Contrasting sociality in two sympatric skink species: *Oligosoma otagense* and *O. grande*

Penny Jacks

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Abstract

The study of sociality in a conservation context is a growing area of science often applied across a variety of taxa, from primates to social insects. However, the study of social systems in in lizards has been limited to just a few species. This study examines the social networks and nature of social interactions in two sympatric lizard species, the Otago skink (*Oligosoma otagense*) and the grand skink (*O. grande*). These two species share a similar biology and are observed cohabiting the same rock tors. However, sociality has not been studied in grand skinks while Otago skinks have been found to form stable social networks in a captive population.

Photographic surveys were conducted over a three-month period at five sites within a wild metapopulation of grand skinks and Otago skinks. These five sites varied in the relative proportion of Otago skinks and grand skinks, from Otago skink dominated sites to grand skink dominated sites. Skink-skink behavioural interactions and basking proximity were recorded and photographs were used to identify the skinks involved in these observations. Pairs of skinks were considered to be interacting peacefully if they were basking within one metre of one another, with interactions categorised into four proximity thresholds: 1m, 30cm, 10cm and touching. An interaction was deemed agonistic if it involved an aggressive behaviour or submissive reaction. Network analysis was conducted to compare the number of interactions between juvenile and adult skinks as well as between Otago and grand skinks. The nature and probability of interactions between and within these groups were also compared. In addition, the presence of tail damage was examined as a potential indicator of the probability of aggressive interactions occurring.

This study found that the social networks and aggregative basking previously observed in a captive population of Otago skinks also occurs in this wild population. The number of Otago skinks interacting decreased as the ratio of grand skinks to Otago skinks increased. In contrast, grand skinks were not seen as seen basking in aggregations and participated in agonistic interactions more often than Otago skinks. Interspecific interactions were rare, consisting of a combination of peaceful and aggressive interactions. The presence of tail damage did not appear to be related to the probability of an individual interacting or involvement in aggressive interactions. However, tail damage was more common at sites that were nearest to a nest of starlings.

It appears both skink species interact less often with conspecifics when the tor is inhabited by a larger number of the other species. Further study is needed in order to understand whether these social interaction rates are associated with population survival and growth. Due to the nature of the Otago skink social structures, it may be beneficial to take existing connected networks into consideration when selecting skinks for translocation. Although, the effects of breaking these networks, such as family groups, on juvenile survival and adult interactions need further research. A multi-year study would increase understanding of the nature of Grand skink agonistic interactions and the stability of pair bonds.

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Introduction

1.1 Animal behaviour as a conservation tool

Animal behaviour research is rarely applied to conservation biology; these two fields are often seen as having little to no direct association, with areas such as animal sociality being some of the least utilised (Berger-Tal et al. 2016; Goldenberg et al. 2019). Since animal populations function in complex and dynamic ecological and social systems, an adaptive management approach is often required to solve conservation issues, drawing from multiple disciplines. The more complete a conservationist's understanding of the functioning of a population within an ecosystem, the greater the ability to predict management outcomes and respond to new challenges (Anthony & Blumstein 2000; Loye & Carroll 1995; Smith et al. 2016). Exceptions where behavioural research has already proven useful when applied to conservation biology include increased understanding of: the effects of climate and anthropogenic changes on populations (Menzel & Feldmeyer 2021); disease transmission (Caillaud et al. 2006); invasive species control (Capelle 2015; Tingley et al. 2013); antipredator behaviour and learning (Ale & Brown 2009; Griffin et al. 2000); habitat restoration (Bennett 2013); human-wildlife conflict (Blackwell et al. 2016); and population genetics and demography (Blumstein 2010; Merenlender 1993). Since uncertainty in management outcomes is often influenced by the behavioural responses of species involved, it is intuitive to consider sociality in conservation plans within a wider scope of group-living species.

Conservation behaviour is a discipline in conservation that "investigates how proximate and ultimate aspects of the behaviour of an animal can be of value in preventing the loss of biodiversity", as described by Buchholz (2007). Current application of conservation behaviour ranges from utilizing sound aversion behaviour in the reduction of gillnet bycatch of the harbour porpoise (*Phocoena phocoena*) by attaching high frequency sound emitting 'pingers' to gillnets (Cox et al. 2003), to reduction of dispersal behaviour when translocating animals such as the jewelled gecko (*Naultinus gemmeus*) using soft release techniques (Knox et al. 2017). This field can enhance understanding of conservation issues including: climate related behaviour (Sørensen & Loeschcke 2002) such as reptiles with philopatric nest sites with temperature-mediated sex determination (Morjan 2003); reintroduction biology, for example translocations of carnivores back into historic ecosystems (Berger 2007); game theory to predict management outcomes (Sutherland 2006); captive breeding management to prevent selection of traits deleterious in the wild (Snyder et al. 1996); teaching advantageous behaviours for release, such as predator aversion (Shier & Owings 2006); sustainable ecotourism practises examining the effects of tourism as a stressor on populations (Walker 2006); and understanding breeding behaviour to enable management of breeding *in situ* and captive breeding (Sousa-Santos et al. 2014). From an analysis of the frequency of occurrence of 10 behavioural themes within conservation literature Berger-Tal et al. (2015) found: movement behaviours such as dispersal and migration were the most commonly studied, foraging behaviours were the second most common theme, while animal personality was the least commonly studied. Though many successful outcomes have arisen from conservation behaviour research, it is still a growing area, with sociality research being one of the least utilised areas (Berger-Tal et al. 2016; Brakes et al. 2019; Somers and Gusset 2009).

Sociality in animals "implies a number of individuals living and/or interacting together, which can lead to complex social relationships and structure", as described by Wey et al. (2008). Sociality research can be used to glean a variety of information about population health, structure and growth. This information has been used to understand: parasite and disease transmission in a population (Bordes et al. 2007; Kappeler et al. 2015); current or predicted population stability and viability as a result of disturbance, fragmentation or dispersal (Maldonado-Chaparro et al. 2018; Slabach 2018); and pair-based management strategies for founder population selection (Kerth 2008; Snijders et al. 2017). Animal social behaviour can also inform conservationists of the mating potential, group membership, territories and parental care of group members; all of which can determine survivability of individuals within a social population (Royle et al. 2012).

Both affiliative and agonistic behaviour are used to understand the social behaviour of a population, with knowledge of these behaviours applicable in a variety of conservation contexts (Foley et al. 2001; Gamradt et al. 1997; Wielebnowski et al. 2002). For example, agonistic behaviours such as infanticide, cannibalism, dominance and male-male aggression are important to understand when housing a species in captivity; these behaviours could inform optimal combinations of individuals and housing densities (Freiria 2006). A study found growth rates in captive saltwater crocodile (*Crocodylus porosus*) hatchlings are lowest at low densities due to the emergence of one dominant individual, but also at high densities where activity is highest as result of frequent interactions (Brien et al. 2016). Understanding how different demographics, such as size categories, interact can also be utilised when managing populations to limit conflict. It is common for interspecific and intraspecific aggression to be initiated by larger individuals when a size difference is observed (Linklater et al. 1999; White et al. 2019; Adriaenssens & Johnsson 2011; Wright et al. 2019), situations in which populations may benefit from partitioning into groups of the same size class when in captivity and during translocation. Behaviours can be an indicator of population health and stability, where agonistic behaviour in the form of territoriality has been used to estimate carrying capacity, comparing territory size versus the area of suitable habitat available (Ayllón et al. 2012). Expanding this application further, the effects of external stressors and anthropogenic effects on populations can be better understood through social behaviour.

Anthropogenic related stressors can affect the nature of interactions, including allowing the incidence of aggression to be used as a tool to assess human effects on population dynamics non-invasively. Taraborelli et al. (2011) propose the monitoring of agonistic and vocalisation behaviours as a non-invasive method of assessing stress levels in wild guanacos (*Lama guanicoe*) during and after live-shearing. The effects of climate change on the social systems of animal populations have also been studied in aquatic some species, including how temperature changes affect the nature of interactions. Changes in the incidence of agonistic behaviour have been found to occur as water temperature increases in crayfish species and brook trout (*Salvelinus fontinalis*), suggesting the effects climate change might have on interspecific competition and potential ecosystem changes as a result (Gherardi et al. 2013; White et al. 2019).

Not only can social behaviours be studied to predict changes in population and improve population management, this line of research can also be used to improve methods used to understand and monitor populations. Agonistic behaviours can affect the representativeness of sampling and populations surveys. Baited camera surveys can be biased in animals displaying territoriality, as observed in pink snapper (*Pagrus auratus*). Agonistic behaviour from aggressors was found to push subordinate snapper away from the camera (Dunlop et al. 2015). A bias is also thought to occur in field surveys, where bolder individuals may be less likely to retreat in the presence of the observer (Cole 1994), and exploration behaviour has been correlated with increased aggression in personality studies (Adriaenssens & Johnsson 2011; Pike et al. 2008).

With our growing understanding and ability to quantify agonistic and social behaviour of animal populations, these areas can continue to enhance a broad range of conservation research and wildlife management, across a variety of taxa.

1.2 Social network analysis in conservation

Social network analysis "addresses the structure of relationships and the mutual interplay between the individual and the group" (Wey et al. 2008). A network consists of a series of nodes (representing individuals) connected by edges (representing interactions between individuals). Quantitative measurements can be taken from the varying number of interactions within a network, to explore group dynamics as well as the involvement of individuals in the group. Social network analysis has become a tool for quantifying sociality in animals in terms of stability of interactions through time, the number of individuals each group member is interacting with, as well as the frequency of interactions between individuals (Croft et al. 2008). Interactions are determined using a variety of measures depending on the nature of the species, ranging from contact behaviours such as grooming, touching and physical attacks to non-contact behaviours such as displacement and proximity; where a pattern of close proximity between individuals that is stable over time is used to determine social bonds (Snijders et al. 2017). The resulting information provides insight into the survival, reproduction and resource exploitation of social groups and their members (Goldenberg et al. 2019).

The development of methods to quantify social systems, such as social network analysis, has advanced the understanding and scope of social population behaviour, resulting in the expansion of social biology into fields outside of behavioural research, including conservation (Blumstein 2010). When social network analysis is applied in a conservation context, the functioning of populations can be better understood and monitoring methods improved. For example, it can be difficult and time consuming to gather population estimates for species that are cryptic or are hard to find. By understanding sociality, there is potential to monitor populations more effectively and efficiently, with social observations being used as indicators of population health through the behavioural patterns. Rates of aggression within a population may reflect population density (Metcalfe & Furness 1987; Knell 2009) or immigration rates (Kawazoe & Sosa 2019). Knowledge of social structure of populations can also be used in combination with areas such as disease transmission, where incidence of disease and parasite presence could be used to predict population densities (Snijders et al. 2017).

The recent development of social network analysis in a biological context has allowed for the expansion of the field of conservation behaviour, contributing to the management of population genetics and demography (Blumstein 2010; Merenlender 1993), translocation success (Goldenberg et al. 2019), investigating anthropogenic effects (Snijders et al. 2017) and understanding disease transmission (Caillaud et al. 2006). Where social associations determine the survival and fitness of individuals in a group, such as in African wild dog (*Lycaon pictus*) populations (Gusset et al. 2006), understanding the position of an individual within a network could improve translocation success as well as reduce effects of the harvest of individuals on the social dynamics of the source population (Wilson et al. 2015). The movement of a whole social grouping or specific individuals can result in fewer mortalities and reduced dispersal upon release than if individuals are chosen randomly (Snijders et al. 2017; Sheir & Swaisgood 2011; Hansen et al. 2009; Blumstein et al. 2009). When individuals are chosen randomly for introduction into a stable population to boost genetic diversity, an unstable social environment can result in reduced breeding success in some species (Linklater et al. 1999). Shier (2006) found that black-tailed prairie dogs (*Cynomys ludovicianus*) translocated with family groups had greater survival rates and breeding success than dogs translocated without relatives. The Allee effect, a common cause of species reintroduction failure, can be reduced and avoided through the use of social network analysis to assess the social functioning of a population, factors contributing to aggression and factors affecting breeding success in the population (Leu et al. 2016).

Understanding and managing social dynamics and demography can aid population survival and success. An unstable social structure for some species can affect the fitness of individuals within the population (Linklater et al. 1999), which may have a negligible effect on population fitness in a large population. However, in small populations or groups, individual effects can have a detrimental effect on overall population or group health (Snijders et al. 2017). Here intervention through strategic manipulation of individuals within a population could be beneficial; in zoos manipulation of groups based on personality and positive interactions is used to increase reproduction in captive breeding programmes (Rose & Croft 2015). In captive populations of rhesus macaques (*Macaca mulatta*) with unnaturally high levels of agonistic interactions, the identification and management of aggressive individuals has reduced agonistic encounters to natural, safe levels (McCowan et al. 2008).

Understanding anthropogenic effects on wildlife populations has growing importance, with the pressure of the expanding global human population continually encroaching on wild places and contributing to decline in wildlife populations. Collection of baseline population structures are important for monitoring anthropogenic changes and effects on individual populations and species; understanding which social structures are most resilient to human induced stressors (Frère et al. 2010; Brent et al. 2015; Williams & Lusseau 2006); as well as minimising effects or predicting impacts of harvest (Williams & Lusseau 2006). Encroachment on habitat is just one impact of human activity, which can cause population fragmentation (Banks et al. 2007), clumping and density increases (Debinski & Holt 2000). These can then lead to higher incidences of aggression and increased spread of disease (Hamede et al. 2009), as well as otherwise unlikely encounters occurring between members of a population (Leu et al. 2016).

Parasite and disease spread in social animals can often be better understood using social network analysis. While techniques to measure the susceptibility of individuals as well as identifying the infection status of every individual of a population can be invasive and intensive, social network analysis can be an effective alternative tool (Tompkins et al. 2011). Social network analysis has been used to effectively predict disease transmission in brushtail possums (*Trichosurus vulpecula*), where closeness and flow-betweeness (two network measures) could be used to predict the spread of the disease *Mycobacterium bovis* between possums (Corner et al. 2003). This technique can predict disease transmission pathways, identify susceptible clusters and centrally connected individuals likely to spread disease widely in populations of social animals (Zohdy et al. 2012). Understanding the social systems of a species potentially enables conservationists to safe-guard populations against disease, predict disease transmission and control infection, as well as aid the conservation of species-specific parasites (Dougherty et al. 2016).

1.3 Sociality in squamates

Current application of animal sociality research largely consists of eusocial insects (Chapman & Bourke 2001; Murray et al. 2009) and charismatic mammals, such as marine mammals (Busson et al. 2019; Smith et al. 2016) and primates (Caillaud et al. 2006; Merenlender 1993); with a general research bias in animal sociality towards mammals, birds and insects (Gardner et al 2016; Krause et al. 2009; Alexander 1974). Doody et al. (2013) state that this taxonomic bias is thought to be exacerbated by the original definition of sociality being based on species with complex mating systems and group structure. Though still debated, they suggest this issue could be resolved using taxa-specific definitions, to allow taxa such as reptiles and amphibians to be explored as social organisms. Reporting of parental-care in lizards, for example, is rare (Somma 2003). However, this disparity when compared with other taxa may be in part the result of differences in how behaviours are expressed. Where the display of parental care in birds, mammals and insects involves meeting the nutritional needs of offspring and providing a form of protection from predation, in reptiles the tolerance of offspring within parental home ranges may be considered parental care (Chapple 2003; Ibargüengoytia & Cussac 2002). The simpler definition of sociality used by Alexander (1974) to mean “group-living” is far more applicable to reptiles, extending this field of study to a taxonomic group often only thought of as displaying solitary and hostile behaviour.

There is a dearth in quantitative research into reptile behaviour, including sociality research (Burghardt 2013). Sociality in lizards is currently thought uncommon (Gardner et al. 2016). This is made apparent in the number of known colonially nesting Australian lizards. Doody et al. (2009) found that only 6% of the Australian lizard species included in their analysis nest colonially. When they analysed a subset of these species that excluded all species that had unknown nesting strategies, the percentage that nest colonially was far higher (86%). From the limited observations of sociality in reptiles, facultative social associations have been found in a broad range of squamate (lizards, snakes and amphisbaenians) species. These range from transient associations to stable aggregative bonds, with parent-offspring aggregations most commonly displayed (Gardner et al. 2015). A common trait associated with sociality in squamates is vivipary, or live-bearing of young (**Figure 1.1**). Halliwell et al. (2017) found that of 1210 squamates, 80% of which were oviparous, there were twice as many viviparous species than oviparous species that displayed social grouping (66 vs 29).

Within social squamate species, kin-based aggregations have been found most commonly in viviparous lizards (**Figure 1.1**).

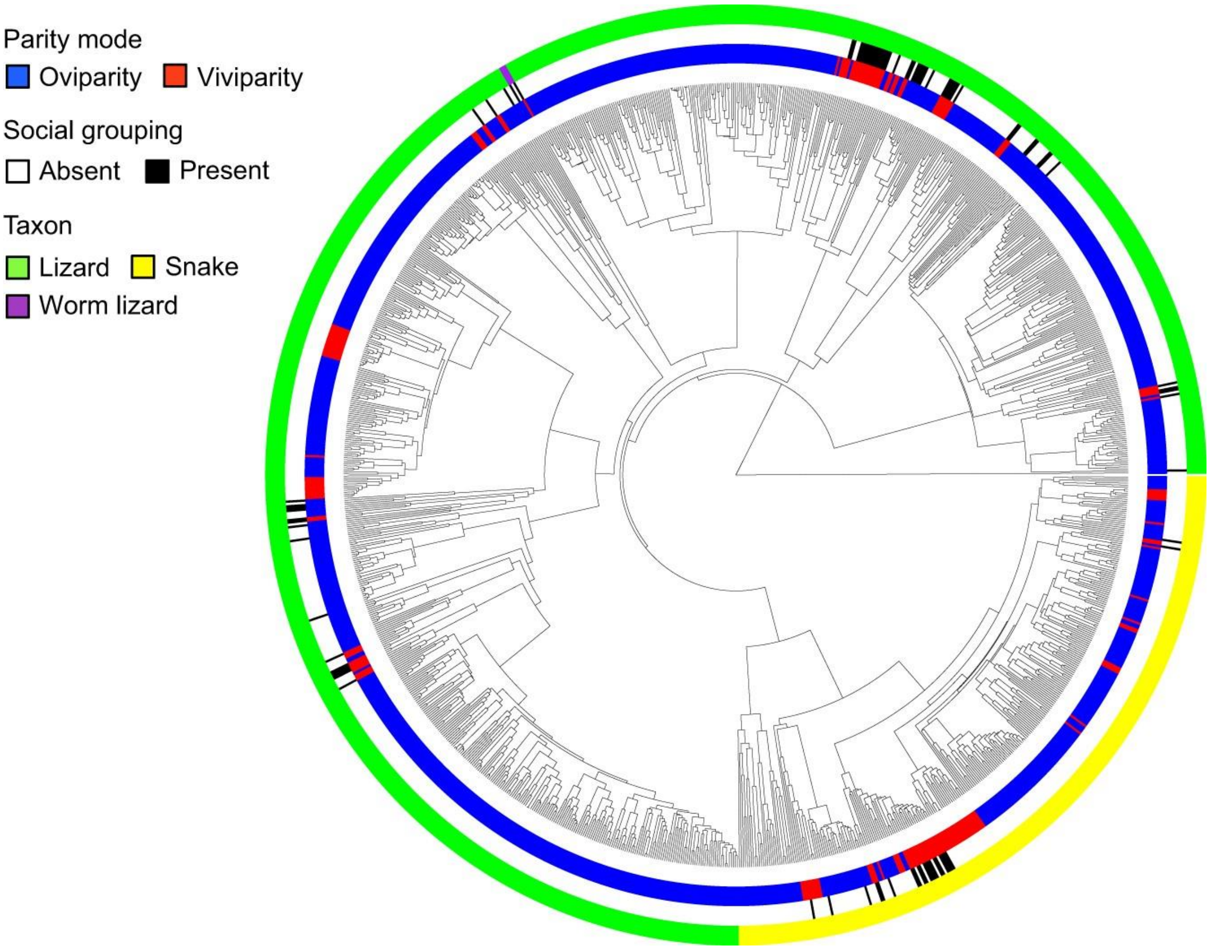


Figure 1.1 Figure retrieved from Halliwell et al. (2017) indicating the presence of social grouping behaviour within squamate species included in the study. A strong correlation was found between vivipary and sociality.

Examples of sociality have been identified anecdotally in several lizard families, including extensive studies within the ancient *Scincidae* family (Bull et al. 2012; Chapple et al. 2012; Gardner et al. 2016; Lukoschek & Shine 2012). Some of the old-world traits featured by this family are thought to influence group living, including viviparity, which is uncommon in more recently diverged lineages of lizards (Connolly & Cree 2008; Cree 1994; Norbury et al. 2006; Molinia et al. 2010). However, not all viviparous squamates form social groups. Life history traits associated with long-lived species are thought to also have a strong correlation with sociality, such as a long lifespan and delayed recruitment (Whiting & While 2017). *Scincidae* is a lineage that commonly has the following features: long-lived, delayed recruitment, small clutch size and viviparous.

1.4 Sociality in *Oligosoma*

Within *Scincidae,* the most studied species known to form stable aggregations are five within the Australian genus *Egernia*: *E. cunninghami* (Stow et al. 2001), *E. kingii* (Masters & Shine 2003), *E. saxatilis* (O'Connor & Shine 2006), *E. stokesii* (Duffield and Bull 2002) and *E. striolata* (Duckett et al. 2012). These taxa are closely related to the New Zealand genus *Oligosoma*. *Oligosoma* species also feature the same life history traits associated with social grouping behaviour typical of these social *Egernia* skink species. All but one *Oligosoma* species, oviparous *Oligosoma suteri*, are live-bearing. These species also tend to be long-lived, have delayed recruitment and many are large bodied (Connolly & Cree 2008; Whiting & While 2017). However, very few behavioural studies have been done on *Oligosoma*, with even fewer on sociality. The Otago skink (*Oligosoma otagense*) is the exception. Known to bask in aggregations of juveniles and adults, a recent study has found that this species forms stable social bonds and aggregate in family groups (Elangovan et al. 2021). *Oligosoma acrinasum* in Fiordland, New Zealand has also been observed communally basking in piles of up to 12 skinks (Thomas 1985).

Using social network analysis, Otago skinks were found to form stable bonds and social networks in a semi-captive population at Orokonui Ecosanctuary (Elangovan et al. 2021). Social network analysis has not been used in other *Oligosoma* species, though many of them share similar life-history traits. The grand skink (*O. grande)* is a sympatric species similar in size, habitat and diet. Both Otago and grand skinks are long-lived and are found to reach more than 16 years of age in the wild (Scharf et al. 2015; Tocher 2009). They also feature delayed recruitment, reaching sexual maturity around the age of 4 years (Molinia et al. 2010). As well as this, they have small clutch sizes with an average of two offspring produced per female each season (Cree 1994). These traits have all been thought to correlate with aggregative behaviour, indicating it is possible grand skinks also display a form of sociality (Chapple 2003).

1.5 Conservation history of the Otago skink and grand skink

New Zealand (Aotearoa) has a history of widespread species decline across a variety of taxa, due to introduced mammalian predators and anthropogenic habitat changes. There is no exception for two of New Zealand’s largest endemic mokomoko (skinks): the Otago skink and the grand skink. Otago and grand skinks were once widespread throughout the Otago region, estimated from sub-fossil evidence to have had a potential range of 1.75 million hectares across Central Otago (Whitaker and Loh 1995). Their distribution was thought to coincide with exposed quartzo-feldspathic schist outcrops present in the Central Otago rain shadow, which is conducive to drier areas with greater sun exposure. However, now these species are restricted to just 8% of this area, in the east-most and west-most areas of their historic range (Norbury et al. 2006; **Figure 1.2**).

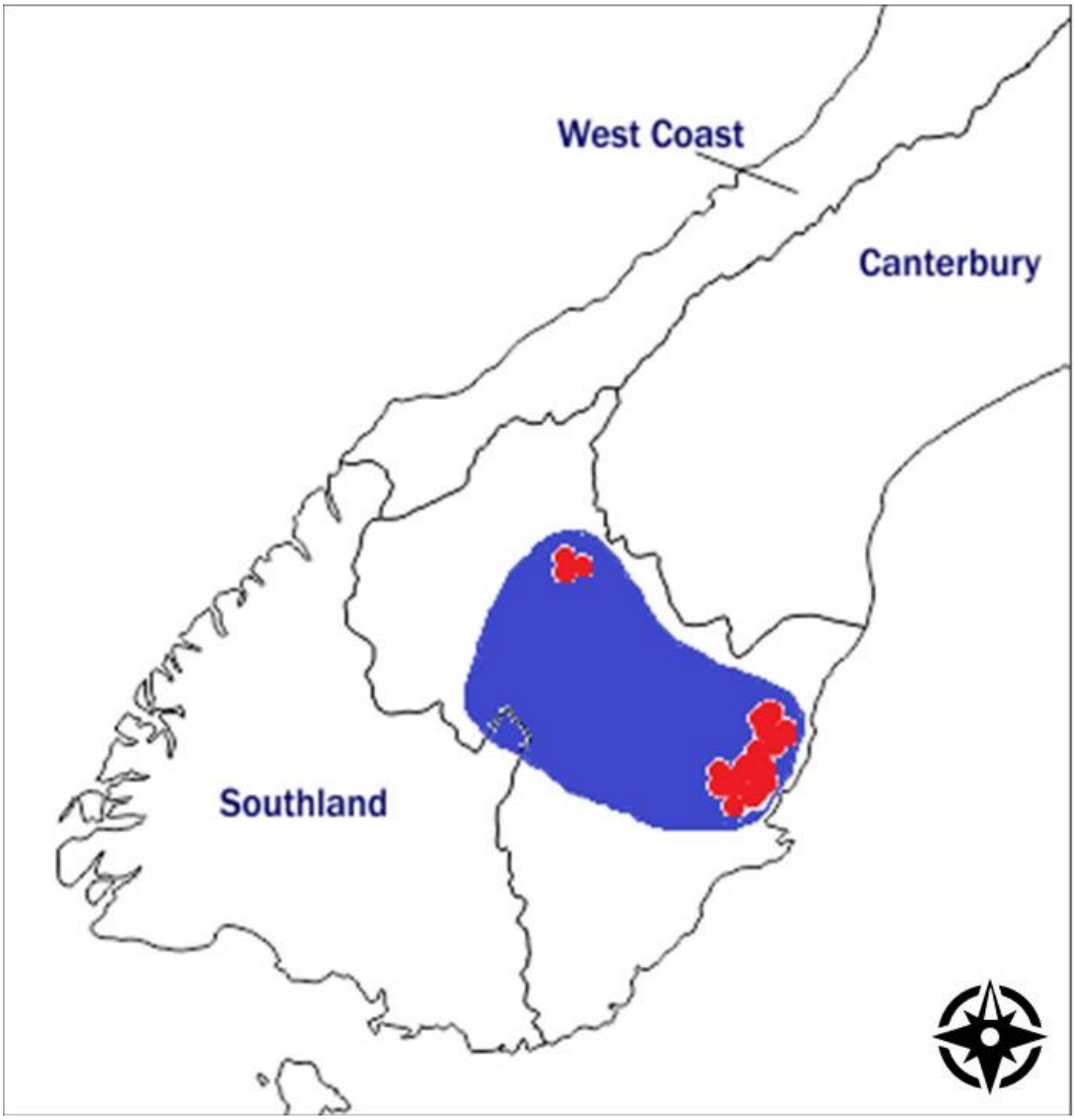


Figure 1.2 Map of the distribution of Otago skinks and grand skinks, showing the historic range (blue), found throughout the Otago region of the South Island of New Zealand, and the current range (red). Small isolated populations now exist in the western and eastern areas of their former range. Map is an adaptation of the distributions described by Norbury et al. (2006) and Patterson (1997).

The remaining skinks reside in small, isolated populations in Ōtī (Macraes)/Middlemarch area in the east, and in the west there are populations scattered between Lake Hāwea and Lindis Pass as well as recent reintroductions to Alexandra (Manuherikia or Areketanara)(Molinia et al. 2010; Patterson 1997; Whitaker and Loh 1995; Whitaker and Housten 2002). According to Hitchmough et al. (2016), both skink species have wild populations of less than 5000 skinks as a result of this range restriction, with a threat classification of Nationally Endangered (Hitchmough et al. 2021).

This range restriction is thought to be a result of habitat modification for mining and agriculture, as well as the spread of introduced mammals. The majority of their former range is now exotic pasture, tussock and shrubland, which promotes less invertebrate life, is more exposed through the elimination of canopy species and has reduced palatable fruiting plant cover. Overall, these habitat changes have reduced the availability of important resources for these two species throughout the landscape (Whitaker & Loh 1995; Tocher 2003).

Otago and grand skinks reside on rock tors within shrub and grassland habitat, the random scattered pattern of said structures giving rise to fragmented metapopulation structures (Coddington & Cree 1997; Germano 2007). There is dietary evidence for occasional foraging away from these tors, for example tutu (*Coriaria*) berries, with trans-tor movement more common where the surrounding vegetation provides dense cover (Patterson 1992). Dispersing individuals may also form transient populations between tors. The nature of these fragmented metapopulations makes them vulnerable to habitat degradation as they are reliant on vegetation for shelter while foraging and traveling between tors, as well as to support year-round food availability. The effects are evident in exotic pasture, where population distribution is more clumped with lower connectivity, likely due to the loss of transient skinks (Whitaker 1996). It is thought transient populations could also reflect the population health of surrounding sub-populations, which act as source populations as they approach carrying capacity (Houghton & Linkhorn 2002), which could also explain this low level of connectivity.

The widespread mammalian predators and competitors in the Central Otago region threaten these skink species further (Tocher 2006). Rabbits (*Oryctolagus cuniculus*) plague this region, both feeding on key fruiting shrubs as well as attracting and supporting populations of mammalian predators such as: feral cats (*Felis catus*), ferrets (*Mustela furo*), stoats (*Mustela erminea*) and weasels (*Mustela nivalis*); all known to feed on skinks as secondary prey (King 2005). In addition to these predators, European hedgehogs (*Erinaceus europaeus*), ship rats (*Rattus rattus*), Norway rats (*Rattus norvegicus*) and mice (*Mus musculus*) are also present in this region, known to also compete for food resources with and potentially prey on Otago and grand skinks (King 2005; Spitzen- van der Sluijs et al. 2009; Tocher 2009). As well as these mammals, there are also suspected native and introduced avian threats in the region, including: magpies (*Gymnorhina tibicen*), little owls (*Athene noctua*), starlings (*Sturnus vulgaris*), and Australasian harriers (*Circus approximans*)(Reardon et al. 2012).

Past conservation efforts have successfully increased numbers in managed populations, with the New Zealand Threat Classification of Otago skinks decreasing from Nationally Crtitical to Nationally Endangered in 2015, the latest classification review (Hitchmough et al. 2016; Towns et al. 2016). These efforts involved management of remaining populations through intensive predator trapping, construction of predator resistant fencing, captive rearing and translocation (Norbury et al. 2014; Reardon et al. 2012). Due to past concern about rapid decline, conservation efforts were concentrated on eastern populations where management was more feasible compared to the scattered populations in the west (Hare et al. 2019). Thriving populations exist within predator resistant fencing, while emergency salvage in 2014 of 85 grand and Otago skinks from genetically distinct western populations was implemented for captive breeding and to a newly built predator exclusion area (Collen et al. 2009; Hare et al 2019). As a result, these two fast declining species have returned to stable and growing populations in the east of their range, where they are managed (Reardon et al. 2012). However, other unmanaged populations have declined, highlighting the dependence of these species on continued management (Reardon et al. 2012).

With some populations now stable, current conservation effort is focused on maintaining and refining proven pest control techniques and on creating secure populations of the western lineage via translocation (Joanne Monks, Department of Conservation, pers. comm.). With a focus on re-establishing populations of both species within their historic range (Lynn Adams, Department of Conservation, pers. comm.), there have been recent translocations of Otago skinks in Alexandra (Hare et al. 2012) and Orokonui Ecosanctuary (Bogisch et al. 2016), a location outside of the known historic range, to successfully establish new populations. Chapple et al. (2012) indicate that Otago skinks are likely to be at the edge of their natural range and suggest future translocations to predator free areas might be beneficial for survival of this species.

A translocation fails when the founding population declines to an unviable density, as a result of mortality, the Allee effect (Stephens & Sutherland 1999) or post-release dispersal for example (Le Gouar et al. 2012), or recruitment is not high enough to establish a stable population (Oro et al. 2011). Social behaviour and intraspecific agonistic interactions can have direct effects on both decline in population membership and recruitment. Battles for dominance, sex bias, mate suitability, previous hierarchical roles, social environment and kinship can all impact the nature of interactions between individuals and thus can impact population survival. Past translocations of Otago skinks have had survival rates of in the first year as high as 68% (Bogisch et al. 2015) and 75% (Hare et al. 2012) within areas of little to no mammalian predator detection. However, annual survival rates have been as low as 0.15 per annum when mice were detected in the year subsequent to translocation (Norbury et al. 2014).

Agonistic behaviour such as cannibalism has been recorded in Otago skinks held in the Orokonui enclosure (Bogisch et al. 2016; Elangovan 2019) which, when occurring in a translocated population, can also affect dispersal rates, and in turn the founder gene pool and demographics (Freiria 2006; Linklater et al. 1999). Being able to reduce cannibalism to maximise survival rates could reduce genetic bottle necks, founder population size requirements, effect on the source population, as well as conservation effort (Parra et al. 2018; Ahlroth et al. 2003; Ottewell et al. 2014). Understanding social dynamics of grand and Otago skinks could inform the selection of founders for translocation by maximising the number of breeding pairs and reducing conflict, leading to increased translocation success rates (Sheir & Swaisgood 2011; Snijders et al. 2017).

Social behaviour could also be explored as an indicator of population health and stability, as the nature of interactions can be affected by factors such as population density and resource availability (Mouton 2011). Male grand skink home range sizes have been found to change depending on food resource availability (Eifler and Eifler, 1999). In Otago skinks there is evidence of adult-adult cannibalism in the Orokonui population (Elangovan et al. 2020), a semi-captive population held at a higher density than found in wild populations. In addition to observed behaviours, skink-inflicted injuries could also be investigated as a possible conservation tool. For example, tail damage could be used to determine the frequency of conflict as well as individual frequency of interaction and network connectedness. Caudal autotomy (tail loss) can occur when some pressure is applied to the tail of an Otago or grand skink. A study by Hare & Miller (2009) found that tail loss in the wild is likely to be influenced by predation, sociality and environmental factors. On islands intraspecific competition has been found to be the most common cause of tail loss (Itescu et al. 2017). Quantifying tail loss occurrence might be an indicator of the frequency of aggressive interactions within the population, the frequency a particular individual is involved in hostile encounters or provide evidence of periods of heightened conflict within the population (Hare & Miller 2009).In these cryptic species with low capture rates, surveys incorporating behaviour observations or related injuries may be an effective method for understanding the density and resource pressure in a population.

1.6 Sympatry in Otago and grand skinks

Otago skinks and grand skinks are two of the largest endemic lizard species in New Zealand, with some Otago skinks reaching 133mm in snout-vent length (SVL), and grand skinks found to reach 118mm in SVL (Tocher 2003). These diurnal skinks occupy tussock grassland habitat of Central Otago (Connolly & Cree 2008; Cree 1994; Norbury et al. 2006). Otago and grand skink species exist sympatrically throughout their eastern range on rock tors, with slight differences in tor preference between the two species. Although, both species have been observed using the same rock tors, grand skinks are more commonly found on ridge tops tors, whereas Otago skinks tend to reside in gullies (Towns 1985). Though Otago skinks and grand skinks live in sympatry, little is known about how these two similar species are able to occupy the same tors, or whether cohabitating populations are stable through time.

The diets of Otago and grand skinks have been found to be similar; rich in fruit during the summer period, with evidence of *Coprosma taylorae* and *Leucopogon fraseri* as well as large-bodied dipterans (*Calliphoridea*) and small-bodied coleopterans (Tocher 2003). However, Otago skinks have shown a preference for small native berries while grand skinks tend to consume higher numbers of invertebrates and tend to have a more generalist diet (Tocher 2001).

As well as diet overlap, there is overlap in habitat choice. Both species require stacked exposed rock tor structures with deep horizontal crevices to provide basking areas and shelter. Tors provide a conglomeration of the essential resources for both these species, resulting in accumulation and higher densities of skinks on the tors themselves. Competition for food resources and space on these tors is thought to have contributed to the evolution of aggregative basking behaviour in Otago skinks, in conjunction with the prolonged contact between slow growing offspring and their parents which is associated with family group aggregation (Whiting & While 2017; Elangovan et al. 2021).

According to Bergmüller & Taborsky (2010), competition between niche sharing species can be a driver for species behaviour changes and behavioural partitioning. There is evidence for agonistic behaviour towards other skinks in both Otago and grand skinks. A study looking at the composition of scat samples for these species found *Oligosoma* spp. present in the diets of both species (Tocher 2003). Cannibalism has also been documented in Otago skinks (Elangovan et al. 2020). Investigation into how Otago skink behaviour towards grand skinks compares with intraspecific behaviour is needed to better understand these agonistic events and hence further understand their sympatric relationship. Behavioural partitioning may occur in these populations, in the form of differences in reactions to skink encounters between species. Population survival could be improved by understanding what factors are allowing these species to coexist, or if this habitat sharing is forced by range restriction and is not sustainable through time.

1.7 Thesis objectives

Understanding the social behaviour of sympatric Otago and grand skink populations, both intraspecific and interspecific, could aid the conservation management of these species independently and as a combined system (Anthony & Blumstein 2000). Recent studies have found Otago skinks do form stable aggregations and social networks through time (Elangovan et al. 2021). However, this has not been investigated in grand skinks, wild Otago skink populations, or in Otago skink populations where grand skinks are present. The aim of this study is to better understand the interactions and social function of Otago and grand skinks, both intraspecifically and interspecifically, in a wild metapopulation.

This aim will be met using the following four objectives:

- Determine the nature and frequency of intraspecific behavioural interactions in grand skink and Otago skink subpopulations, using network analysis to characterise the social structure of these subpopulations. Since the *Oligosoma* genus, to which the Otago skink and grand skink belong, possess life-history traits that have been associated with the evolution of sociality in other lizards (Connolly & Cree 2008; Whiting & While 2017), I predict that both species will display behaviours associated with sociality. Otago skinks are known to form social networks in one captive population, with stable groups of juvenile skinks observed basking on top of adult skinks (Bovill 2018; Elangovan 2019). Therefore, it is expected that this social structure will also be found in these wild subpopulations and most intraspecific interactions will be peaceful, with juvenile and adult skink aggregative basking expected to be observed. Some aggressive interactions between Otago skinks are also expected as these have been recorded in previous studies (Bovill 2018; Elangovan 2019). It is predicted that grand skinks will also display a degree of sociality as they share many of these sociality-associated traits with the Otago skink. However, as they are sympatric it is likely this behaviour differs from the Otago skink as interspecific resource competition is often a driver of species behaviour partitioning (Bergmüller & Taborsky 2010). Since grand skinks are not known to display aggregative basking involving direct contact, a non-contact basking distance between skinks will be used to define a social interaction to investigate if this species is also social. I predict a higher incidence of aggression between grand skinks since this species does not tend to bask as close together as the Otago skink. I also predict that some peaceful basking interactions will be observed, but further apart than the interactions seen between Otago skinks.

- Investigate the frequency and nature of behavioural interactions between Otago and grand skinks in shared environments of varying ratios of grand skinks to Otago skinks. When species that occupy the same niche occur simultaneously within an ecosystem there is likely to be conflict as a result of resource competition, with previous evidence of both skink species preying upon other skink species (Tocher 2003). Cannibalism has been observed in Otago skinks (Elangovan et al. 2020) and consumption of other *Oligosoma* species has been recorded in both Otago skinks and grand skinks (Tocher 2003). I predict that there will be more aggressive interspecific interactions as the tor population of each species approaches an even ratio, in line with this previous evidence of interspecific conflict.

- Determine if the nature or occurrence of social interactions varies between juvenile and adult skinks. There are distinct age classes in both Otago and grand skink populations as a result of a combination of delayed recruitment and juveniles remaining among the parent population after birth. For this study, skinks are grouped into two age-classes (juvenile and adult). Since Otago skinks are known to form family groups, I predict adult and juvenile Otago skinks will be more likely to be involved in peaceful social interactions than adult and juvenile grand skinks. It is expected that adult skinks are more likely to display aggression, with infanticide recorded in adult Otago skinks. Adult grand skinks are known to demonstrate aggressive behaviours during the breeding season (Eifler & Eifler 1999), and since our study will take place during this time I expect adult grand skinks will be more likely to have aggressive interactions than juvenile grand skinks.

- Examine the presence of tail damage as a possible proxy to determine the frequency of conflict as well as individual frequency of interaction and network position. Understanding whether or not tail damage in individuals is correlated with the stability or types of interactions occurring in a population could be useful in a conservation context. Quantifying tail loss occurrence might be an indicator of the frequency of aggressive interactions within the population, the frequency a particular individual is involved in hostile encounters or provide evidence of periods of heightened conflict within the population (Hare & Miller 2009). In lizards, the tail is utilized for stored lipid resources (Clark 1971), putting individuals with recent tail loss at greater risk of demise during starvation periods. Therefore, it is predicted that skinks in this study with tail loss or tail damage are involved in aggressive encounters less often than those without damage, as a strategy to avoid further tail loss and conserve energy resources.

Chapter 2

Materials and methods

2.1 Study site

This research was conducted within the Wildlife Site in the Redbank Conservation Area in Ōtī (Macraes), Central Otago, New Zealand (45°27′00″S 170°26′24″E). The study location is fully fenced with predator resistant fencing, constructed in 1999 around pre-existing grand and Otago skink metapopulations sharing the same rock outcrops. This location is at an altitude of 400-600m, consisting of many tall exposed Haast schist rock tors and outcrops surrounded by native tussock (*Chionochloa rigida*, *C. rubra*), introduced grasses, woody shrubs (*Leptospermum scoparium*), golden speargrass (*Aciphylla aurea*) and mountain flax (*Phormium cookianum*).

Five sites within this area were examined in this study, all of which were a collection of closely connected tors separated by the tall tussock matrix (**Figure 2.1**).

Figure 2.1. Map of the study site showing the location of all five tor sites at the Wildlife Site, Macraes. Aerial photograph was taken from Google Earth (12.05.20). Outlined in white are the five sites, labelled with the number allocated to the largest tor at the site. These tors were numbered by the Department of Conservation in previous Otago and grand skink surveys.

Site boundaries were determined as the point at which there was at least five metres of separation between tors at that site and any other tor, including any exposed rock within this area that is safely accessible for monitoring. These sites were chosen based on the approximate ratios of Otago to grand skinks, with ratios ranging from Otago skink dominated sites to grand skink dominated sites, in order to explore the effects of this habitat sharing on sociality in both species. These ratios were estimated using data from previous DOC surveys (Unpublished data, Department of Conservation). Sites were also chosen based on the size and structure of the exposed rock, with each site consisting of a tall main tor surrounded by smaller tors and ground level exposed rock.

2.2 Tor descriptions

Site 6 (**Figure 2.2**) consists of DOC labelled tors 6-8. It is the north-east most site, made up of one main tor at the top of a gully, and- three smaller tor clusters at the base of the main tor, on the side of the gully.

Figure 2.2. East side of main tor of site 6 at the Wildlife Site, Macraes. Photograph taken by Penny Jacks, 2019.

The main tor has a large, deep crevice that continues diagonally from the base of east side upwards to the highest point, which was a common area of activity (**Figure 2.2**). There are not many rock crevices at this site, with most skink shelter in the form of small slabs and a few larger crevices. The highest densities of skinks were seen on a collection of smaller rock tors at the northern base of the main tor. The exposed rock is surrounded by long tussock and introduced grasses. This collection of tors receives sunlight earliest each day, as well as being highly exposed to wind due to its tall shape. In this study the skink population at site 6 was approximately 98% Otago skinks and 2% grand skinks.

Site 17 (**Figure 2.3**) consists of DOC tors 17-21, located on the south bank of the northern gully between site 6 and site 33, separated from these areas by rock tors, tussock and introduced grasses.

Figure 2.3. East side of the last three main tors of site 17 at the Wildlife Site, Macraes. Photograph taken by Penny Jacks, 2019.

This site is a collection of long, tall tors running in a line perpendicular to the gully. There is also a ground level area of exposed rock to the north-east of this section where skinks were also observed. The tors at this site had a high number of crevices. However, there was more separation between tors, as well as shorter vegetation with more moss ground cover. Skinks at this site were most often found on the tors furthest from the gully and on the highest points of the tors, which were less shaded throughout the day. In this study the skink population at site 17 was approximately 73% Otago skinks and 27% grand skinks.

Site 33 (**Figure 2.4**) consists of DOC labelled tors 33 to 36.

Figure 2.4. East side of largest tor at site 33 at the Wildlife Site, Macraes. Photograph taken by Penny Jacks, 2019.

This site is located south-east of site 17, along the same gully. The tors are similar in shape and size to site 17, though the largest tors here are taller and feature more crevices. There are more overhanging layers at this site, resulting in more shaded areas on the tors. The surrounding vegetation consists of more long grass than at site 17. There is also a larger ground level rock area than at sites 17 and 6. In this study the skink population at site 33 was approximately 85% Otago skinks and 15% grand skinks.

Site 137 is made up of DOC labelled tor main tor 137 and small stack tor 137a. Site 137 is the west most site, made up of one long main tor, with three smaller tors at the north end, as well as a small tall tor 137a on the east side of the south end (**Figure 2.5**).

Figure 2.5 South end of the main tor at site 137 taken from the east, with the tall rock stack tor 137a in front at the Wildlife Site, Macraes. Photograph taken by Ricardo Rocha Mello, 2019.

The main tor does not have deep crevices, with only slabs as refuges and a few small plants on the top and at the base of the tor. The east and north sides of this main tor are bare and have almost no refuges while the southern-most side is vegetated with mosses and low-growing plants. At the north end of the main tor there are three smaller tors and at the south end is another tor made up of layers of large slabs and rock with many crevices. Tor 137a is to the east of the main tor and has many slabs at the base. Skinks were often seen making their way down the sides of this tor from the top. In this study the skink population at site 137 was approximately 21% Otago skinks and 79% grand skinks.

Site 125 includes DOC labelled tors 125 to 127. This is the south-east most tor in this study, as well as the furthest from any other tors in this study. It is made up of one main tall tor (**Figure 2.6**) surrounded by ground level exposed rock, mosses and grasses.

Figure 2.6. East side of the main tor at site 125 at the Wildlife Site, Macraes. Photograph taken by Penny Jacks, 2019.

There are many loose slabs at this site as well as dried branches surrounding the main tor. This site is the last to receive sunlight and is the most shaded of the five tors. The main tor itself has layered sides with overhangs and crevices, and is divided into two sections by a deep, vegetated crevice. The southern section has large stacked slabs on top, and adult skinks were often observed here. The northern section has some smaller slabs on the top but has fewer refuge opportunities. In this study the skink population at site 125 was approximately 24% Otago skinks and 76% grand skinks.

2.3 Data collection

Data collection consisted of two separate periods: a non-invasive photographic survey period, which took place over 26 days from February to May 2019, and seven days of capture sessions in November and December 2019.

2.3.1 Photographic surveys

The photographic surveys were conducted by a team of three researchers and consisted of visual observations combined with photographs for identification of individual skinks. Throughout the photographic survey observation period, data collection began between 8am and 10am and ended by 7pm (GMT + 13h) each day, with observation time recorded in GMT + 13h. When observing the tors we maintained a standard walking speed and only observed each section of a tor once. The observation time at each site was between 10 minutes and an hour, varying between sites and days because of the differences in tor formations at each site and the time taken to record observations. The first site for each day changed on a rotating basis, starting at the site adjacent to the first site of the previous collection day in an anti-clockwise direction. We visited each site once every day, rotating through sites in an anticlockwise direction.

Observation of a site started with circling of the site from 10-15m away, examining the tors and flat rock through a camera lens. We then slowly moved to within five metres from the site and circled again. Tors were observed in a spiral movement starting at surrounding ground-level exposed rock at the base of the tor and working up to the highpoint. Where it was safe to do so, the individual tors taller than the observer were climbed slowly to observe the top of the tor. No further observations of the sides of the tor were made after climbing the tor. Due to the structure of some of the tors, some areas were excluded consistently throughout the whole study because they were either unsafe to access or there was not a way to observe the area without disturbing it during the approach, including high overhanging ledges on the sides of tors.

The observations made throughout this period involved recording every grand and Otago skink that was sighted at the five sites. For each observation we recorded: the location; age-class estimate (adult or juvenile; **section 2.2.5**); number of skinks in the observation and, if there were multiple skinks present, the nature of the interaction (aggressive or peaceful); along with corresponding photos to identify individuals (**section 2.2.3**). Observations were made collaboratively by all team members over the first few days to establish consistent methodology before any observations were recorded independently by team members, and we periodically compared our estimates throughout the survey period to ensure data were recorded consistently.

An interaction was defined as an observation involving two or more skinks in close proximity. Interactions were categorised into four distance thresholds, which were estimated as the shortest distance between two skinks. Distances were judged from less than 3m away, using the original locations of skinks observed. If skinks were first seen at a greater distance, then the observers approached the location before estimating the distance between skinks. The original locations of skinks were possible to locate due to the detailed and varied nature of the ground cover and rock, with many lichens, mosses, small plants and distinct rocks throughout. The categories used in field observations were 1m, 30cm, 10cm and touching. Each interaction category includes all interactions that occurred at that distance or closer, so the 30cm distance threshold included all interactions in the 10cm and touching categories. For an observation to be recorded as an interaction there had to be a line of sight between each skink, for example: two skinks may have been 30cm apart but be on different layers of the tor or have an obstruction between them, such as a rock or plant, inhibiting a line of sight. Without a line of sight between two skinks it is not known whether they were aware of each other. Therefore, whether they were behaving in response to one another (**Figure 2.7**).

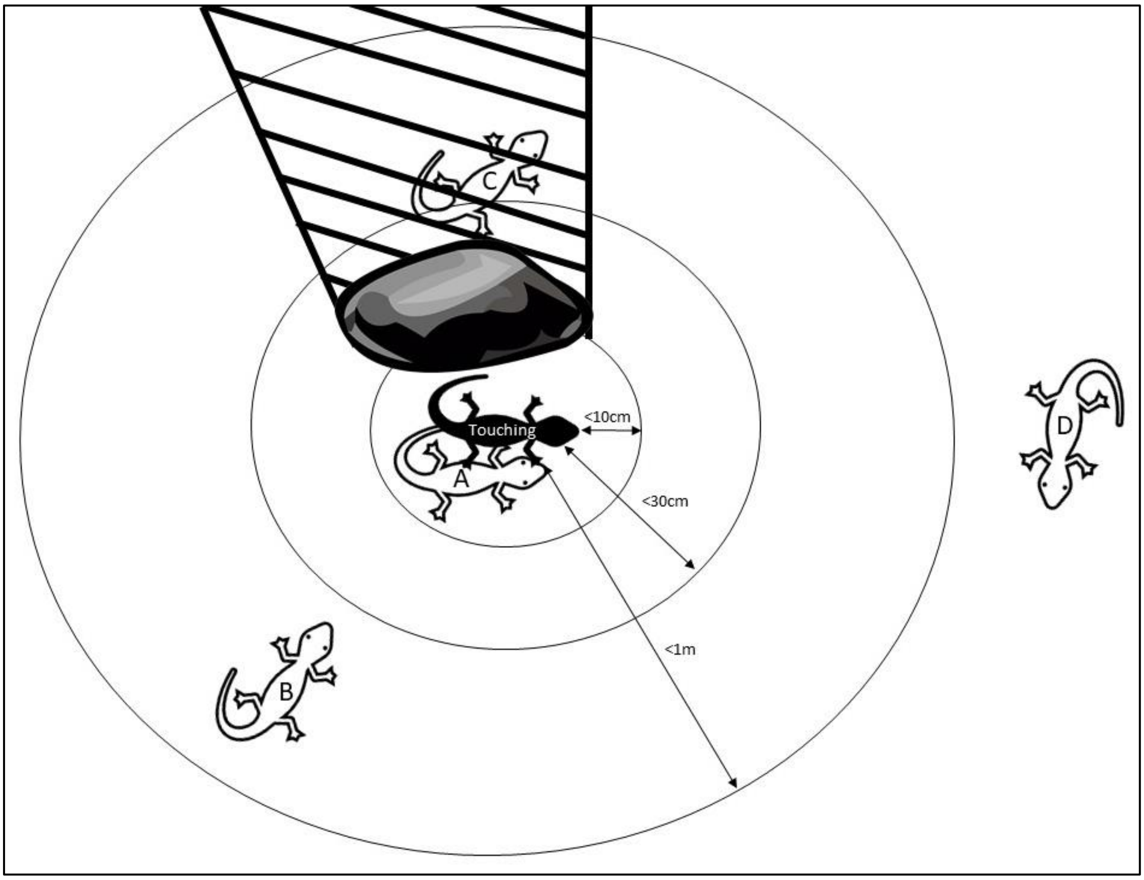


Figure 2.7. Diagram displaying the various proximity measures. Each ring represents a distance of 10cm, 30cm and 1m from the skink in question (solid black), with the smallest proximity measure (touching) being any skink that is physically touching that skink. All skinks within a determined distance (shown here as one of the circles) are considered to be interacting if they are within that proximity threshold, including those at smaller thresholds. The exception to this is if one or both skinks do not have a line of site between them, as it is not clear whether both are aware of the other. The area marked with thick dashed lines represents the area of view obscured by the rock in the diagram. In this scenario, the only skink considered to be interacting with the solid black skink when using a 30cm distance interaction threshold is skink A, as there is not a line of sight between the solid black skink and skink C, while B and D are greater than 30cm away. If a proximity threshold of 1m was used, both A and B are considered to be interacting with the solid black skink.

For each observation, skinks were recorded as interacting or not under each of the four proximity categories. If a skink was identified in two or more observations within the same observation period then only data from the first observation was included in analyses.

An interaction was also classified as peaceful or aggressive. Peaceful interactions were defined as an interaction that did not appear to induce an aggressive reaction from either individual, for example two skinks basking in close proximity while both lying flat against the substrate. An aggressive interaction was defined as an interaction consisting of the display of an aggressive or submissive behaviour or both. Aggressive behaviours observed included: biting, push-up position (**Figure 2.8**), tail wagging or sudden approach towards another skink resulting in displacement or avoidance behaviour from the other skink.

Figure 2.8. Demonstration of the push-up behaviour, a sign of an aggressive encounter, displayed by an adult grand skink at the Wildlife Site, Macraes. Photograph taken by Penny Jacks, 2019.

Submissive interactions were determined when aversion was observed or there was movement of a skink away from another in direct association with a behaviour from the aggressor. Submission was also recorded when a skink increased its speed of movement when moving from or past a skink in view then slowing in speed once out of view of that skink, if other reasons such as feeding and aggression towards others could be ruled out.

2.3.2 Diet observations

Throughout this period, additional observations were recorded separately if consumption of food items was observed, including lichens, insects and berries. If the opportunity was available, photos were taken to capture these observations as well as a full description of the event. Records of these dietary observations are presented in **Appendix 1**.

2.3.3 Photographic identification

Individual Otago and grand skinks have unique patterns that cover the whole skink, which allow them to be reliably identified by eye from photographs (**Figure 2.9**).

Figure 2.9. An example of photographic identification of individual Otago skinks and grand skinks by eye. Using the unique patterns, “a” can be identified as the same skink as “b”, and “d” is the same skink as “f”. Coloured squares of the same colour surround approximately the same area on each of the skinks, indicating examples of markings used to recognise individual

skinks. Photographs taken at the Wildlife Site, Macraes by Penny Jacks and Ricardo Rocha Mello, 2019.

Photographic identification was used to identify individual skinks involved in each observation in order to perform social network analysis. To identify each skink a photographic library was created cumulatively for each site, with photographs from every new observation compared to photographs of all individuals previously identified as unique and added to the library if deemed to be a new individual. This identification method is standard practise for non-invasive DOC census surveys of these two species and is a reliable tool (Germano 2007; Reardon 2012). The unique patterning on Otago and grand skinks is stable through time, with recognisable change in just 2% of the population studied by Reardon et al. (2012) between years. Changes in skink appearance in this 2% were at the scale level and did not result in unrecognizable change in the overall pattern on the skink. Therefore, making it a reliable identification method.

Whenever possible, photos were taken of the full body, top and sides, to allow individuals to be identified at a variety of angles. Any area of the skink, apart from the tail, could be used for identification. A pattern match was found at a minimum of two sections of the body before it was confirmed as the same individual. A skink was only confirmed as a unique individual if both sides of the skink were identified as belonging to the same skink and were different from every other skink in the library. There were 17 observations that did not have usable photographs, in which case these observations were excluded from the dataset. There were three skinks that could not be confirmed as unique skinks as the photographs taken were only of a small area on the body, so were also excluded from the dataset.

2.3.4 Capture sessions

Seven capture sessions took place in November and December of 2019 in order to gather information on body size, body condition, sex and age. Skinks were captured around the neck via noosing using a thin hollow metal tube and fishing line as described by Reardon and Norbury (2004). Skinks were also caught by hand where possible. Only skinks that were out of crevices or close to the edge of crevices were captured; no stone turning was done to avoid damage to skinks. Skinks were held in cotton bags in the shade until they could be processed. Masking tape was used to mark the capture location of each skink with a corresponding bag number, allowing the skinks to be released back to their original location. Skinks were weighed using a Pesola spring balance (to the nearest 0.5g). Vernier callipers were used to measure head width (to the nearest 1mm). A ruler was used to measure snout-vent length (SVL), tail length and tail regeneration length where applicable (to the nearest 1mm). A skink was recorded as having tail damage if regeneration was present or a recent injury to the tail was evident, inflicted prior to handling. Sex was determined by first gently palpating the abdomen to check if the skink was pregnant, then via hemipene eversion if not determined to be pregnant. Small juvenile skinks were not sexed, as sex cannot be determined accurately until they begin to reach maturity.

2.3.5 Age classes

Age-class was determined by body size, using two categories: adult and juvenile. Skinks were categorized by eye throughout the observation period to avoid the disturbance involved with capturing lizards to take measurements. An age-class was given for each observation, from which the mode age-class was used for each skink. The accuracy of the mode age-classes were tested by comparing them to age-class categories described by Collen et al. (2009) for the subset of individuals who were also captured and measured during the capture sessions. Individuals with an SVL measuring at least 101mm in Otago skinks and at least 78mm in grand skinks were considered adults, with skinks below these sizes considered juveniles. Of the 52 skinks that were sighted on more than two days, that were also caught during the capture sessions, 94% of the measured age-classes matched the mode ages. The three mode age-classes that did not match measured ages were all within 10mm of the adult size category, one of these being just 2mm larger than the mode age category and the other two 10mm and 1mm below the mode age category. The 2mm discrepancy may have been due to growth during the lag time between the observation period and capture sessions. Since mode and measured age-classes matched for the majority of these skinks, mode age-class was used as skink age, with mode age-classes replaced with measured age-classes in the two skinks with measured age-classes (juvenile) below their mode age-classes (adult).

2.4 Social network analysis

In order to investigate the patterns of interactions at each site and network structure in the Otago and grand skink sub-populations I performed social network analysis. Social network analysis uses interactions observed between two individuals (nodes) to construct links (edges) indicating some level of interaction. This is repeated for all individuals in the population or sample until all interactions are represented by edges, thus creating a social network. The social network diagrams constructed in this study consist of nodes that each represent a unique skink and edges that represent at least one interaction between two skinks. These edges are weighted, increasing in thickness with the number of interactions between a pair of individuals. Only individuals that were sighted on three or more days throughout the study period were used in the network analysis to reduce the chances of including transient individuals.

The package asnipe version 1.1.11 (Farine 2018) was used in R version 4.0.1 (R Core Team 2020) to construct social networks for each site separately, including both species at each site. Initially networks were constructed for each of the four interaction threshold categories; 1m, 30cm, 10cm and touching. The simple ratio index (SRI) was derived for each pair of individuals in each network, which was calculated as the number of times a pair of skinks were observed together divided by the number of times they were seen independently, together and in other interactions (Croft et al. 2008). A SRI value is a number between 0 and 1, where 1 indicates that whenever two skinks were sighted they were always together, whereas a score of 0 indicates that two skinks were never seen interacting. SRI values formed the edges in the social networks. From this, network diagrams were made in igraph (Csardi & Nepusz 2006) using the function “plot.igraph”.

Networks with a proximity parameter of one metre and networks with a proximity parameter of thirty centimetres had a similar number of edges at two of the sites (**Table 2.1**). However, there was a substantial drop in the number of edges at four of the five sites when comparing networks with these more generous parameters to networks with a proximity parameter of ten centimetres and touching (**Table 2.1**). Thirty centimetres is the approximate total body length of an adult Otago or grand skink (Cree 1994), so considered the most biologically relevant of the two larger parameters. With thirty centimetres also being the more conservative measure of these two parameters, it was used in network comparisons. Touching was also used as a distance parameter when comparing site networks, due to the difference in nature between contact and non-contact peaceful interactions. Comparing both proximity parameters, thirty centimetres and touching, individuals that exhibited on-top or touching group basking behaviour, associated with courtship behaviour or family groups in Otago skinks (Elangovan et al. 2021), can be distinguished from non-contact group basking.

Table 2.1 The total number of edges calculated using the four proximity thresholds at each site, including both Otago and grand skink interactions.

Site	**Touching**	**10cm**	**30cm**	**1m**
6	66	92	112	114
17	2	2	8	8
33	12	16	20	40
125	4	22	36	68
137	6	6	38	54

As well as constructing network diagrams, five network measures were calculated for networks calculated from the 30cm proximity measure to gain more understanding about the sub-population structures. To explore how social and connected the skink sub-populations at each site were overall I calculated network density. Network density was calculated using the function “edge_density” in igraph, which is the total number of edges in a network divided by the number of edges it could potentially have if every individual interacted with every other individual. This value between 0 and 1 indicates the network is entirely connected if the value is 1; as this value approaches 0 the number of individuals interacting are few, with a value of 0 expected in solitary species.

To examine how often individuals belonging to each species or age class are interacting, I calculated strength using the function “strength” in igraph. Strength is calculated as the sum of the edge weights connected to a node, calculated for each node. A high value here indicates a high number of interactions with other skinks: a value could be equally as high in a situation where multiple interactions occurred between a couple of skinks or where fewer interactions occurred between many skinks. This measure can inform us about how often individuals are interacting. When the mean strength is calculated for a group it can be used to understand how many interactions occurred, indicating patterns of interaction commonality within demographics or species. However, to understand how many skinks are interacting within a group network, degree is more informative.

I calculated degree in order to determine the number of individuals each skink is interacting with, to give an idea of how interconnected each network or demographic is. This was done using the function “degree” in igraph, which gives a count of the number of edges connected to a node, calculated for each node. If this value is low (close to 0) for an individual then the individual, assuming it has been re-sighted many times, is likely to either be solitary or may interact with a couple of individuals only. In contrast, if an individual has a high degree value then it is interacting with many different individuals. When the mean degree is compared between types it is expected that a social population would have a high value, with the majority of members connecting with multiple group members.

The mean degree and strength were calculated for both species at the two interaction distance thresholds (touching and 30cm), and for the two age-classes within each species (30cm threshold only). The difference in mean degree and strength between age-classes and distance thresholds was compared using a randomisation test with 10000 permutations.

Clustering within a skink social network could reflect the nature of interactions occurring, for example: where interactions are based on family groups, a population would be expected to consist of distinct clusters of adults and juveniles; in contrast a less aggregative social system would be expected to have a highly connected network with little to no clustering. To determine whether networks were clustered I used the modularity function “cluster_walktrap” in igraph. This function calculates the most likely number of defined clusters present in the network and gives an overall modularity score for the network. The modularity score is a value between 0 and 1 that compares the density of edges within clusters with those between clusters. A score close to 1 is considered high and indicates distinct clusters with a low number of connections between clusters as might be seen if a population consists of distinct pairs, family groups or other small clusters of individuals; or repeated agonistic encounters between certain individuals only. In contrast, a score close to 0 indicates a lack of distinct clusters, which could result from a population that is not interacting or is highly interconnected. Modularity was tested for each network from a 30cm distance threshold.

The final network measure used was assortment using the function “assortment.discrete” in assortnet (Farine 2016), giving an assortativity coefficient between -1 and 1 as a measure of how likely individuals of a particular type (e.g. sex; males and females) are to interact with another individual of the same type. A value close to 1 indicates that individuals are more likely to interact with those of the same type. A value close to -1 indicates that individuals are more likely to interact with those of a different type. If individuals display no affinity for either type selected then this value will approach 0. Here assortment was used as a measure of how likely skinks were to interact with other members of the same species, in order to determine whether interspecific sociality exists between these two species, as well as if skinks tend to interact more often with skinks of the same age class. An assortment value close to 1 for age class could indicate that adult skinks tend to only interact with adult skinks, which may occur due to with mating behaviour, territoriality or perhaps avoidance of larger skinks by juvenile skinks. On the other hand, if parental care is taking place it would be expected that juveniles would interact with both adults and juveniles (siblings), resulting in an assortativity coefficient close to 0.

Both species were compared first to investigate whether the two species interact more often intraspecifically, interspecifically or interactions were likely randomly occurring. These types were then bisected to compare interactions of adults and juveniles of the same species as well as species differences within the two age-classes. The types compared within the networks constructed from 30cm interaction threshold data were: Otago skinks with grand skinks; juvenile grand skinks with juvenile Otago skinks; juvenile Otago skinks with adult Otago skinks; adult grand skinks with adult Otago skinks; and juvenile grand skinks with adult grand skinks.

The Benjamini-Hochberg method (Haynes 2013) was used to determine the significance of results for degree, strength, difference in degree and difference in strength. This method is used to calculate conservative critical values when the same test is repeated multiple times on different samples. This method calculates a significance threshold for each statistical test, to reduce the number of false discoveries when a test is repeated over simultaneous independent or dependent statistical tests. These values are calculated for each test separately by first ordering the original p-values from smallest to largest, multiplying them by the number of simultaneous tests and then dividing by the rank order.

2.5 Factors influencing interactions

Two Generalised Linear Mixed Models (GLMM) were used to test whether skink age, species, time of day or site (tor) had an effect on the occurrence and nature of interactions observed among skinks. The dataset used in these two models consisted of all sightings of Otago and grand skinks throughout the photographic survey period, excluding any skinks that were only sighted once during this 3-month survey period. R packages lme4 (version 1.1-21; Bates et al. 2015) and car (version 3.03; Fox & Weisberg 2019) were used in R version 4.0.1; (R Core Team 2020) to run these models.

For both models, the fixed effects included were: skink age-class (juvenile or adult), species (Otago or grand skink), time of day (morning (8:00 – 10:59; GMT +13), midday (11:00 – 13:59; GMT +13) or afternoon (14:00 – 19:00; GMT +13)) and site (6, 17, 33, 125 and 137). Tail damage and sex were not included as factors in the models because the sample size of skinks caught during the capture sessions, ranging from just 7 to 21 skinks at each site. Sex and the presence of tail damage were only determined for the skinks caught during these capture sessions. A smaller sample of these skinks caught had a known sex since some of these skinks were too young to be sexed.

The first GLMM was used to determine which of the fixed effects (skink age, species, time of day or site) influenced the probability of skinks interacting with each other (at a 30cm proximity threshold). An interaction threshold of 30cm was chosen here as it seemed the most appropriate for comparisons between both species. The 10cm and touching thresholds greatly reduced the number of interactions, while the 30cm and 1m thresholds gave a similar number of interactions at two of the sites and a smaller reduction of the number of interactions compared with the 10cm threshold at the other three sites (**Table 2.1**). With 30cm being the more conservative of these two larger thresholds (30cm and 1m) it was chosen to be used in this model. The choice for 30cm over 1m reduces the chance of falsely recorded interactions resulting from circumstantial proximity at prime basking locations. Thirty centimetres is also more biologically relevant for grand skinks than a smaller threshold, as they did not display the same touching group basking behaviour seen in Otago skinks. This proximity measure is similar to the 0.5m threshold used by Germano (2007) at the same field site.

The second GLMM model examined if the same list of fixed effects (skink age, species, time of day or site) influenced the probability of skinks being involved in aggressive interactions. This model included all skink observations from the dataset, both interactions and observations that were not interactions, with observations that involved aggression indicated using a binomial scale (0=no aggression, 1=aggression). The response variable in this model was whether or not an observation was an aggressive interaction, regardless of proximity. Interactions were determined by a proximity threshold of 1m since all interactions involving an aggressive display could be deemed an interaction.

Interactions between fixed effects time of day and species, age-class and species, and time of day and age-class were also considered in the final models. Time of day and species, and age-class and species interactions did not have a significant effect on either the probability of a skink being involved in an aggressive interaction or whether or not it was involved in an interaction. Therefore, these interaction factors were not included in the final models. However, there was a significant effect of the time of day and age-class interaction factor in both models, which was included in the final GLMM models. The response variables for these models were whether or not the skink interacted and whether or not the skink was involved in an aggressive interaction (interacted=1, did not interaction=0), so were modelled as a binomial distribution with a logit link. Individual identification number and date were included as random effects in both models to account for both individual skink behavioural differences and day-to-day variation in site conditions.

2.5.1 GLMM model checking

Singularity in the GLMM models was checked for using the function “isSingular” in package lme4. The result for both original models was that there was singularity in the models. The Bound Optimization by Quadratic Approximation (BOBYQA) optimiser was applied to both models to enable model convergence, which removed the singularity.

Collinearity was tested using the Variance Inflation Factor (VIF), which was calculated for each variable. All variables had a VIF value less than 11, with two sites having values greater than 9 (site 125 and site 137). Exploratory analysis indicated there was a slight correlation between time of day and site, with some tors having a greater number of observations in the morning than the afternoon or vice versa. This probably results from the structure and positioning of tors affecting heating time and shadowing, and thus basking opportunities. Patterns showed in the model output were as expected from preliminary exploration of the data, while both these variables are important factors, so they were both retained in the model.

Overdispersion in the models was tested using a dispersion parameter; there was no indication of overdispersal in the interaction (<30cm) GLMM ($c = 0.79$), whereas the aggression GLMM was slightly under-dispersed ($c = 0.40$).

2.6 Factors influencing tail damage

Tail damage was investigated as a possible indicator for the frequency of aggressive encounters in sub-populations of Otago and grand skinks. The probability of a skink having a damaged tail was compared between age classes, sexes and whether an individual was involved in at least one aggressive interaction, using a Generalised Linear Model (GLM). A subset of the dataset in **section 2.3**, made up of the 59 skinks that were caught during the capture sessions, was used for this analysis. Each row in this subset represented a unique skink, with aggression classified as a factor with two groups (0=was not recorded participating in an aggressive encounter, 1=participated in an aggressive encounter occurring at 1m or less) and the proportion of interactions occurring less than 30cm apart that individual was involved in (number of interactions the individual was involved in / total number of observations for that individual). The response variable was whether or not the skink had tail damage, observed as either regrowth present or an incomplete tail (0= complete tail, 1= tail damage), which was modelled as a quasibinomial distribution with a logit link due to it being binomially distributed. The predictor variables investigated were: whether or not the observation was involved in at least one aggressive interaction, the proportion of observations of the individual that were interactions, species (Otago or grand), site (6, 17, 33, 125 or 137), age (adult or juvenile), and the degree and strength of the skink in the 30cm threshold network as described in **section 2.4**. Sex was not included as a predictor variable as the sample size was too small, since sex could only be accurately determined in adults.

2.6.1 GLM model checking

Collinearity was checked for by calculating the Variance Inflation Factor for each variable, where all variables had a value less than 11, indicating low levels of collinearity in strength and degree. Through preliminary exploration of all response variables, no visible effect of collinearity was found. Dispersion was checked using a dispersion parameter, which gave a value of 1.02, indicating the model was not over dispersed.

Chapter 3

Results

A total of 244 skinks (146 Otago skinks, 98 grand skinks) were identified from the 1087 observations (423 involving Otago skinks, 671 involving grand skinks) in the dataset. The mean number of times an individual skink was sighted throughout the three-month observation period was 5.2 (SD=5.1), with a mean of 6.6 (SD=6.2) for grand skinks and 3.3(SD=2.7) for Otago skinks. Seven of these observations involved both Otago and grand skinks. Across all observations, 18.7% of observations were considered interactions (using a 30cm threshold). Although, this varied between species and sites (**Table 3.1**). Of the interactions occurring (30cm threshold), the proportion of Otago skink observations that were interactions ranged from 9% to 23% across the five sites and in grand skinks 0% to 9% across sites (**Table 3.1**). The number of skinks identified at the different sites ranged from 37 to 66 (**Table 3.1**). However, daily numbers sighted were much lower (**Table 3.1**), and this was also evident in the number of skinks caught during the capture sessions at each site (between 7 and 21).

Table 3.1. Summary of the numbers of skinks found at the five sites. “N” is the total count of skinks, “Mean daily count (SD)” is the mean number of skinks recorded at a site (irrespective of species), “Mean Sighted (SD)” is the mean number of times each individual skink was sighted (standard deviation), “Species (N)” is the count for the specified species, “Species/ N” is the proportion of the total number of skinks that are the specified species, “Adult (N)” is the adult count, “Juvenile (N)” is the juvenile count, “Male (N)” is the male count, “Female (N)” is the female count, “Sex Unknown (N)” is the count of skinks with an unknown sex, “$N_{interact}/N_{obs}$ 1m” is the proportion of observations that were deemed interactions at a threshold of 1m, “$N_{interact}/N_{obs}$ 30cm” is the proportion of observations that were deemed interactions at a threshold of “30cm, $N_{interact}/N_{obs}$ 10cm” is the proportion of observations that were deemed interactions at a threshold of 10cm, “$N_{interact}/N_{obs}$ t” is the proportion of observations that were deemed interactions when touching. Sex was determined for some skinks during the capture sessions, while the “Sex Unknown” category represents skinks that were not caught during these sessions or were too young to sex.

Site	**N**	**Mean daily count (SD)**	**Species**	**Mean Sighted (SD)**	**Species (N)**	**Species/ N**	**Adult (N)**	**Juvenile (N)**	**Male (N)**	**Female (N)**	**Sex Unknown (N)**	**$N_{interct}/N_{obs}$ 1m**	**$N_{interct}/N_{obs}$ 30cm**	**$N_{interct}/N_{obs}$ 10cm**	**$N_{interct}/N_{obs}$ touch**
6	50	8.2(5.2)	Otago	4.3(3.2)	49	0.98	17	32	1	1	47	0.31	0.23	0.18	0.07
			grand	3.0(0)	1	0.02	0	1	0	0	1	0	0	0	0
17	37	5.6(3.1)	Otago	2.4(2.1)	27	0.73	20	7	0	3	24	0.10	0.10	0.03	0.02
			grand	9.4(9.5)	10	0.27	9	1	3	2	5	0.08	0.06	0.02	0.01
33	53	9.0(5.4)	Otago	3.6(2.7)	45	0.85	26	19	7	4	34	0.23	0.11	0.07	0.04
			grand	6.8(6.2)	8	0.15	5	3	2	0	6	0.09	0.06	0	0
125	66	13.3(6.5)	Otago	3.0(1.9)	16	0.24	10	6	1	2	13	0.24	0.09	0.07	0.04
			grand	6.4(5.5)	50	0.76	24	26	3	5	42	0.23	0.09	0.04	0.01
137	38	11.0(4.6)	Otago	5.0(3.7)	8	0.21	6	2	1	2	5	0.26	0.17	0.09	0.09
			grand	9.3(6.9)	30	0.79	14	16	4	3	23	0.17	0.05	0	0

3.1 Factors influencing interactions

Otago skinks were significantly more likely to interact with other skinks than grand skinks, where skinks were considered to be interacting if they were within a critical proximity of 30cm (**Table 3.2**; **Figure 3.1**).

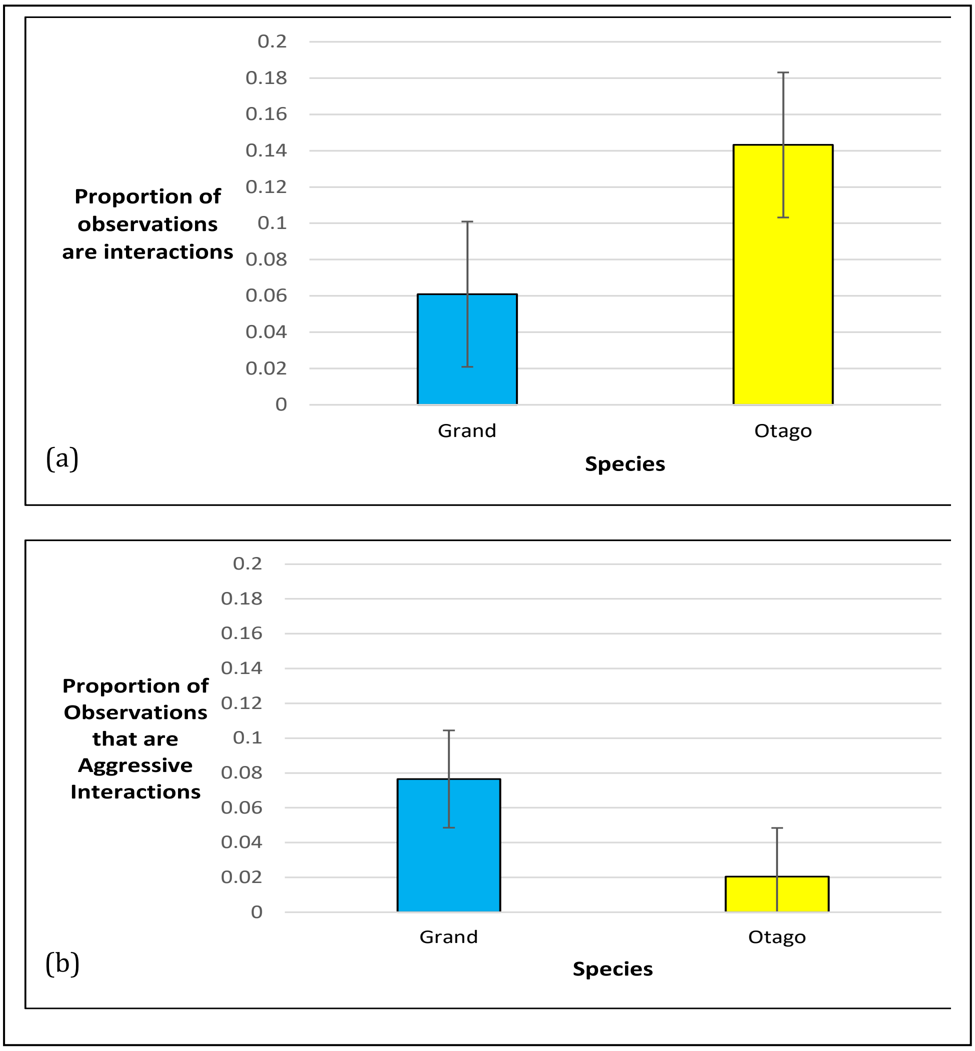


Figure 3.1 The proportion of observations that were interactions (a, 30cm threshold) and the proportion of observations that were aggressive interactions (b) for grand skinks (n=99) and Otago skinks (n=145). The proportion was calculated from the total number of observations for that species only. Error bars represent standard error.

However, Otago skinks were significantly less likely to be involved in aggressive interactions than grand skinks (**Table 3.2**; **Figure 3.1**). This difference in aggression is consistent with field observations of these species. The behaviour of grand skinks in the field was often observed as being avoidant and reactive to the presence of nearby skinks or skink activity, often displaying the push-up position. Otago skinks tended to display a relaxed posture lying flat on the substrate unless another skink, either Otago or grand skink, was displaying an aggressive behaviour within close proximity (pers. obs.).

The probability of interactions occurring significantly decreased throughout the day, with interactions most likely to occur in the morning and least likely to occur in the afternoon (**Table 3.2**; **Figure 3.1**). There was also a significant decrease in the probability of aggressive interactions occurring from midday to the afternoon (**Figure 3.2**).

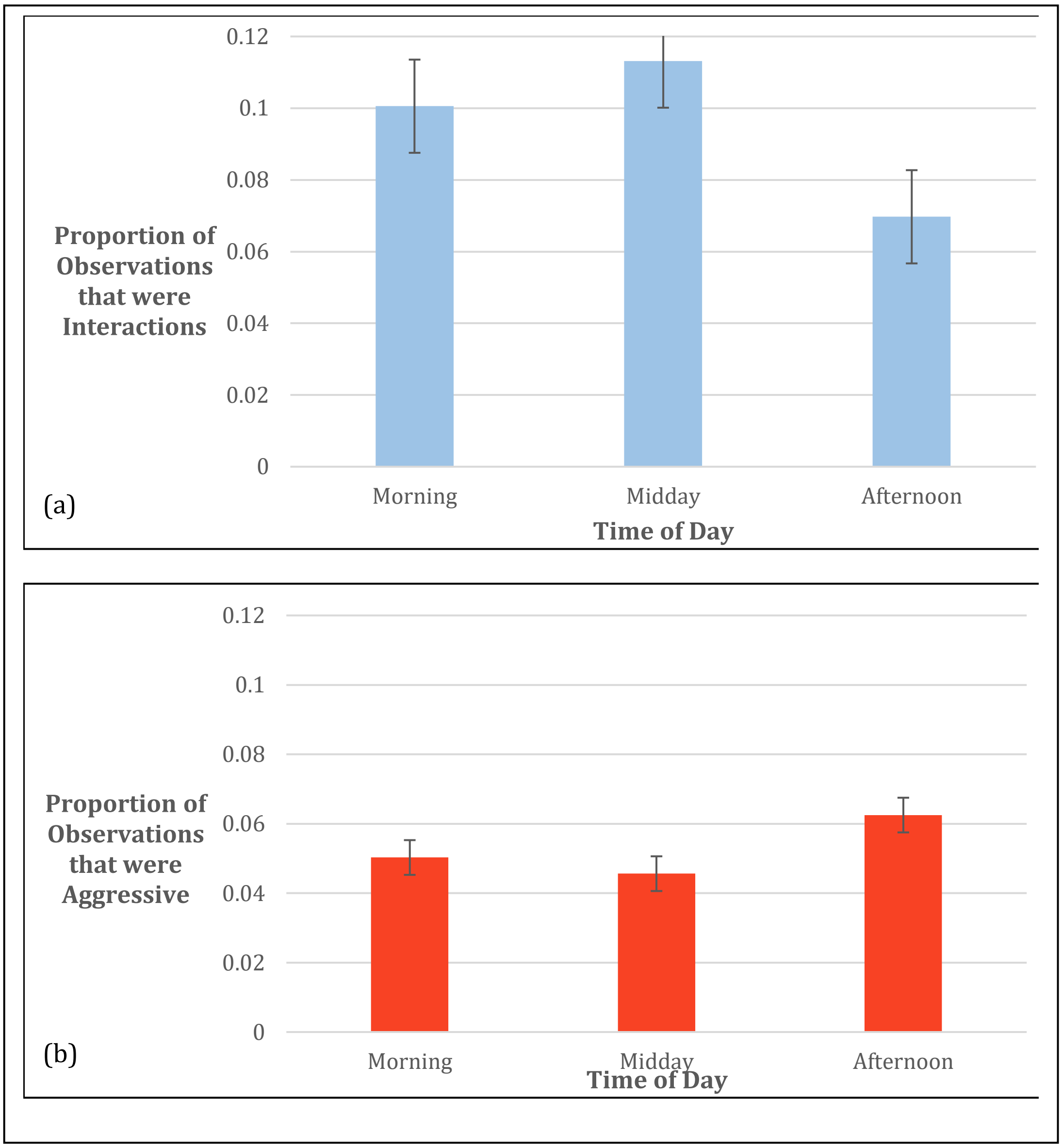


Figure 3.2 The proportion of total observations that were interactions (a; threshold 30cm) and the proportion of total observations that were aggressive interactions (b) at the three time categories (morning, midday and afternoon). This includes both grand skink and Otago skink populations (n=244). Error bars represent standard error.

The probability of interactions occurring varied significantly between sites, with interactions least likely to occur at sites 17 and 33 while most likely to occur at the Otago skink dominated site, site 6 (**Table 3.2**). However, there was not a significant difference in the probability of aggressive encounters occurring between sites (**Table 3.2**).

While the age-class of a skink did not affect the probability of it interacting, it did have a significant effect on the probability of a skink being involved in aggressive interactions, with adults more likely to be involved in aggressive interactions than juveniles (**Figure 3.3**).

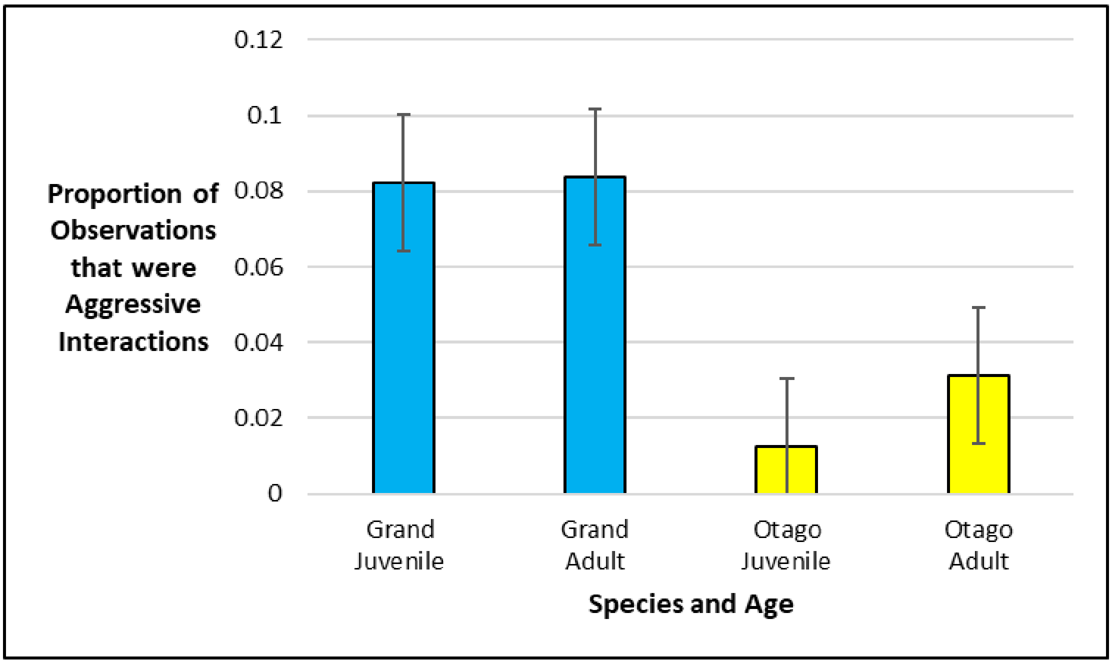


Figure 3.3 The proportion of observations that were aggressive interactions for juvenile and adult skinks by species (Otago and grand; n grand juvenile=47 , n grand adult =52 , n Otago juvenile=66, n Otago adult=79). The proportion was calculated from the total number of observations for that species only. Error bars represent standard error.

Time of day and age-class also had a significant combined effect on the probability of aggressive encounters occurring, with aggressive encounters significantly more likely in juvenile skinks occurring at midday, whereas the probability of aggressive encounters in adult skinks was highest in the afternoon and lowest at midday (**Table 3.2**).

Table 3.2 Results from two GLMM analyses examining fixed effects: time of day, age, species, site and interaction factor between time of day and age (time of day:age); on interactions measured as <30cm and whether an observation was an aggressive interaction. Reference categories for: time of day is morning, age is juvenile, species is grand, site is site 6 and time of day:age is morning and juveniles. In the GLMM with interaction (<30cm proximity threshold) as the response variable, individual skink (variance = 0.15, Std Dev = 0.39) and date (variance = 0.37, Std Dev = 0.61) were included as random effects. In the GLMM with aggression interaction as the response variable, individual skink (variance = 0.18, Std Dev = 0.42) and date (variance = 0.60, Std Dev = 0.78) were included as random effects.

Interaction type	**Effect**	**Chi-square**	**p**	**Category**	**Model Coefficient**	**SE**
<30cm	Time of Day (Morning)	11.57	**<0.01**	Midday	-0.01	0.34
				Afternoon	-0.97	0.38
	Age (Juvenile)	0.70	0.40	Adult	0.33	0.39
	Species (Grand)	8.21	**<0.01**	Otago	0.70	0.24
	Site (site 6)	26.13	**<0.01**	17	-1.35	0.35
				33	-1.26	0.28
				125	-0.94	0.32
				137	-1.17	0.33
	Time of Day:Age (Morning:Juvenile)	4.86	0.09	Adult:Midday	-0.51	0.44
				Adult:Afternoon	0.28	0.48
Aggression	Time of Day (Morning)	0.57	0.75	Midday	0.77	0.63
				Afternoon	-0.30	0.70
	Age (Juvenile)	0.20	0.65	Adult	0.94	0.66
	Species (Grand)	11.42	**<0.01**	Otago	-1.45	0.43
	Site (site 6)	2.83	0.59	17	1.27	0.89
				33	1.00	0.86
				125	1.28	0.85
				137	1.01	0.86
	Time of Day:Age (Morning:Juvenile)	12.47	**<0.01**	Midday:Adult	-1.76	0.74
				Afternoon:Adult	0.15	0.79

3.2 Social network analysis

The sizes of the networks examined here ranged from 14 skinks to 41 skinks (**Table 3.3**). Of the five sites, there were only three Otago-grand edges (**Figure 3.4:** a & e), with a total of three aggressive interactions between adult skinks occurring and 6 peaceful interactions occurring within 1m.

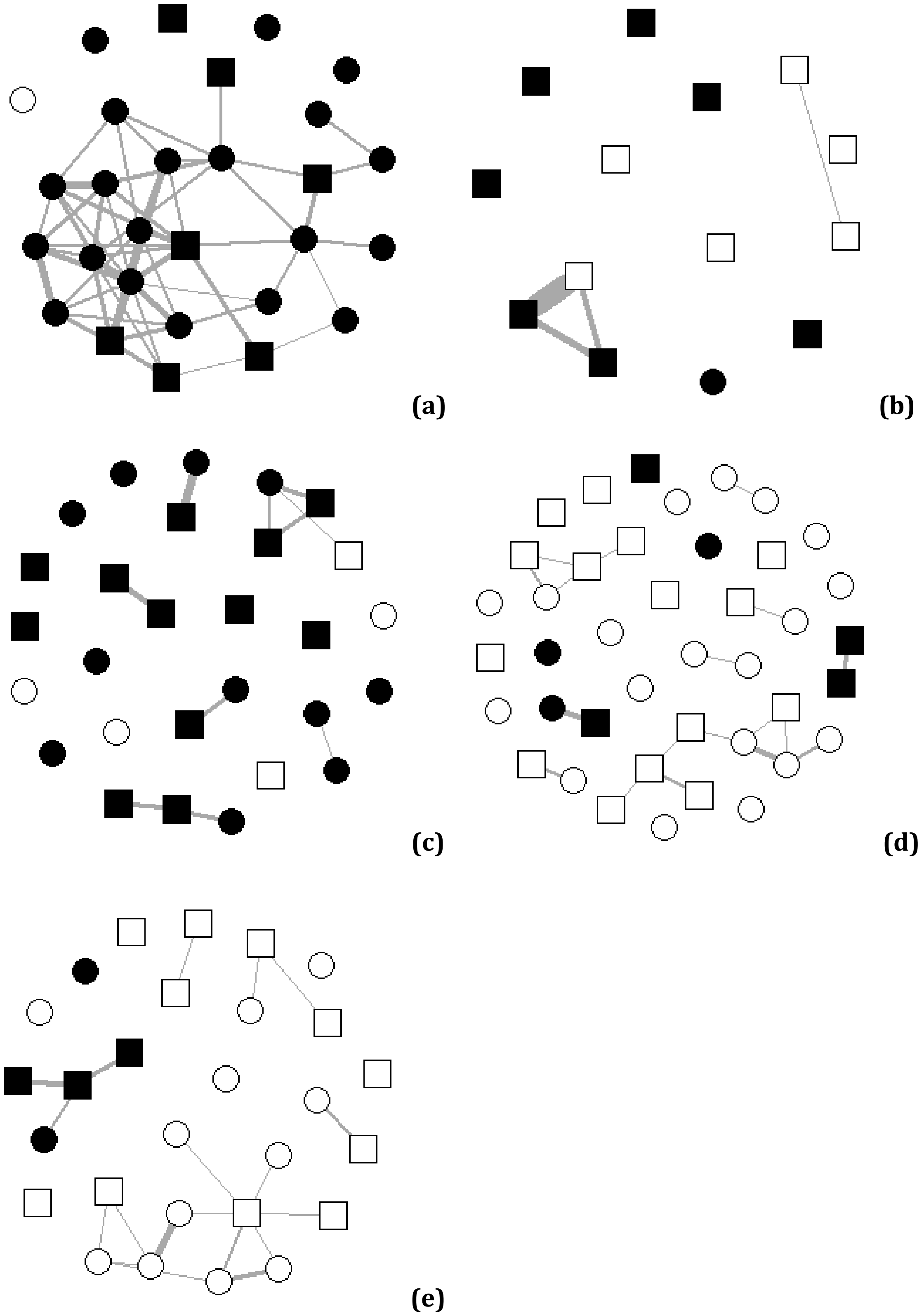
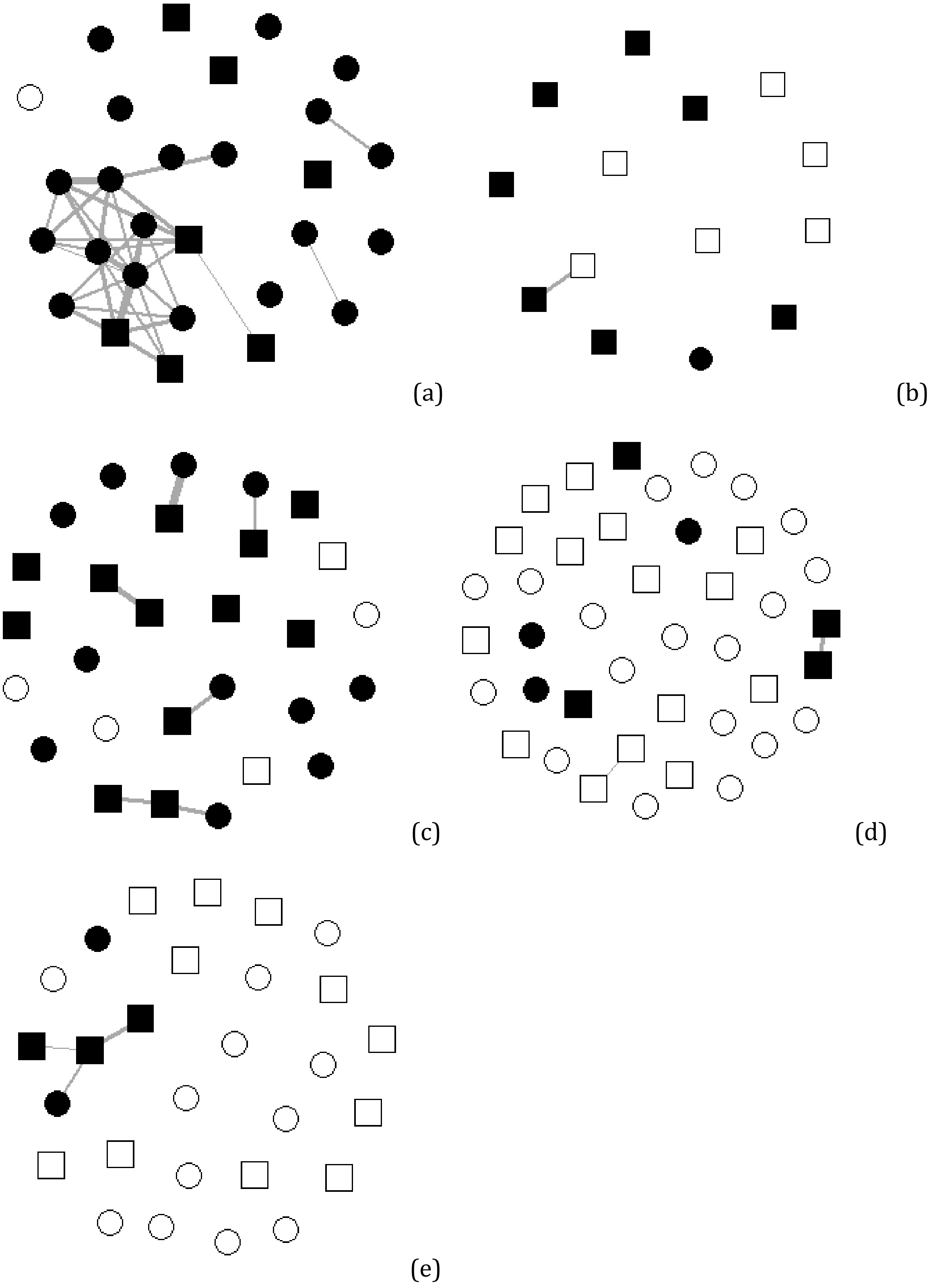


Figure 3.4. Network diagrams constructed using 30cm as the proximity threshold to determine if an observation was an interaction. (a) site 6, (b) site 17, (c) 33, (d) 125, (e) 137. White nodes represent individual grand skinks and black nodes represent individual Otago skinks. Square nodes represent adult skinks, and circle nodes represent juvenile individuals.

Otago-grand interactions were observed at three of the five sites (17, 33 and 137), with the sites without these interactions being the Otago dominated site and one of the grand dominated sites (sites 6 and 125). Three of these interactions occurred at a distance greater than 30cm or at least one of the skinks was only sighted once, so were not included as edges in these network diagrams (**Figure 3.4** & **3.5**).



(a) (b)

(c) (d)

(e)

Figure 3.5. Network diagrams constructed using skinks touching as the proximity threshold to determine if an observation was an interaction. (a) site 6, (b) site 17, (c) 33, (d) 125, (e) 137. White nodes represent grand skinks and black nodes represent Otago skinks. Square nodes represent adult skinks, and circle nodes represent juvenile individuals.

One of the grand skinks at site 137 participated in an aggressive encounter with an Otago skink as well as in a peaceful interaction with another Otago skink. One grand-Otago edge consists of peaceful interactions observed on three separate days at site 17. When the 30cm distance parameter was used, there was only one connection between grand skinks of the five sites, between two adult skinks (**Figure 3.5**: d).

Table 3.3. Summary of the numbers of skinks in the subset used in network analysis, excluding all individuals sighted on less than three days. N is the total count of skinks, Mean resight (SD) is the mean number of times each skink was re-sighted (standard deviation), Species (N) is the count for the specified species, $N_{species}$/ N is the proportion skinks that are the specified species, Adult (N) is the adult count, Juvenile (N) is the juvenile count, Male (N) is the males count, Female (N) is the female count, Sex Unknown (N) is the count of skinks with an unknown sex, $N_{interact}/N_{obs}$ 1m is the proportion of observations that were deemed interactions at a threshold of 1m, $N_{interct}/N_{obs}$ 30cm is the proportion of observations that were deemed interactions at a threshold of 30cm, $N_{interct}/N_{obs}$ 10cm is the proportion of observations that were deemed interactions at a threshold of 10cm, $N_{interct}/N_{obs}$ t is the proportion of observations that were deemed interactions when touching.

Site	**N**	**Species**	**Mean resight (SD)**	**Species (N)**	**$N_{species}$/ N**	**Adult (N)**	**Juvenile (N)**	**Male (N)**	**Female (N)**	**Sex Unknown (N)**	**$N_{interact}/N_{obs}$ 1m**	**$N_{interact}/N_{obs}$ 30cm**	**$N_{interact}/N_{obs}$ 10cm**	**$N_{interact}/N_{obs}$ touch**
6	28	Otago	6.4(2.3)	27	0.96	8	19	1	1	25	0.21	0.20	0.13	0.04
		grand	3(0)	1	0.04	0	1	0	0	1	0.00	0.00	0	0
17	14	Otago	4(2)	8	0.57	7	1	0	3	5	0.03	0.03	0.00	0
		grand	13(5)	6	0.43	6	0	3	2	1	0.03	0.01	0	0
33	28	Otago	5(2.1)	23	0.82	12	11	6	3	14	0.13	0.08	0.07	0.06
		grand	8(5)	5	0.18	2	3	2	0	3	0.02	0.00	0	0
125	41	Otago	3.9(1.1)	8	0.20	5	3	0	1	7	0.15	0.07	0.07	0.03
		grand	8.5(4.7)	33	0.80	15	18	1	5	27	0.12	0.07	0.03	0
137	28	Otago	6(2.8)	5	0.18	3	2	1	2	2	0.15	0.15	0.11	0.11
		grand	11(5.8)	23	0.82	11	12	4	3	16	0.10	0.06	0	0

The proportion of skinks connected in a network was highest at the Otago skink dominated site, with a network edge density higher than any other site (**Table 3.4**). The site with the lowest network edge density was the grand skink dominated site 125 (**Table 3.4**).

Mean strength and degree differed significantly between Otago and grand skinks at site 137, where both the mean degree and mean strength were higher in Otago skinks than grand skinks when using the touching proximity threshold (**Table 3.4**). There was one small cluster of four Otago skinks interacting at this site. However, no grand skinks were seen touching here. In addition, at site 125 mean strength differed significantly between species in the network using touching as the proximity measure, with strength slightly higher in Otago skinks than grand skinks (**Table 3.4**). This site had the only grand-grand touching interaction involving an aggressive encounter. Only one pair of Otago skinks touching at site 125, which occurred on two occasions. There were no significant differences in mean degree or strength between Otago and grand skinks at any of the other sites.

There was no difference in the mean degree and strength between adults and juvenile skinks of the same species within any of the networks (**Table 3.5**). The number of edges was not high enough for both species at a single site to allow for comparisons between the same age classes of the two species at any of the sites (**Table 3.5**).

Table 3.4. Difference between Otago and grand skink network mean degree, mean strength, and edge density. These values are calculated from networks constructed from observations deemed interactions at 30cm apart and touching. P-values are based on a randomised two-sided test with 1000 permutations. A "-" is used where there was not a large enough sample size to make a calculation.

Site	**Interaction parameter**	**Difference in degree means**	**p**	**Difference in strength means**	**p**	**Edge density**
6	<30cm	-	-	-	-	0.15
	touching	-	-	-	-	0.09
17	<30cm	0.167	0.942	0.005	0.120	0.04
	touching	-	-	-	-	0.01
33	<30cm	0.626	0.302	0.081	0.110	0.03
	touching	0.513	0.614	0.067	0.210	0.02
125	<30cm	0.370	0.800	0.014	0.758	0.02
	touching	0.227	0.274	0.03	**0.046**	<0.01
137	<30cm	0.191	0.562	0.038	0.898	0.05
	touching	1.200	**<0.001**	0.094	**<0.001**	0.01

Table 3.5. Difference in mean degree and mean strength between adult and juvenile skinks when split by species (interaction parameter <30cm). Here "O" represents Otago skink and "g" represents grand skink. "Sum of edges" indicates the sum of edges between skinks, categorized into grand skink intraspecific "g with g", Otago skink intraspecific "O with O" and interspecific "O with g" edges. A "-" is used where there was not a large enough sample size to make a calculation. P-values are based on a randomised two-sided test with 1000 permutations.

Site	**Difference in degree (O adult vs O juvenile)**	**p**	**Difference in degree (g adult vs g juvenile)**	**p**	**Difference in strength (O adult vs O juvenile)**	**p**	**Difference in strength (g adult vs g juvenile)**	**p**	**Sum of edges**		
									g with g	**O with O**	**O with g**
6	0.59	0.72	-	-	0.06	0.61	-	-	0	63	0
17	-	-	-	-	-	-	-	-	1	1	2
33	0.28	0.82	-	-	0.04	0.43	-	-	0	9	1
125	-	-	0.34	0.83	-	-	0.01	0.37	16	2	0
137	-	-	0.05	0.19	-	-	0.04	0.66	16	3	0

There was high modularity at the site dominated by grand skinks (site 125; **Table 3.6**), with the number of groups at this site also high. There was a large proportion of skinks at this site not observed interacting, likely influencing this high modularity score as well as a small mean group size (mean group size = 1.58; site 125; **Table 3.6**). An Otago skink dominated site (site 33; **Table 3.6**) also had a high modularity score as the majority of skinks at this site were not seen interacting, while some pairs of Otago skinks were seen together on multiple days. This is reflected in the small mean group size for this site (mean group size = 1.47; site 33; **Table 3.6**) The Otago skink dominated site (site 6; **Table 3.6**) had a low modularity score. This is an indicator that the network at this site is more connected overall compared to the networks of other sites. However, the mean group size is similar to the other four sites, which range from 1.27 to 2.15 across sites (mean group size for site 6 = 1.87; **Table 3.6**).

When comparing age-classes by species and age-classes within species, the assortment values indicate that there is not a high probability for skinks to associate with other skinks of the same age-class (**Table 3.7**).

Table 3.6. Modularity, mean group size, number of groups (groups) and largest group size (max group size) based on networks consisting of both grand and Otago skinks at each of the five sites, using 30cm as the interaction threshold.

Site	**Modularity**	**Mean group size**	**Max group size**	**Number of groups**
6	0.18	1.87	7	15
17	0.07	1.27	3	11
33	0.79	1.47	4	19
125	0.80	1.58	5	26
137	0.68	2.15	6	13

Table 3.7 Assortment values comparing juvenile and adult skinks by species (Otago and grand), as well as species difference overall and by age-class (juvenile and adult) for networks calculated using a 30cm interaction threshold.

	Otago juvenile vs adult			**Grand juvenile vs adult**			**Adult grand vs Otago**			**Sum of edges**		
Site	**Juvenile**	**Adult**	**P**	**Juvenile**	**Adult**	**p**	**Grand**	**Otago**	**p**	**Grand**	**Otago**	**Both**
6	0.59	0.05	0.48	-	-	-	-	-	-	0	63	0
17	-	-	-	-	-	-	-	-	-	1	1	2
33	0.06	0.34	0.65	-	-	-	-	-	-	0	9	1
125	-	-	-	-	-	-	-	-	-	16	3	0
137	0	0.77	0.20	0.39	0.10	0.96	0.29	0.71	0.10	16	2	0

3.3 Factors influencing tail damage

Tail damage was recorded in 33 of the 59 skinks caught during the capture sessions, with variation in the number of skinks that had damaged tails at each site (percentage of skinks with tail damage: site 6 = 0, site 17 = 87.5%, site 33 = 60.0%, site 125 = 35.7%, site 137 = 69.2%). The probability of a skink having tail damage was significantly different between sites, where the site with the highest ratio of Otago skinks to grand skinks had a much lower probability of tail damage than the other four sites (**Table 3.8**). This pattern is evident in the percentage of skinks with tail damage, with the population consisting of 98% Otago skinks having 0 skinks with tail damage, while the other sites had varying percentages of skinks with tail damage (**Figure 3.6**).

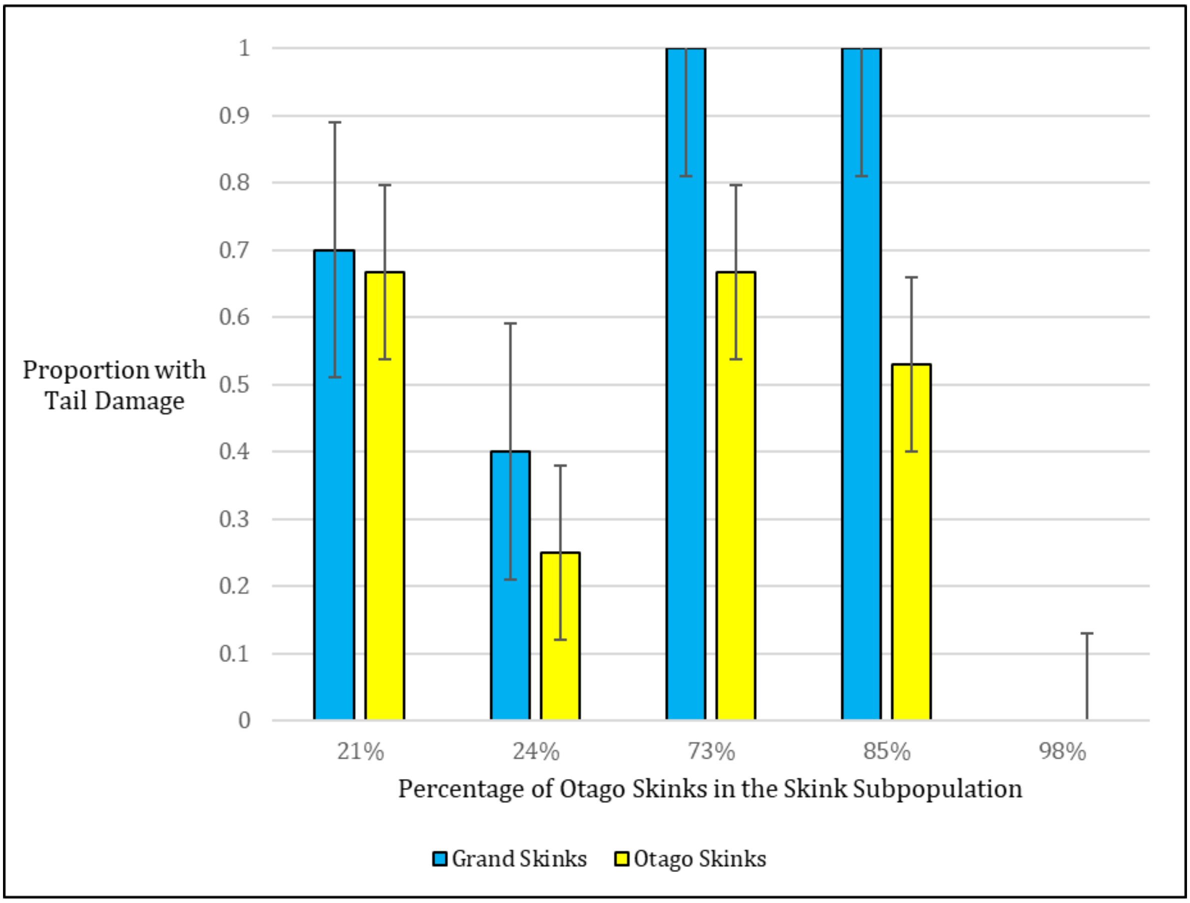


Figure 3.6 The proportion of skinks with tail damage at each of the five site percentages of Otago skinks, calculated as a percentage of the combined total of grand and Otago skinks found at that site (n= 50, 37, 53, 66 and 38). Proportions are calculated as the number of skinks with tail damage of a particular species (grand or Otago), from the subset of skinks caught during the capture sessions. Error bars indicate the standard error.

However, the standard error for all sites is very high (SE=1739), indicating that this result may not be representative of the pattern in the true populations, as the sample sizes were small at each site.

Age-class also had an effect on the probability of tail damage, where adult skinks were significantly more likely to have tail damage than juvenile skinks (**Table 3.8**; **Figure 3.7**).

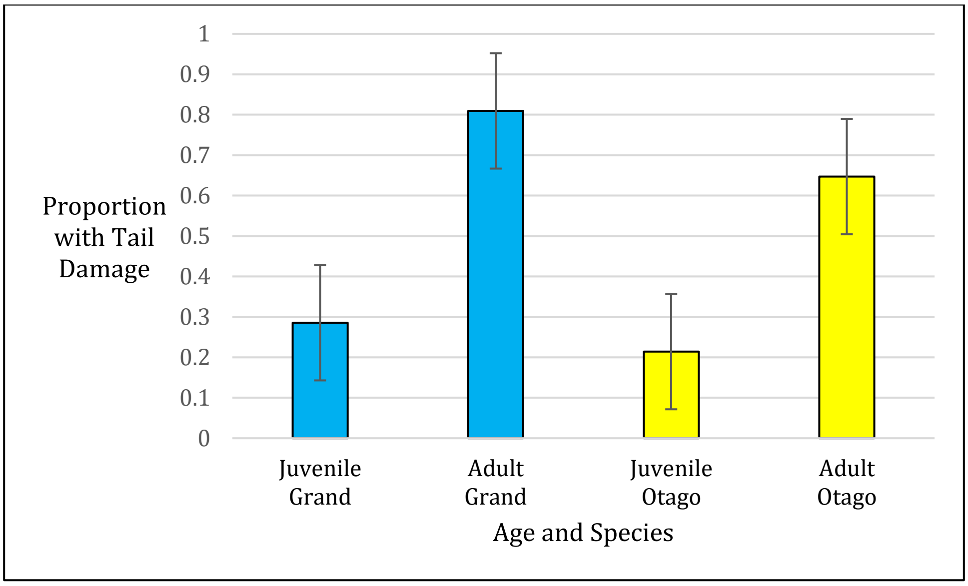


Figure 3.7 The proportion of adult and juvenile skinks split by species with tail damage, from skinks caught during the capture sessions. Proportions were calculated from the total number of skinks within each subset (juvenile grand skinks n=47, adult grand skinks n=52, juvenile Otago skinks n=66, Adult Otago skinks n=79). Error bars represent standard error.

The probability of a skink having tail damage was not correlated with either whether or not a skink participated in interactions or participated in aggressive interactions, nor the network node strength or degree (**Table 3.8**). There was also no significant difference in incidence of tail damage between Otago and grand skinks (**Table 3.8; Figure 3.8)**.

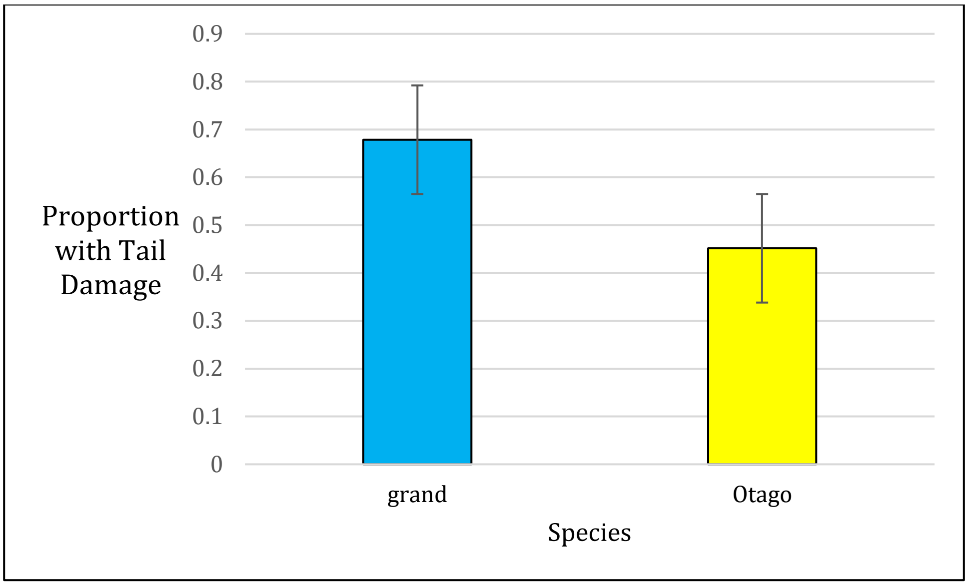


Figure 3.8 The proportion of grand skinks (n=99) and Otago skinks (n=145) with tail damage from skinks captured during the capture sessions. Proportions were calculated from the total number of skinks caught for that species. Error bars represent standard error.

Table 3.8. Model coefficients for fixed effect factors in a GLM examining the effect of species, whether an observation is an interaction using threshold <30cm, and age on the presence or absence of tail damage. The reference categories are as follows: species is grand, age is adult, aggression is none, site is site 6.

Factor		**Model Coefficient**	**Standard Error**	**P value**
Species (grand)		-1.24	0.26	0.08
<30cm interacting		-3.77	3.44	0.72
Age (adult)		-2.68	0.92	**<0.01**
Aggression (no)		0.40	0.85	0.77
Strength		10.58	12.52	>0.99
Degree		-0.69	1.09	0.17
Site	17	17.47	1738.61	**0.04**
	33	17.27	1738.61	
	125	14.61	1738.61	
	137	15.97	1738.61	

Chapter 4

Discussion

This study aimed to increase understanding of the interactions and social function of Otago and grand skinks, both intraspecifically and interspecifically, in a wild metapopulation. The aggregative behaviour and social behaviour of Otago and grand skinks was found to be contrasting. This is consistent with the idea that species with overlapping niches can drive behavioural partitioning (Bergmüller & Taborsky 2010). The Otago skinks in this study were found to be interacting more often than grand skinks under the parameters of this study, at all distance thresholds examined. Of the interactions that occurred, both grand and Otago skinks participated in peaceful interactions more often than aggressive interactions. However, the proportion of all interactions that were aggressive was higher in grand skinks than Otago skinks. Grand skinks were observed displaying avoidant and reactive behaviour towards nearby skinks, while Otago skinks tended to display a relaxed posture lying flat on the substrate unless another skink, either Otago or grand skink, was displaying an aggressive behaviour within close proximity. These contrasting behavioural patterns parallel the pattern of basking proximity we observed in both species, with peaceful interactions occurring between Otago skinks at closer proximity than grand skink. Most peaceful interactions between grand skinks occurred at 30cm or greater.

4.1 Intraspecific sociality of Otago skinks and grand skinks

In this study, Otago skinks were more likely to interact with conspecifics than grand skinks, with the majority of the interactions taking place between conspecifics in both species. This observation aligns with the observation made by Eifler & Eifler (1999), who found that grand skinks did not interact often. Otago skinks were less likely to be involved in aggressive interactions than grand skinks. In a previous study, female grand skinks were found to display aggression more often towards the breeding season (around March; Eifler & Eifler 1999), which began in the middle of my observation period. This mating behaviour likely contributed to the higher rates of aggression seen in grand skinks.

Modularity scores for each network indicate there are differences in the number of groupings present at each site. One of the sites dominated by grand skinks was found to have the highest modularity score and highest number of groupings, a result of many individuals not interacting with other skinks and many single interactions between two individuals. In contrast, the site with the highest percentage of Otago skinks (site 6) had low modularity with a smaller number of groups, resulting from a population consisting of a large inter-connected network with fewer skinks that did not interact. This was more consistent with the pattern observed in previous studies of an Otago skink population (Bovill 2018; Elangovan 2021). Another site that also had a higher number of Otago skinks than grand skinks (site 33) had a high modularity score due to fewer interactions observed at this site. This site consisted of multiple small and large tor sections, some separated by vegetation, with suitable basking locations spread throughout the site. Site 6 is dominated by a large single tor, with basking sites concentrated in a smaller area. This difference in habitat structure may be more conducive to the aggregation of skinks at site 6 compared with site 33.

The site with the highest percentage of Otago skinks, where only one grand skink was sighted, was found to have the highest number of connected individuals. This was the only site that had one large network of skinks that included the majority of Otago skinks at this site (30cm proximity parameter), consistent with networks observed in the Orokonui semi-captive population (Bovill 2018; Elangovan et al. 2021). However, the number of connected individuals in a subpopulation appears to decrease as the percentage of Otago skinks decreases, where grand skink dominated sites had fewer connected individuals. In the presence of high numbers of grand skinks, perhaps aggregative basking behaviour does not occur as frequently due to differences in the social behaviour of grand skinks and Otago skinks. Changes in social behaviour in response to the presence of grand skinks may reduce the number of peaceful interactions and create barriers between Otago skinks on the same tor. Limited resources, such as locations with earlier sun exposure, that sympatric species both require have been found to be sources of intraspecific competition in other lizard species (Žagar et al. 2015). Žagar et al. (2015) observed that resource (basking area) interception occurs between the two sympatric species (*Podarcis muralis* and *Iberolacerta horvathi)* in the form of interspecific agonistic interactions. Langkilde et al. (2005) observed that in a lab setting resource competition between two sympatric scincid species (*Egernia saxatilis* and *Eulamprus heatwole*) resulted in a change in behaviour of the smaller *Eulamprus heatwole*, which developed an earlier retreat behaviour when the *Egernia saxatilis* approached compared with the reaction time of *Eulamprus heatwole* when housed with a conspecific. With the populations of grand skinks and Otago skinks in the Wildlife Site enclosure thought to be at carrying capacity (Joanne Monks, Department of Conservation, pers. comm.), finite availability of prime microhabitats on the tor structures are likely to encourage competition and consequently agonistic behaviour between grand and Otago skinks. What should not be overlooked though, is sites with a larger percentage of grand skinks in this study also had a lower number of Otago skinks. With fewer conspecifics present, the probability of seeing Otago skinks interacting may have been reduced.

From this study, grand skinks do not appear to display the same sociality and social networks that has been documented in Otago skinks. It does not appear grand skinks form highly connected social networks as is seen in Otago skink populations. Grand skinks that did interact interspecifically tended to interact with only one or two other skinks. This is consistent with a study by Eifler & Eifler (1999), who found grand skinks do not tend to interact intraspecifically. In terms of selection of grand skinks for translocation or captive housing, it appears that randomly selecting individuals is not likely to affect the social environment of the chosen individuals or host population as they do not appear to form complex social networks. However, further research over multiple breeding seasons is needed in order to determine if stable pair bonds are formed between the few adult grand skinks that were seen interacting peacefully, to determine if it would be advantageous to keep these pairs together.

These two sympatric species have contrasting behaviour as consistent with other sympatric social lizard species *Egernia saxatilis* and *Eulamprus heatwole*. *Egernia saxatilis* is skink species that forms family groups similarly to the Otago skink (O'Connor & Shine 2006), whereas *Eulamprus heatwole* tends to display aggression often intraspecifically, forming dominance hierarchies (Kar et al. 2017). The aggressive larger *Egernia saxatilis* induces avoidant behaviour in the smaller *Eulamprus heatwole* (Langkilde et al. 2005). This parallels the avoidant behaviour exhibited by the grand skink in response to the presence of the Otago skink. It is not known whether grand skinks or Otago skinks also form complex dominance hierarchies, with intraspecific aggression occurring in populations of both species it would be worth investigating to gain a better understanding of the functioning of these intraspecific agonistic interactions.

4.2 Interactions between Otago and grand skinks in shared environments

There were only 3 edges in network diagrams (interactions proximity threshold 30cm) between Otago and grand skinks across all of the sites. These were a combination of peaceful and aggressive interactions between the two species. Agonistic interactions are common between sympatric lizard species, with mechanisms such as scent recognition used to distinguish between conspecifics and other species (López & Martín 2002). The few interactions between Otago skinks and grand skinks could be due to energy conserving behaviour involving territoriality and avoidance to prevent encounters and conflict between species. López and Martín (2001) found that agonistic encounters between Iberian wall lizards (*Podarcis hispanica*) were shorter and were less likely to become physical in lizards with a greater size difference. In the same study, when two of the same lizards had an agonistic interaction for a second time it was likely to be shorter than the previous, which was thought to be due to the ability to recognise individuals and remember the outcomes from previous encounters. Otago skink and grand skink populations may also possess the ability to avoid interspecific aggressive interactions through recognition of individuals and species, potentially reducing the number of interspecific interactions overall.

The peaceful interspecific interactions observed involved skinks basking within 30cm of each other. However, no peaceful touching occurred. These peaceful interactions were unexpected, since conflict is known to exist between these two species, as well as evidence of predation of grand skinks by Otago skinks (Tocher 2003).

In the oviparous long-tailed skink, *Mabuya longicaudata*, females perform parental care by protecting the nest from predators. Huang (2006) found that females can differentiate between sympatric lizards and snakes that prey on long-tailed skink eggs from harmless species, guarding eggs and reacting with aggression towards the predators. It is possible that the aggressive behaviour between grand skinks and Otago skinks could not only be the result of competition, but also a result of predation occurring between these species.

It appears from this study that Otago skinks and grand skinks behave similarly to other social skink species, including species in the *Egernia* genus. Aggression occurs between other sympatric skink species, while some have shown to develop avoidance and energy saving strategies in order to cohabit areas without compromising body condition and fecundity (Langkilde & Shine 2004, 2005, 2007; López & Martín 2002; Žagar et al. 2015).

4.3 Comparing juvenile and adult interactions

There was no difference found in the probability of interactions and the probability of aggressive interactions between adult and juvenile age-classes of both Otago and grand skinks. However, grand skinks of both age classes were more likely to be involved in agonistic interactions than both Otago skink age classes.

The behaviour of the two age classes in Otago skinks was as expected. The behaviour of juvenile Otago skinks was expected to be similar to adult Otago skinks since this species is known to engage in aggregative basking involving both adult and juvenile skinks (Elangovan et al. 2021). Both age-classes were found to be as likely to be involved in aggressive interactions. They were also found to interact between and within age classes, touching as well as group basking at a distance.

It was expected that there would be increased avoidance behaviour in juvenile grand skinks and increased aggression in adult grand skinks, as this species is not known to bask in juvenile-adult groups. However, both age-classes had a similar probability of partaking in an aggressive encounter. The aggressive interactions between adult grand skinks are likely to be related to mating behaviours, as female grand skinks have been observed increasing aggression during mating season when pursued by males (Eifler & Eifler 1999). Juvenile aggression is common in other lizard species, including the Grenada bush anole (*Anolis aeneus*)(Stamps & Krishnan 1994). In the veiled chameleon (*Chamaeleo calyptratus*) early-life interactions were found to directly impact the nature of interactions in later life stages (Ballen et al. 2014). Noble et al. (2014) has suggested social learning through demonstration by conspecifics may be more common in reptiles than previously thought. These aggressive interactions seen in juvenile grand skinks may an example of this social learning, perhaps practising aggressive and submissive behaviours.

Juvenile grand skinks were not found touching during an interaction with adult grand skinks, contrasting the aggregative basking seen in Otago skinks (Elangovan et al. 2021). However, adult and juvenile grand skinks were observed interacting at 30cm apart. In a larger lizard species ranging between 40-60cm in body length, the sleepy lizard (*Tiliqua rugosa*), an interaction distance of 14m has been used for social network analysis using GPS loggers to determine the position of individuals (Leu et al. 2016). This distance was decided as it is within the visual perceptual range of this species (Auburn et al. 2009). Therefore, though grand skinks do not display aggregative basking where conspecifics are touching, this species may also be a social lizard.

4.4 Factors influencing tail damage

Tail damage was not found to be associated with either aggressive behaviour or interactions. This indicates that other factors may have a greater influence on tail damage than the intraspecific social stability and nature of interactions occurring in these populations.

Adult skinks tended to have tail damage more often than juvenile skinks, as well as there being differences in the number of skinks with tail damage between sites. This is consistent with other studies, which found the probability of tail loss increased with age (Bateman & Flemming 2009; Chapple & Swain 2004). It would be expected that adult skinks have tail damage or regrowth more often, since the probability that a skink had encountered a situation in its lifetime that would trigger caudal autotomy would increase over time. The larger body size and slower locomotion of adult skinks compared to juvenile skinks is likely to make them easier targets for predation, as found with the metallic skink (*Niveoscincus metallicus*)(Chapple & Swain 2004). With increased predation risk, the risk of tail loss is likely to increase

There was variation in tail damage between sites, which could reflect variation in the quality of retreats, local predation events, evidence of recent or past changes in social dynamics or differences in environmental features that would trigger tail loss or prevent escape (Hare & Miller 2009). Throughout the photographic survey period starlings were present around some of the sites (6, 17 and 33) which are known to prey upon skinks (Reardon et al. 2012). Of these, sites 17 and 33 had two of the highest percentages of skinks with tail damage of the five sites, where all grand skinks examined for tail damage had tail damage at both sites (**section 3.3**). There may be potential to use tail damage as an indicator of predation events as the sites with the highest proportion of skinks with tail damage were also those closest to a starling nest. Further investigation is needed to determine whether caudal autotomy is common with starling predation, and how often these events are fatal. Caudal autotomy has been shown to result in reduced body condition and mobility in some lizard species (Althoff & Thompson 1994; Chapple & Swain 2002; 2004). If fatalities or caudal autotomy are common with starlings present, it could be advantageous to remove them from known Otago and grand skink locations to reduce the risk of population decline. Further, to expand this investigation to the effects of other known predators to determine whether tail damage could be used to indicate predation rates.

At these two sites, where 100% of grand skinks surveyed had tail damage, were also dominated by Otago skinks with 73% and 85% of the skink populations being Otago skinks. As the probability of tail damage is significantly higher here than at the two sites with low Otago skinks, agonistic interactions and predation events may be occurring between these species with Otago skinks “winning” these interactions more often. Further investigation into the interspecific effects of these two species sharing tors in the absence of predation is needed to better understand whether this is occurring, using a managed population such as the recently translocated populations at Mokomoko Dryland Sanctuary, Alexandra. This area of research could aid future decisions surrounding transportation, housing and translocation decisions, where these two species may be more likely to thrive separately than in shared habitat.

4.5 Conclusions

- From this study it appears social networks and aggregative basking occur in wild sub-populations of Otago skinks. Grand skinks on the other hand do not appear to display the same aggregative basking, nor do they appear to interact socially as often as Otago skinks. From this study it does not appear that grand skinks exist in complex social networks in the same way Otago skinks do.

- Grand skinks were more likely to interact aggressively than Otago skinks. However, both species were more likely to interact peacefully than aggressively. The nature of interactions involving juvenile skinks and involving adult skinks of the same species was similar.
- Grand skinks and Otago skinks rarely interact at a distance of 1m or less at these five sites. The interactions observed between these species were a combination of both peaceful and aggressive interactions.
- The nature of the interactions a skink is involved in does not appear to affect the probability of the skink having tail damage. However, the probability of tail damage varied between sites, indicating environmental factors may have a greater effect on tail loss than interactions with other skinks.

4.6 Management implications and future directions

It appears there may be a cost for populations of both grand skinks and Otago skinks when they share habitat. Though few interactions were observed between these lizards, the site with the highest percentage of Otago skinks had the most connected networks, behaving similarly to the semi-captive population studied previously (Elangovan et al. 2021). However, as the percentage of Otago skinks decreased the social networks separated into small clusters. If stable social networks have survival benefits, including reduced intraspecific conflict and enable an earlier predator response in Otago skinks, as has been found in the sleepy lizard (Bull & Pamula 1998), then understanding of conditions that encourage these to form would have great benefit to the species. Further research is needed to better understand the effects of these different population structures on population health. Determining whether there is a significant cost to grand and Otago skink sharing habitat could enhance reintroduction programs, giving both species a better chance to thrive in new habitat.

Otago skinks have now been found to form social networks in captive and wild populations. This knowledge can be applied to selection of skinks for translocation. A deliberate approach to choosing skinks would benefit both the source population and the survival of translocated skinks. If known social groups and stable pairs are selected then disruption and conflict in the source population may be reduced, for example separating mates may encourage skinks to seek out new mates, potentially resulting in conflict with skinks in stable pairs. Translocation of known stable pairs or clusters may also reduce chances of conflict and dispersal in the founding population, since, if individual recognition is similar to in *Podarcis hispanica*, social standing and bonds between skinks will already be established (López & Martín 2001).

However, from this study it does not appear that grand skinks have complex social systems like the Otago skink. Further study outside of the breeding season and using larger interaction distance thresholds are needed to confirm whether social bonds occur within small groups or pairs. If social bonds do not appear to be present in this species, a random selection method for choosing skinks to translocate would be suitable as the chance of conflict between any two individuals of the same type would be equal to any other.

From this study, tail loss does not appear to be an indicator for population health and social stability. Alternatively, it could be used as an indicator of the presence of some cryptic predators with low detectability. In this study there appears to be an association between the two sites nearest to nesting starlings and an increased probability of tail damage. Further investigation is needed to determine the probability of caudal autotomy in these skink species with various predators.

Grand skinks in this study were more likely to have tail damage than Otago skinks. However, the presence of other predators including starlings are likely to have contributed to this tail loss. Further investigation into the effects of habitat sharing with Otago skinks on tail loss in grand skinks in the absence of predation is needed to better understand whether interspecific agonistic interactions between these species are increasing the number of tail autotomy events. This area of research could aid future decisions surrounding transportation, housing and translocation of these sympatric species, where these populations may be more productive when kept separate.

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Appendices

Appendix 1: Diet observations

Otago skinks were observed hunting down and eating honey bee (*Apis mellifera*)(Fig A.1.1) and German yellowjacket (*Vespula germanica*) (Fig. A.1.2 & A.1.3). Grand skinks were observed hunting and eating cicada (species unknown)(Fig. A.1.4) and flies (species unknown)(Fig. A.1.5).

Figure A.1.1 Otago skink holding a recently caught honey bee (*Apis mellifera*). Photograph taken by Ricardo Rocha Mello, 2019.

Figure A.1.2 Otago skink gripping a struggling German yellowjacket (*Vespula germanica*). Photograph taken by Ricardo Rocha Mello, 2019.

Figure A.1.3 Otago skink holding the now deceased German yellowjacket (*Vespula germanica*). Photograph taken by Ricardo Rocha Mello, 2019.

Figure A.1.4. Grand skink transporting a struggling cicada (species unknown) to a hide where it was consumed. Photograph taken by Ricardo Rocha Mello, 2019.

Figure A.1.5. Grand skink in pursuit of a fly (species unknown). Photograph taken by Penny Jacks, 2019.