; Table 4.2; Figure 4.2).

Table 4.1. LMMs testing if number of kleptoparasites (*A. antipodianus*) influenced the condition of other spiders in the web (host: *C. foliata* and kleptoparasites: *A. antipodianus*)

Coefficients	Estimate	Std. Error	t value	*P*-value
Argyrodes antipodianus				
(Intercept)	4.12	0.38	10.83	**<0.001**
No. *A. antipodianus* in web	3.05	2.97	1.03	0.31
Cambridgea foliata				
(Intercept)	1.23	0.30	4.15	**<0.001**
No. *A. antipodianus* in web	0.02	0.13	0.11	0.91

P < 0.05 indicated in bold

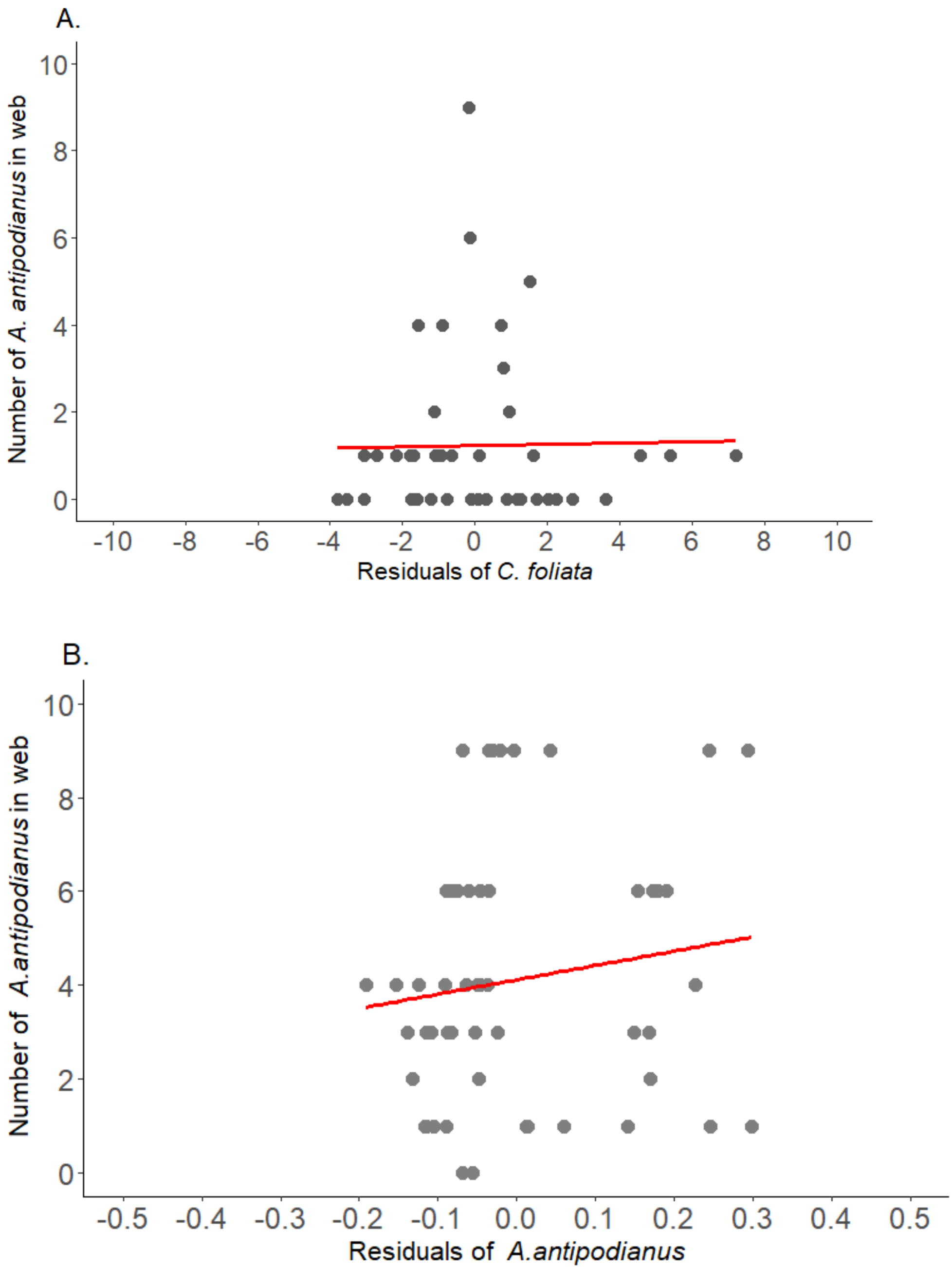

Figure 4.1: A. Plot of *C. foliata* body condition (residuals) against how many kleptoparasites (*A. antipodianus*) were found in the web when they were collected. **B.** Plot of *A. antipodianus* body condition (residuals) against how many kleptoparasites were found in their host web. Red lines represent the linear regression lines.

Table 4.2. LMM testing whether percentage weight change over the duration of the experiment was influenced by treatment, species or the interaction between treatment and species*.

	Estimate	Std. Error	df	t value	*P*-value	Variance	Std.dev
Random effect (Container_ID)	-	-	-	-	-	541.20	23.26
Residual	-	-	-	-	-	1707.40	41.32
(Intercept)	-53.04	13.14	62.17	-3.88	**<0.001**	**-**	**-**
Cambridgea control	53.94	26.96	37.58	2.00	**0.05**	-	-
Treatment 1 kleptoparasite	14.50	19.36	62.17	0.75	0.46	-	-
Treatment 2 Kleptoparasite	13.94	20.49	33.94	0.68	0.50	-	-
Species (*Cambridgea*)	53.09	20.66	16.79	2.57	**0.02**	-	-
Treatment (*Argyrodes* control: *Argyrodes antipodianus*)	44.44	26.67	16.79	1.67	0.11	-	-

P < 0.05 indicated in bold

*Reference categories: *Argyrodes* control (treatment), *Argyrodes antipodianus* (species) and *Argyrodes* control: *Argyrodes antipodianus* (treatment:species interaction)

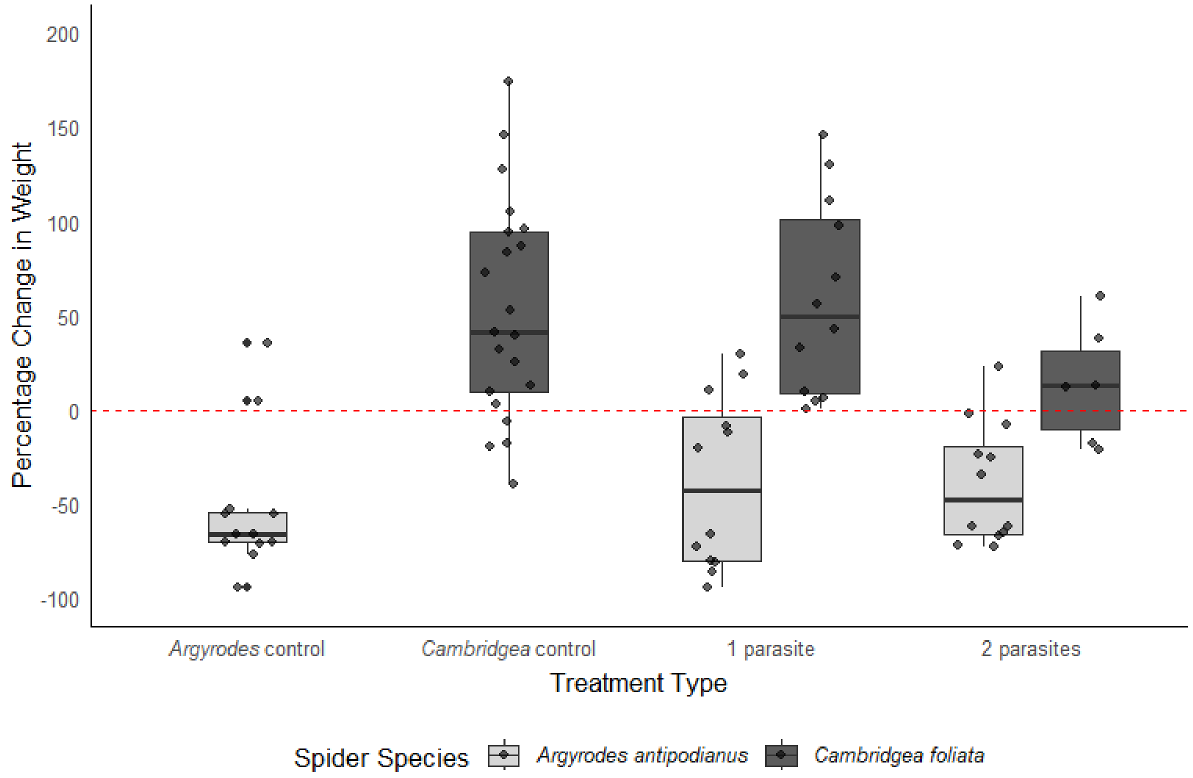

Figure 4.2: Percentage weight change of *C. foliata* and *A. antipodianus* over the experimental duration.

Thirty-five *A. antipodianus* and two *C. foliata* died during the experiment. In total, 30 trials had to be excluded from the experiment. For example, if one kleptoparasite died in the two kleptoparasite treatment, the host would then have only one kleptoparasite for the remainder of the experiment. I found that there was no difference between treatments in the number of deaths that occurred (Table 4.3; Figure 4.3).

Table 4.3. GLM comparing the number of deaths across the four treatments*.

	Estimate	Std. Error	Z value	*P*-value
(Intercept)	-0.41	0.46	-0.89	0.37
Treatment *Cambridgea* control	-18.16	1458.51	-0.01	0.99
Treatment 1 kleptoparasite	-1.15	0.62	-1.85	0.06
Treatment 2 kleptoparasite	-0.21	0.53	-0.40	0.69

P < 0.05 indicated in bold

*Reference category: *Argyrodes* control

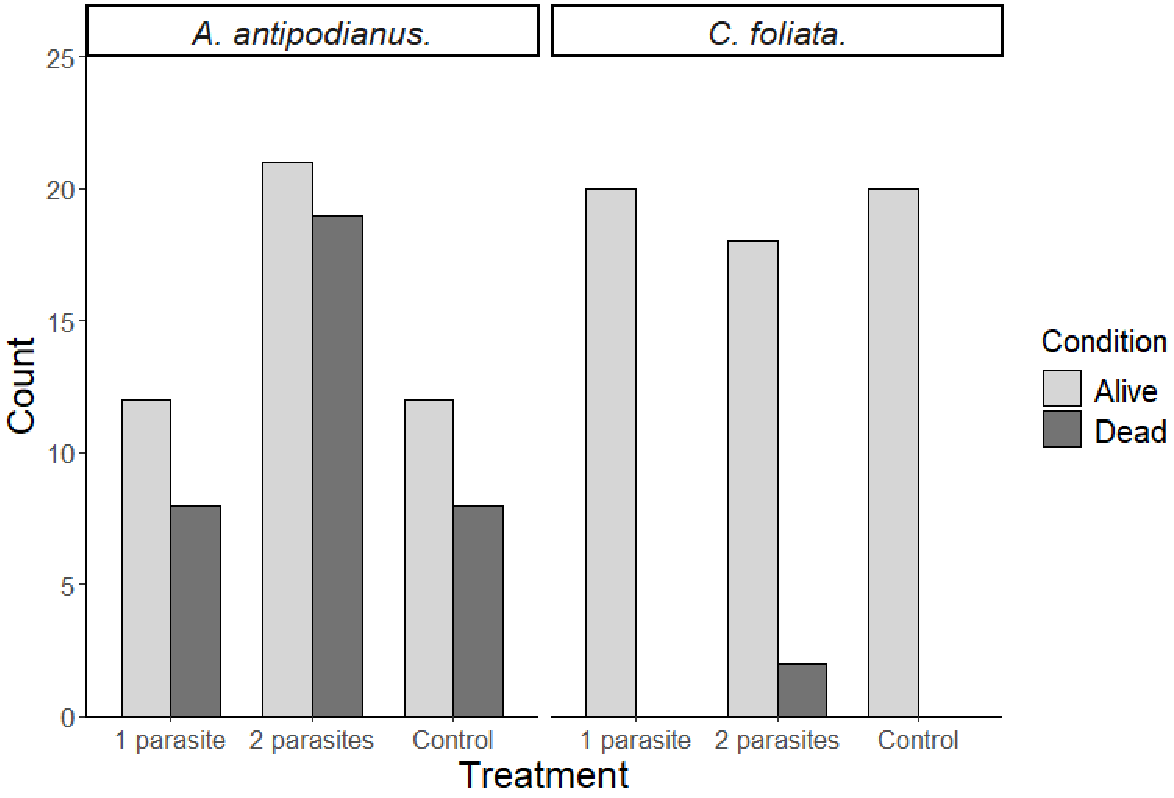

Figure 4.3: Counts of how many individuals of each species in each treatment died during the experimental period.

4.5 Discussion

I did not find a relationship between the number of *A. antipodianus* living in the web of a *Cambridgea foliata* and the weight of either kleptoparasite or host spiders. There was no relationship in the field between the body conditions of hosts and the number of kleptoparasites present in the web, or in my experimental lab study. Other studies have found that the presence of four *A. antipodianus* reduced the weight of *Trichonephila plumipes* (previously *Nephila plumipes*) (Latreille et al., 1804), an orb-weaving host (Grostal & Walter, 1997). However, my results showed that body condition of *C. foliata* in the field did not correlate with the number of *A. antipodianus* found in their webs (as measured by the residuals of a regression between weight and size which can represent recent feeding history and are often an indicator of body quality) (Jakob et al., 1996; Wilder et al., 2016; Wolters, 2019). This suggests that *A. antipodianus* do not select host *C. foliata* based on recent feeding history, otherwise we would expect a relationship between *C. foliata* body condition and the number of kleptoparasites in their web.

My field observations found no relationship between the body condition of the kleptoparasites and how many kleptoparasites were found in the webs of *C. foliata*. This firstly suggests that *A. antipodianus* is not very competitive in the webs of their sheet web hosts. If *A. antipodianus* aggressively competed for hosts, we would expect an inverse relationship between the body condition of *A. antipodianus* and the number of kleptoparasites with larger individuals more likely to win competitions and therefore to be sole occupants of a host web, and smaller individuals being forced to share hosts (Whitehouse, 1997a). Intraspecific aggression seems to be rare among *A. antipodianus*, mostly occurring during mating events and even then, only rarely (Whitehouse, 1991).

Interestingly, *A. miniaceus* (Doleschall, 1857) have better foraging outcomes when they feed alone rather than with conspecifics present (Yu et al., 2022). If a similar pattern was happening here, we would expect *A. antipodianus* by themselves to have a better body condition than those in larger groups, however this was not the case. Secondly, the lack of a relationship between body condition and number of kleptoparasites suggests that *A. antipodianus* don't work together to kleptoparasitise hosts because we would expect that a higher number of individuals in a web would result in kleptoparasites with better body conditions.

Argyrodes antipodianus lost weight regardless of treatment in my experiment. The universal weight loss of *A. antipodianus* as well a substantial number of deaths during the experiment suggest that *A. antipodianus* was unable to kleptoparasitise *C. foliata* effectively in the lab. In the field, I often observed *A. antipodianus* in the support and knockdown threads of *C. foliata* webs which are used to knock flying insects down into the sheet below where the host spider catches and consumes them (McCambridge et al., 2019). In the lab, I had to take the lid off the experimental arenas whenever I fed or weighed the spiders. If *C. foliata* attached their knockdown threads to the lids of their arenas they would have been regularly broken during feeding and weighing. The regular destruction of the *C. foliata* support threads may explain why *A. antipodianus* were unable to effectively kleptoparasitise the *C. foliata* in the lab.

In my study I used mealworms as a feeding insect for the *C. foliata*. *C. foliata* webs are designed to catch flying prey. Ground dwelling beetle larvae, such as mealworms, are unlikely to be commonly caught by *C. foliata* naturally (McCambridge et al., 2019). The kleptoparasitic behaviours of *A. antipodianus* may not have been able to adapt to this new prey type (Whitehouse, 2016).

A common strategy employed by *A. antipodianus* when kleptoparasitising the orb weaver *S. pustulosa* is to build a scaffold web close to or attached to the host web and move between the two webs (Whitehouse, 1988). Further, *S. pustulosa* use non-cribellate, sticky silk, a type of silk with glue-like droplets to trap prey (Whitehouse, 1988). However, *A. antipodianus* struggle to walk on cribellate silk, a type of silk that employs small silk fibrils in order to ensnare prey, which *C. foliata* uses (Forster, 1967; McCambridge et al., 2019; Whitehouse, 1988). This also could have influenced their ability to kleptoparasitise *C. foliata* in my laboratory experiment.

Alternatively, my results could indicate that *A. antipodianus* do not kleptoparasitise *C. foliata* at all. *Argyrodes antipodianus* commonly kleptoparasitise *S. pustulosa* in the field (Whitehouse, 1986). Based on previous studies on *A. antipodianus* behaviour, we can presume that *A. antipodianus* are entering the webs of *S. pustulosa* primarily to feed (Whitehouse, 1986). The difference in shape and silk type of the *C. foliata's* sheet web and the *S. pustulosa's* orb web may mean that *A. antipodianus* can only effectively kleptoparasitise *S. pustulosa's* webs. If this were true, then it would indicate that *A. antipodianus* are entering the webs of *C. foliata* for reasons other than foraging.

One potential reason for *A. antipodianus* to enter the webs of *C. foliata* is for protection. *C. foliata* webs are often larger, denser and constructed along three planes compared to the two-dimensional webs of *S. pustulosa* (Graf & Nentwig, 2001; McCambridge et al., 2019). The tightly packed threads of *C. foliata* webs may allow *A.*

antipodianus to detect predators early, impede the ability of a potential predator to catch *A. antipodianus,* or offer multiple avenues of escape for *A. antipodianus*.

Another possibility for why *A. antipodianus* enter the webs of *C. foliata* is to use the webs as a refuge during reproduction. There is little literature on the lifecycle of *A. antipodianus*, but the related *A. ululans* (Cambridge, 1880) construct their eggs sacs in the webs of their social, sheet web hosts, *Anelosimus eximius* (Keyserling et al., 1884), and guard them for 17-28 days (Cangialosi, 1990). Juvenile *A. ululans* also scavenge in the webs of *A. eximius* (Cangialosi, 1990). If the reproductive cycle of *A. antipodianus* is like *A. ululans*, then *A. antipodianus* may use *C. foliata* webs as nurseries, with juvenile *A. antipodianus* scavenging from the webs of *C. foliata* until they disperse and kleptoparasitise the webs of *S. pustulosa.* A more in-depth study into the reproduction and lifecycle of *A. antipodianus* would be needed to test this hypothesis.

It is possible that *A. antipodianus* is in a kleptobiotic or commensal relationship with *C. foliata*. To examine this, I would run four complementary tests. Firstly, I would examine if *A. antipodianus* are stealing prey from *C. foliata* through direct observations*.* Secondly, I would examine how *A. antipodianus* walks on the sheet and support threads of the webs of *C. foliata* similar to previous tests of *A. antipodianus* on *S. pustulosa* silk (Whitehouse, 1988). This test would help to determine if silk type prevents *A. antipodianus* from effectively kleptoparasiting *C. foliata.* Thirdly, I would test if effects on the fitness of *A. antipodianus* on the host only become apparent after a large number of *A. antipodianus* are present in the web (i.e., nine kleptoparasites, the largest number of *A. antipodianus* I observed in the web of a single host in my natural history survey (Chapter Two)). Further, using mated female *C. foliata* would allow me to measure and compare the weight, size and number of spiderlings between kleptoparasitised and non-kleptoparasitised mothers as a more direct measurement of fitness. I would also conduct another field survey using mark recapture techniques to monitor the survival and reproductive success of *A. antipodianus* in *S. pustulosa* and *C. foliata* webs.

In conclusion, my combined field and laboratory results suggest that there is no foraging benefit for *A. antipodianus* when living in groups in the webs of their hosts. However, my results also suggest that *A. antipodianus* may struggle to effectively kleptoparasitise *C. foliata*, which may contribute to *C. foliata* tolerating a large number of kleptoparasites in their webs. Further research is needed to test and potentially reassess if the relationship between *A. antipodianus* and *C. foliata* is kleptoparasitic, kleptobiotic or commensal.

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Chapter 5

General discussion

In my thesis, I investigated the relationship between *Argyrodes antipodianus* (Cambridge, 1880) and its New Zealand hosts *Socca pustulosa* (Walckenaer et al., 1841) and *Cambridgea folitata* (Cambridge, 1879). I also explored the potential for beneficial intraspecific interactions among *A. antipodianus.* The results of my field study suggest that *A. antipodianus* more commonly kleptoparasitise the orb weaver *Socca pustulosa* over the sheet-web spider *Cambridgea foliata* (Chapter Two). I also found that *A. antipodianus* were mostly found alone in host webs, rather than in groups (Chapter Two). *A. antipodianus* commonly kleptoparasitises hosts with large webs rather than small webs. I hypothesise that this is because a host is less likely to abandon a larger web and will therefore tolerate more *A. antipodianus* activity because *A. antipodianus* presence positively correlated with host site fidelity. I found that *A. antipodianus* do not appear to be attracted to airborne chemical cues from potential hosts or conspecifics (Chapter Three). My field and experimental data suggest that the number of kleptoparasites in a web do not affect the body condition of the host (*C. foliata*) or kleptoparasite (*A. antipodianus*) (Chapter Four). Overall, my results indicate that *A. antipodianus* do not gain a foraging benefit from forming groups in host webs.

5.1 Factors affecting sociality in *Argyrodes antipodianus*

My results provide evidence contrary to my hypothesis that *A. antipodianus* gain a foraging benefit by aggregating together in a host web. In field surveys, I found that individual *A. antipodianus* were more common than groups of *A. antipodianus* in host webs. If there was a fitness advantage to being in a group for the purposes of feeding, we would expect grouping behaviours to be selected for and therefore *A. antipodianus* groups to be a more common occurrence than solitary *A. antipodianus*. Although surprising, my results are in line with *A. miniaceus* (Doleschall, 1857) that have better feeding outcomes when alone than in a group (Yu et al., 2022). I had hypothesised that *A. antipodianus* has better feeding outcomes in a group because *A. flavipes* (Rainbow, 1916) lives communally and subdues prey (Whitehouse & Jackson 1998). However, *A. flavipes* is not kleptoparasitic (Whitehouse & Jackson, 1998). This study was done in the spring and for that reason many of the *A. antipodianus* may have been coming out of their overwintering phase and therefore were seeking shelter rather than food which could have potentially biased the results (Whitehouse, 1986). My olfactometer experiments suggest that *A. antipodianus* do not use airborne chemical cues to locate conspecifics, suggesting in turn that *A. antipodianus* do not actively seek each other out. Further testing of the use of silk chemical cues is needed before completely ruling this out. My field surveys also indicate that *A. antipodianus* frequently moves between hosts, a conclusion supported by Whitehouse and Jackson, (1993) who performed a mark recapture survey of *Argyrodes antipodianus* in New Zealand (Whitehouse & Jackson, 1993). Adults that move frequently between host webs may increase their chance of finding a mate (Jellen et al., 2007). However, it seems that *A. antipodianus* do not remain together long enough to form stable, long-term relationships like other social spiders as other social spiders form groups for reproduction, whereas *A. antipodianus* appear to form groups for foraging purposes (Uetz & Cangialosi, 1986; Ward &

Enders, 1985; Whitehouse & Jackson, 1993; Whitehouse & Lubin, 2005). Once on a web together, males and females may identify each other using contact pheromones in web silk, common among theridiids (Scott et al., 2018, 2018; Whitehouse, 1991; Whitehouse & Jackson, 1994). *A. antipodianus,* while tolerant of conspecifics, do not appear to work together (Whitehouse, 1997).

5.2 Comparison to other social spiders

Argyrodes sit within the family Theridiidae, which has the most social spiders of any spider family (Agnarsson, 2004). While *A. antipodianus* is tolerant of conspecifics, it does not share the same level of cooperation as other social spiders both in and outside of Theridiidae (Whitehouse, 1997). Some social spiders construct their webs close to conspecifics but still maintain their own territory and defend their web against intruders (Ward & Enders, 1985). Other social spiders take this further and co-operatively construct webs and overpower prey caught in the web (Binford & Rypstra, 1992; Ward & Enders, 1985). Many social spiders form groups for reproductive purposes and share the cost of parental care (Avilés & Guevara, 2017; Whitehouse & Lubin, 2005). Cooperation for reproduction in spiders can result in reduced genetic variability in the population due to a decrease in the dispersal rate of offspring and therefore an increase in inbreeding (Avilés & Guevara, 2017; Whitehouse & Lubin, 2005). *A. antipodianus* has very little parental care which mostly involves the mother guarding the egg sac for a few days before it hatches, as such *A. antipodianus* maintains a high dispersal rate.

Most social spiders are found in the tropics, perhaps because the insects large enough to make sociality profitable tend to be found in the tropics (Nentwig, 1985).

Increased prey capture allows social spiders to feed their offspring more, promoting reproductive success (Avilés & Guevara, 2017) Since *A. antipodianus* steals prey rather than subduing it themselves they do not need to work together to catch prey and since they do not provide parental care, they do not concern themselves with feeding their offspring (Whitehouse, 1997; Whitehouse & Lubin, 2005). While some *A. antipodianus* may tolerate each other long enough for multiple individuals to feed from the same prey item as their host (a particularly profitable strategy for *A. antipodianus*) it doesn't necessarily give them a better outcome (Whitehouse, 1997). Also, social spiders working together to catch prey engage in intraspecific aggression after a kill, with silk throwing, web shaking and prey stealing all being observed (Binford & Rypstra, 1992). However, intraspecific competition among *A. antipodianus* on a host web risks them being detected, which could lead to them being chased, caught and eaten by the host, or the host abandoning its web in which case *A. antipodianus* can no longer exploit it (Whitehouse, 1997). The cooperative behaviours of other social spiders is used as a way to offset the costs constructing a web, capturing prey and raising young (Binford & Rypstra, 1992; Nentwig, 1985). *A. antipodianus* do not need to work cooperatively to offset these costs as they steal these resources from their hosts or do not provide for their young. *A. antipodianus* has significant differences in ecology from other social spiders. However, this doesn't entirely explain why they aren't social as many other kleptoparasitic animals do work cooperatively.

5.3 Comparison to other social kleptoparasites

I hypothesised that *A. antipodianus* work in groups to co-operatively steal prey from hosts. Previous studies found that *A. antipodianus* move between host webs and conspecific aggregations in a manner similar to the fission-fusion dynamics of dolphins (Aureli et al., 2008; Whitehouse & Jackson, 1993; Whitehouse & Lubin, 2005). I predicted that this similarity in group formation may also mean that *A. antipodianus* forage cooperatively. While I was unable to systematically test this here, my observations suggest that *A. antipodianus* do not forage cooperatively. I usually found only one *A. antipodianus* in a host web. If *A. antipodianus* do forage together, it is not common.

If cooperative kleptoparasitism offered a greater fitness advantage than solitary kleptoparasitism, it follows that aggregations of *A. antipodianus* should be more common than lone *A. antipodianus,* although the presence of individuals entering webs for shelter rather than foraging can't be discounted. My experiments found no benefit to two *A. antipodianus* in a host web compared to one individual in a host web, or an individual living without a host web (Chapter Four). I believe this may be due to a difference in foraging behaviour between *A. antipodianus* and other social kleptoparasites. Unlike other social kleptoparasites such as spotted hyenas (*Crocuta crocuta*) (Erxleben, 1777) and glaucous-winged gulls (*Larus glaucescens*) (Naumann et al., 1840) which work in groups to harass a host away from its catch, *A. antipodianus* foraging tactics favour not being detected by the host when stealing prey (Herbert et al., 2019; Lehmann et al., 2017; Whitehouse, 1997). Detection by the host could lead to *A. antipodianus* being chased, caught and eaten by a potential host (Whitehouse, 1997). Also, hosts of kleptoparasites abandon webs if they detect too many kleptoparasites in their webs (Grostal & Walter, 1997). Avoiding detection by the host is more likely when *A. antipodianus* are alone rather than in a larger group and thus being alone may be more advantageous than in other kleptoparasites.

5.4 Why *Argyrodes antipodianus* form groups if not for cooperation

While some species of *Argyrodes* congregate in aggregations of 40+ individuals in the web of a single host, this is quite rare (Vollrath, 1979). Previous work has found that it is much more common for *Argyrodes*, including *A. antipodianus*, to congregate groups of two to five individuals (Grostal & Walter, 1999; Vollrath, 1979). This is in contrast to my natural history observations (Chapter Two) where I usually found *A. antipodianus* alone in host webs. This discrepancy may be because other studies of *A. antipodianus* have been completed in their Australian range, where their chosen host produces an orb web which *A. antipodianus* seem to prefer (Grostal & Walter, 1999). However, in both my study and Grostal & Walter (1999) there was a positive correlation between *A. antipodianus* presence and the size of the host web.

Grostal and Walter (1999) also found a positive correlation between kleptoparasitic load and host web size, while I found that hosts with *A. antipodianus* present were less likely to abandon it. I hypothesise that this is due to *A. antipodianus* selecting hosts with larger webs because these hosts are less likely to abandon them having invested more time, energy and silk into constructing the web. As a result, *A. antipodianus* may exploit the greater potential for prey capture that a larger web provides with less risk of the host abandoning the web (Harmer et al., 2015). Grostal & Walter (1999) also noted that more *A. antipodianus* were found in the webs of female hosts being courted by males. This suggests that *A. antipodianus* take advantage of the opportunity to kleptoparasitise the female while she is distracted by a males' courtship (Grostal & Walter, 1999). It may be that *A. antipodianus* are more likely to form aggregations when resources are abundant (e.g. when a host has a large web and therefore catches more prey), or when the host is less likely to notice or respond to high levels of kleptoparasite activity. Aggregations in these scenarios may not be driven by cooperation, but by maximising opportunities to exploit resources, either through access to prey or the ability to take advantage of a vulnerable host.

5.5 Kleptoparasitic vs kleptobiotic relationships

My results suggest that *A. antipodianus* may have a kleptobiotic or commensal relationship with its sheet web host, *C. foliata.* My field studies demonstrated that *A. antipodianus* kleptoparasitises *C. foliata* less often than its orb weaver host *S. pustulosa*. *Argyrodes* species often rely on orb weavers for food, and other studies of *A. antipodianus* found that they have specialised behaviours when feeding with an orb weaver host, including *S. pustulosa* (Whitehouse, 1986; Whitehouse et al., 2002). These behaviours include attaching a support web to the host web to move around the web as well as feeding on prey items from the side of the web opposite to the host (Whitehouse, 1986). Both of these are done in an attempt to avoid being noticed by the host (Whitehouse, 1986). The results of my fitness experiments also indicate that *A. antipodianus* struggled to kleptoparasitise *C. foliata* in the lab. Therefore, I speculate that *A. antipodianus* may enter the webs of *C. foliata* for reasons other than foraging. One reason may be that *C. foliata* webs offer more protection from predators than *S. pustulosa* webs. *Cambridgea foliata* webs are larger, denser and built in three dimensions compared to *S. pustulosa* webs. Theoretically, this would make it easier to detect an approaching predator due to the increased number of threads in the web, as well as providing more places for *A. antipodianus* to escape to compared to *S. pustulosa* webs (Graf & Nentwig, 2001; McCambridge et al., 2019; Mortimer et al., 2016, 2018). Another potential reason to enter the webs of *C. foliata* could be that the larger *C. foliata* webs provide *A. antipodianus* with ample space with which to mate and lay egg sacs, with *C. foliata* serving as nurseries for *A. antipodianus*. Studies of other *Argyrodes* species such as that of *A. ululans* found they laid their egg sacs in the barrier webs of their host and remain inactive, guarding the egg sac until it hatches approximately 17-18 days after laying (Cangialosi, 1990). If *A. antipodianus* has a similar breeding cycle then *C. foliata* would make better egg laying sites than *S. pustulosa* as *C. foliata* construct similar sheet shaped webs to *Anelosimus eximius*, the host of *A. ululans* (Cangialosi, 1990; McCambridge et al., 2019b). However, I do not believe reproduction to be the sole reason that *A. antipodianus* enters the webs of *C. foliata* as I also observed juveniles on the webs of *C. foliata*.

Another potential reason *A. antipodianus* enters the webs of *C. foliata* could be it has a more predatory relationship with *C. foliata* than *S. pustulosa. A. antipodianus* often kleptoparasitise the webs of orb weavers, such as *S. pustulosa* (Whitehouse, 1986, 2016). Laboratory experiments show little difference in the time it takes naïve adult *A. antipodianus* to use the best strategy for kleptoparasitism compared to *A. antipodianus* that have been trained to kleptoparasitise *S. pustulosa* from birth (Whitehouse, 2016). However, individuals can be trained to better catch the spiderlings of hosts with males showing the most improvement, demonstrating that spiderling predation is potentially a facultative trait that can be improved with experience (Whitehouse, 2016). I speculate that while *A. antipodianus* may not be able to kleptoparasitise *C. foliata* the same way they kleptoparasitise *S. pustulosa,* they may opportunistically predate *C. foliata* spiderlings. This would explain why my field survey (Chapter Two) found more *A. antipodianus* in the webs of *S. pustulosa* as kleptoparasitism is the more common strategy (Whitehouse, 1986). It would also explain why none of the *A. antipodianus* gained weight during my fitness experiments (Chapter Four) as there were no spiderlings for them to predate.

5.6 Next questions and future research

My research has raised new questions about where on the spectrum of kleptoparasitism to commensalism the relationship between *A. antipodianus* and their hosts lies. It has also raised questions about how *A. antipodianus* locate their hosts and other conspecifics. In this section, I will outline two sets of experiments that could add further insight to help answer these questions.

My experiments with *C. foliata* and *A. antipodianus* demonstrated that they struggled to kleptoparasitise *C. foliata* under laboratory conditions. This has led me to believe that *A. antipodianus* may not have a kleptoparasitic relationship with *C. foliata* and instead may have a kleptobiotic or even commensal relationship. For this reason, I suggest conducting a series of systematic behavioural observations of *A. antipodianus* in the webs of *C. foliata.* Observations of *A. antipodianus* and *C. foliata* movements in webs would allow for the assessment of how often *A. antipodianus* feed from the same prey item as *C. foliata*, and how often *A. antipodianus* shows interest in a potential prey item. Observations like these could help to determine if *A. antipodianus's* behaviour in *C. foliata* webs is similar to their behaviour in other host webs such as those of *S. pustulosa* and *T. plumipes* (Grostal & Walter, 1997, 1999; Whitehouse, 1986, 1997). I would then run another fitness test this time using a flying prey item as *C. foliata* webs are more likely to catch flying insects and therefore *A. antipodianus* are more likely to know how to kleptoparasitise them. The purpose of this test would be to quantify the effect on fitness of *A. antipodianus* on *C. foliata.* I would use large, net cages (40cm x 40cm x 40cm) instead of plastic boxes for the arenas, providing space for *C. foliata* to build webs similar in size to webs in nature. I would compare the effects of a large number of *A. antipodianus* (nine, which was the largest number of *A. antipodianus* I found in a single web during my natural history surveys (Chapter Two)) on the fitness of *C. foliata* to the effects of no kleptoparasites on *C. foliata*. Using a larger number of kleptoparasites in the web than I used in Chapter Four may generate more pronounced effects of kleptoparasitism on *C. foliata*. The results from this experiment, combined with direct observations of the feeding behaviour of *A. antipodianus* in the web will help to determine the relationship between *A. antipodianus* and *C. foliata*. If *A. antipodianus* gain weight while *C. foliata* lose weight, then the relationship is kleptoparasitic. If *A. antipodianus* gain weight and *C. foliata* have no change in weight, then the relationship is kleptobiotic. If *A. antipodianus* lose weight and *C. foliata* have no change in weight, then the relationship is commensal.

The second experiment will test how *A. antipodianus* locates and chooses its hosts. I found that *A. antipodianus* did not approach airborne chemical cues released by potential hosts and conspecifics and speculated that they use other cues to find hosts (Chapter Three). These cues may include chemical cues on the web silk, cues from prey in the web, or a combination of host cues and conspecific cues. While my survey data did not indicate that prey items in a web were an important factor in kleptoparasitism by *A. antipodianus,* prey availability is an important factor for other species of *Argyrodes* (Hénaut et al., 2005). Further studies are needed to assess the importance of captured prey items in a host web to *A. antipodianus* finding and kleptoparasitising a host. I suggest running a test using a Y maze with strips of blotting paper containing the silk of a host on one side and the silk of a non-host spider on the other side to see which, if any, *A. antipodianus* chooses. This will help determine if silk is important for host location.

Once the cues that *A. antipodianus* uses to locate their hosts are determined I would test whether *A. antipodianus* have a host preference. My natural history observations showed that more *S. pustulosa* were kleptoparasitised than *C. foliata*, but the number of kleptoparasites in the webs of each host were similar (Chapter Two). I would also test the factors that influence host choice by *A. antipodianus*., such as the presence of conspecific cues combined with host cues. My observations and others have suggested that *A. antipodianus,* along with other members of the *Argyrodes* genus, prefer hosts with large, long lived webs (Dash & Sivaperuman, 2023; Grostal & Walter, 1999; Miyashita, 2002). A next step would be to empirically test this.

5.7 Conclusions

I found that *A. antipodianus* kleptoparasitised the orb weaver *S. pustulosa* more than the sheet web spider *C. foliata.* My experiments suggest that *A. antipodianus* struggle to kleptoparasitise *C. foliata*, which means that why *A. antipodianus* enter the webs of *C. foliate* is uncertain. Although *A. antipodianus* and other species of *Argyrodes* are often found in groups in host webs, I usually found just one *A. antipodianus* in a host's web. Host spiders with *A. antipodianus* tended to have higher site fidelity than host spiders without *A. antipodianus.* I believe this may be due to *A. antipodianus* preferring hosts with large webs and therefore the hosts being less likely to abandon a large web that they have invested in. *A. antipodianus* do not respond to airborne chemical cues from potential hosts or conspecifics under laboratory conditions. However, further research is needed to confirm these results and identify the cues that *A. antipodianus* uses to locate hosts. Despite *A. antipodianus* being tolerant of conspecifics, my observations suggest they do not cooperate in order to facilitate kleptoparasitism, nor gain a foraging advantage from aggregating in a host web. My research has also raised new questions regarding *A. antipodianus'* status as a kleptoparasite or a kleptobiont in the webs of *C. foliata*. *Argyrodes antipodianus* are an excellent model species for testing questions about how intraspecific interactions influence kleptoparasitic relationships.

5.8 References

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