Social networks and social stability in a translocated population of Otago skinks (Oligosoma otagense)

Vanitha Elangovan1, Luke Bovill1, Alison Cree1, Joanne M. Monks1,2 and Stephanie S. Godfrey1

1Department of Zoology, University of Otago, Box 56, Dunedin, New Zealand
2Department of Conservation, Dunedin, New Zealand
*Author for correspondence (Email: vanithaelangovan21@gmail.com)

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Abstract: The social behaviour of New Zealand’s native lizards is poorly understood. We explored the social behaviour of the Otago skink (Oligosoma otagense), one of New Zealand’s largest and rarest species of lizards. The Otago skink has previously been observed in the wild in pairs and groups, but little else is known about its social structure. Regular photo surveys were conducted from November 2017 to October 2018 to identify skinks and the social interactions among them. Skinks were observed to be either solitary or interacting in groups consisting of two to eight individuals. Social network analysis was used to determine the strength of the interactions between adult males, adult females, subadults and juveniles. We assessed the stability of social interactions in the population over time by comparing the persistence of social interactions between seasons (summer, autumn/winter and winter/spring) while taking into account the size and composition of a social group. Interactions between adults and subadults were stable across autumn/winter and winter/spring whereas juveniles showed no stability in their interaction patterns during this time. During the course of the study, there was an overall stability in the social networks, indicating that the stability of social interactions present in the translocated population is largely driven by the adults and subadults in the enclosure. Our work suggests that incorporating an understanding of sociality into capture procedures may minimise disruption to social structures and ultimately improve outcomes of translocation.

Keywords: Ōrokonui Ecosanctuary, social behaviour, social network analysis, translocated population

Introduction

The study of sociality in lizards has traditionally focussed on their territorial and mating behaviour (Whiting & While 2017). Recently, however, growing evidence has shown that sociality in lizard systems is more than just an artefact of sexual selection and territoriality (Whiting & While 2017). Sociality in lizards occurs across a range of species, and aggregations can vary in size (Gardner et al. 2016). The reasons for lizard aggregations can include ecological or physiological drivers (Schutz et al. 2007). Aggregations that are ecologically driven generally occur due to limitations in key resources such as food, refuge sites and oviposition sites (Graves & Duvall 1995; Schutz et al. 2007). Alternatively, aggregations can also occur for defence against predators, or for reproductive or thermal benefits (Rabosky et al. 2012).

The emergence and evolution of sociality in reptiles have been strongly associated with species that exhibit two life-history traits: viviparity (Halliwell et al. 2017b), and longevity (Ridley et al. 2004). The physical proximity between a mother and her offspring in viviparous reptiles may favour an evolutionary transition towards group living (Halliwell et al. 2017b). In New Zealand, unsurprisingly given the relatively cool climatic conditions, many lizard species are both viviparous (Cree & Hare 2016) and long-lived (Cree 1994) making them an excellent group to investigate the occurrence of social behaviour. Understanding sociality in lizards can subsequently lead to the development of conservation strategies, given that social relationships within a population may have an influence on fitness measures such as reproduction and survival (Snijders et al. 2017).

Among New Zealand’s lizards, aggregative social behaviour has been described in several species including the Raukawa gecko Woodworthia maculata (previously Hoplodactylus maculatus) and Duvaucel’s gecko (Hoplodactylus duvaucelli), as well as the Otago skink (Oligosoma otagense) (Hare & Hoare 2005; Germano 2007; Barry 2010; ). Woodworthia maculata have previously been observed in an unusually large and densely packed aggregation of 94 individuals, comprising 39 juveniles, 11 males, and 44 females (Hare & Hoare 2005). The densely packed aggregation was observed in a bait box that had been deployed on an offshore island to control rodent incursions (Hare & Hoare 2005). On a smaller scale, Duvaucel’s geckos have been seen in aggregations of up...
to eight individuals in diurnal retreat sites, with aggregations usually consisting of a single male with one or more females (Barry et al. 2014). Similarly, aggregations of Otago skinks have been observed in wild populations (Coddington & Cree 1997; Germano 2007). Pairs were seen over a five-month study period for up to three weeks at a time (Coddington & Cree 1997). Whilst most pairs comprised a male and a female, some same-sex pairs have also been observed (both male-male and female-female) (Germano 2007). Larger social groups of three or four individuals, comprising both adults and juveniles have also been observed, in another study conducted over a period of five months, from December 2003 through April 2004 (Germano 2007). On several occasions, female-juvenile pairs were observed basking together (Germano 2007). However, it is unknown how long interactions last for, and whether there is any seasonality to these interaction patterns. In our study, we examined the social behaviour of Otago skinks in an outdoor enclosure over the course of 11 months.

The Otago skink is the largest and one of the rarest species of New Zealand lizards (Whitaker & Loh 1995; Hitchmough et al. 2016), and is classified as Endangered by IUCN standards and as Nationally Endangered under the national threat classification criteria of the Department of Conservation, New Zealand (Hitchmough et al. 2016). Otago skinks are a strongly saxicolous species, with a preference for schist rock outcrops that have extensive surfaces with numerous crevices, fissures and loose slabs (Towns & Daugherty 1994; Coddington & Cree 1997). Their populations are endemic to the tussock-grassland habitats of the Otago region in the South Island (Cree 1994; Tocher 2003).

Over the past few decades, the distribution of Otago skinks in the wild has declined, and their geographic ranges have severely contracted, leaving the species in relict populations (Whitaker & Loh 1995). The decline in numbers of Otago skinks can be largely attributed to habitat degradation (Whitaker & Loh 1995) and the invasion of mammalian and avian predators (Reardon et al. 2012). Currently, the only large population that exists is at Macraes, in addition to smaller wild populations in Central Otago near Lake Hawea (Reardon et al. 2012). The control of introduced mammals via the extensive use of mammal-proof fences and trapping has enabled the recovery of Otago skink numbers at Macraes (Reardon et al. 2012). Recently, individuals have been translocated into a fenced sanctuary near Alexandra (G. Norbury, Central Otago Ecological Trust, pers. comm.). In addition, a small translocated population of Otago skinks in an outdoor enclosure at Ōrokonui Ecosanctuary was established in November 2013; these skinks were translocated from a captive-bred population (Bogisch et al. 2016).

In this study, we aimed to quantify the aggregative behaviour, interaction patterns, and the stability of interaction patterns over time in Otago skinks at Ōrokonui. In addition, we documented the changes in interaction patterns in the population over time with and without the presence of juveniles. Skinks were considered interacting when they were seen touching, or were within 10 cm of one another (Bogisch 2014). An association, however, is defined as a stable interaction between skinks for an extended period of time (i.e. between seasons). As sociality is a fundamental aspect of living, studying the sociality of Otago skinks can be of value towards understanding the complex behavioural dynamics of a translocated population. Obtaining a better insight into the sociality of captive Otago skinks may then allow for the improved management of this population at Ōrokonui and in other potential captive or managed populations, including in situations that involve reintroductions or removal of individuals.

Methods

Study site

This study was conducted at Ōrokonui Ecosanctuary, a mainland reserve near Waitati on the South Island of New Zealand (45°46′S, 170°36′E). The ecosanctuary contains 307 hectares of remnant and regenerating native forest, as well as exotic grassland and shrubland (Bogisch et al. 2016). The reserve is surrounded by an 8.7 km predator-resistant metal mesh fence (Jarvie et al. 2015; Tanentzap & Lloyd 2017). The 2-m high fence was erected in 2007 and mammalian predators have almost completely been eradicated (Bogisch et al. 2016; Tanentzap & Lloyd 2017). On 20 November 2013 (late austral spring), 30 Otago skinks were released into an outdoor enclosure at Ōrokonui. The skinks were obtained from either zoos or private collections in the North Island (Bogisch et al. 2016). The oval-shaped enclosure has an approximate area of 109 m² (Bogisch et al. 2016) and consists of schist and other rock slabs, as well as tussocks and native shrubs, in order to closely resemble the skinks’ natural habitat. The rock tors in the enclosure provide the skinks with retreat sites that are 200–650 mm deep (Bogisch et al. 2016).

Reference photographs and sample collection

On 27 November 2017, 20 skinks (12 adults, 6 subadults, and 2 juveniles) were captured from the enclosure. The skinks were handled following procedures approved by the University of Otago Animal Ethics Committee (permit number D82/17). Skinks were caught using a lizard lasso (i.e. a loop of string with a sliding knot at the end of a pole) and were weighed and measured. Sexing of the skinks was based on the presence of hemipenal ridges in males (Holmes & Cree 2006). In this study, the snout-vent-length (SVL) of the skink determined whether it was an adult, subadult or juvenile. Skinks with an SVL of more than 100 mm were considered adults and skinks with an SVL of less than 70 mm were considered juveniles (Collen et al. 2009). Skinks whose SVLs measured between 70 mm and 100 mm were considered subadults (Collen et al. 2009). Other measurements recorded were each skink’s mass, tail length, and head width. The skinks were also photographed and the best photographs depicting the left- and right-hand sides of each skink, as well as the dorsal surface, were archived in a photo library for individual identification. Then the skinks were returned to the site of capture.

Visual Photographic Surveys

Field work for this study was carried out between 24 November 2017 and 24 October 2018, constituting three defined survey periods (seasons); Summer (24 November 2017 to 4 February 2018), Autumn/Winter (17 April 2018 to 14 July 2018), and Winter/Spring (28 July 2018 to 24 October 2018). In order to document the social relationships between Otago skinks, visual photographic surveys were conducted; these involved photographing the lizards that were seen in the enclosure, and recording the location, date and time of each observation. For each observation, location information included on which of the eight rock tors it had been seen and where on the rock tors it had been seen (top, middle or bottom). Photographs were taken using a Panasonic Lumix DMC-FZ1000, with a 16×
optical and a 4× digital zoom. Visual observations and the photographs enabled us to determine whether skinks were seen alone or interacting with one another in a group. Interactions were defined by whether skinks were seen touching or within 10 cm of another skink (Bogisch 2014).

In general, photographic surveys were conducted twice per day, three times a week, between 0930 and 1230 (NZ Standard Time). However, in the austral winter (June, July and August) surveys were conducted twice per day, once a week between 1200 and 1500 (NZ Standard Time), when the weather was warm enough for the skinks to bask. In total, 112 photographic surveys were conducted over 57 days. Two surveys (separated by at least one hour to allow skinks to resettle if disturbed) were conducted on each trip to Ōrokonui during 52 out of 57 days. On five days, only the morning survey was conducted due to unfavourable weather in the afternoon. The enclosure was walked around twice during each survey and the skinks were photographed (the second search was included to minimise the chance that skinks had been missed in the first round). Skinks that were re-photographed in the second round were eliminated from the data set during the processing of photographs. As a result, each individual and interaction were represented at most once in each survey (with up to two surveys each day) to avoid pseudoreplication.

### Identification of individual skinks

Individual skinks were visually identified by one researcher, with reference to a photo library, using unique features in their appearance, especially the distinctive curvilinear black and gold markings between the nose and foreleg region (Gebauer 2009; Reardon et al. 2012). For skinks that had no prior capture photographs (predominantly juveniles that were born in the enclosure in February 2018), individual identification was based on markings that were unique and stable over time. Photographs of the 11 juveniles born between February and April 2018, depicting their left- and right-hand sides, were then added to the existing photo library.

### Social Network Analysis

The association strength between individuals was measured using the simple ratio index (SRI) (Croft et al. 2016) in R (R Development Core Team 2016), using the package aspine (version 1.1.10) (Farine 2015). The SRI refers to the probability that a pair of individuals have been observed together given that one of the individuals has been seen, and this measure was derived for each pair of skinks. The SRI was calculated as the number of times two skinks in a pair were seen together divided by the total number of times each individual had been observed (regardless of whether it had been seen alone, or with any other skink) within each season. A network was formed for each season using the R packages aspine, version 1.1.10 (Farine 2015) and igraph, version 1.2.2 (Csardi & Nepusz 2006). The nodes represented the individual skinks, and the edges represented the interactions (SRI) between skinks. The thickness of the edges represented the strength of the interaction with an SRI value, with thicker edges having a higher SRI.

To describe the general structure of the networks, the density and clustering coefficient were calculated for each network. The density of a social network refers to the proportion of possible edges that are present between individual skinks (Faust 2006). A density of one would reflect a very densely connected population in which all skinks are connected to all other skinks in the population (Faust 2006). The clustering coefficient refers to the probability that the individuals directly connected to a particular skink are also connected to each other (McAssey & Bijma 2015). Therefore, a high clustering coefficient (close to one) would reflect a high level of cliques in a population (Makagon et al. 2012). To identify how often each age group (which was defined by the SVL of each skink) and sex was seen interacting with each other, the proportion of edges (interactions) that occurred between the different ages and sexes of individuals in each season was also calculated. These procedures were performed using the R package assortnet version 0.12 (Farine 2014).

To analyse the overall stability of the networks, the SRIs between pairs of skinks were compared between summer and autumn/winter, and between autumn/winter and winter/spring. In other words, the strength of association between each interacting pair of skinks was compared between the seasons, to test whether pairs of skinks that interacted strongly (or weakly) in one season, also interacted strongly (or weakly) in the next season. Simple ratio indices were also compared in the same way among only juveniles between autumn/winter and winter/spring, and the same was done for adults and subadults together, during the same period, allowing us to determine whether age-group had an effect on the overall stability of the network. All comparisons between networks over time were conducted using the analysis MRQAP with double-semi-partialing (R packages: aspine version 1.1.10) against 1000 permuted data sets. Statistical significance was set at $p < 0.05$.

### Results

In total, 1057 observations of skinks were made on 57 days from November 2017 to October 2018. Of these observations, 182 (17.2%) were of skinks in groups (an aggregation of 2 or more skinks). The median size of skink groups was 2 (range = 2–8). The different types of observations made, as well as the network density, clustering coefficient and the mean number of observations per skink are summarised in Table 1. The networks in all three seasons were considered to have

### Table 1. Types of observations during the three different seasons: summer, autumn/winter and winter/spring.

<table>
<thead>
<tr>
<th>Types of Observations</th>
<th>Summer</th>
<th>Autumn/winter</th>
<th>Winter/spring</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of skinks</td>
<td>19</td>
<td>32</td>
<td>32</td>
</tr>
<tr>
<td>Number of sessions</td>
<td>51</td>
<td>26</td>
<td>32</td>
</tr>
<tr>
<td>Number of observations</td>
<td>401</td>
<td>259</td>
<td>397</td>
</tr>
<tr>
<td>Number of interactions</td>
<td>90</td>
<td>50</td>
<td>42</td>
</tr>
<tr>
<td>Network density</td>
<td>0.140</td>
<td>0.178</td>
<td>0.074</td>
</tr>
<tr>
<td>Clustering coefficient</td>
<td>0.494</td>
<td>0.590</td>
<td>0.319</td>
</tr>
<tr>
<td>Mean observations per skink ± SD</td>
<td>26.3 ± 10.1</td>
<td>10.2 ± 5.7</td>
<td>13.6 ± 7.3</td>
</tr>
</tbody>
</table>
A large proportion of the network edges (interactions) observed in summer occurred between adult males and females (33.4%; Table 2). However, there was a slight increase in female-juvenile interactions (from 16.6% to 18% in winter/spring (Table 2). Interactions between adults (males and females) and subadults decreased from 12.6% in summer to 2% in winter/spring (Table 2). In winter/spring, however, the percentages of these interactions increased slightly to 7.8% and 5.2% for male-subadults and female-subadult interactions respectively (Table 2).

In autumn/winter, a large proportion of the interactions observed occurred between juveniles (51.0%), but these constituted a smaller proportion of the interactions observed in winter/spring (30.8%, Table 2).

Overall, there was a significant relationship between the interaction strengths (SRI) between pairs of skinks through time (summer to autumn/winter, Table 3, Fig. 2a; autumn/winter to winter/spring, Table 3, Fig. 2b). In each of these cases, there were a large number of pairs that never interacted in either season and a small number of pairs that maintained strong associations in each season, both of which contributed to the significant relationship between the two seasons. In order to determine how the 15 juveniles in the population contributed to the network stability, only the pairwise interactions of the juveniles were analysed (Fig. 2c). There was no significant relationship between the interaction strengths formed by juvenile skinks in autumn/winter and those formed in winter/spring (Table 3). When the presence of juveniles was omitted from the network, however, there was a significant relationship between the interaction strengths formed between the adults and subadults in autumn/winter with those formed in winter/spring (Table 3; Fig. 2d). In this comparison, there was also many pairs that never interacted in either season, and four pairs that maintained strong associations in each season, and these contributed to the significant relationship between the two seasons.

Discussion

The social network of Otago skinks in an outdoor enclosure at Ōrokonui Ecosanctuary showed a high degree of stability.

Table 2. Percentages of the different types of network edges (interactions) seen amongst Otago skinks at Ōrokonui Ecosanctuary. The various types of interaction are recorded for summer, autumn/winter and winter/spring.

<table>
<thead>
<tr>
<th>Interaction type</th>
<th>Summer (%)</th>
<th>Autumn/winter (%)</th>
<th>Winter/spring (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult Interactions</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male-male</td>
<td>4.2</td>
<td>1.0</td>
<td>2.6</td>
</tr>
<tr>
<td>Male-female</td>
<td>33.4</td>
<td>4.2</td>
<td>10.4</td>
</tr>
<tr>
<td>Female-female</td>
<td>0.0</td>
<td>1.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Adult and Subadult Interactions</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male-subadult</td>
<td>12.6</td>
<td>2.0</td>
<td>7.8</td>
</tr>
<tr>
<td>Female-subadult</td>
<td>12.6</td>
<td>2.0</td>
<td>5.2</td>
</tr>
<tr>
<td>Subadult-subadult</td>
<td>4.2</td>
<td>2.1</td>
<td>2.6</td>
</tr>
<tr>
<td>Adult-Juvenile Interactions</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male-juvenile</td>
<td>16.6</td>
<td>12.6</td>
<td>18.0</td>
</tr>
<tr>
<td>Female-Juvenile</td>
<td>12.6</td>
<td>18.8</td>
<td>18.0</td>
</tr>
<tr>
<td>Subadult-Juvenile</td>
<td>0.0</td>
<td>5.2</td>
<td>5.2</td>
</tr>
<tr>
<td>Juvenile-Juvenile</td>
<td>4.2</td>
<td>51.0</td>
<td>30.8</td>
</tr>
</tbody>
</table>

Table 3. Comparison of the interaction strengths (simple ratio index; SRI) observed between the different time periods for Otago skinks at Ōrokonui Ecosanctuary. Comparisons were made for the overall population, as well as for when juveniles were considered on their own. A comparison was also made for when adults and subadults were considered on their own. P-values that are significant (P < 0.05) are in bold.

<table>
<thead>
<tr>
<th></th>
<th>Overall: Summer vs autumn/winter</th>
<th>Overall: Autumn/winter vs winter/spring</th>
<th>Juveniles: Autumn/winter vs winter/spring</th>
<th>Adults and subadults: Autumn/winter vs winter/spring</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of skinks</td>
<td>19</td>
<td>32</td>
<td>13</td>
<td>19</td>
</tr>
<tr>
<td>Coefficient</td>
<td>0.212</td>
<td>0.072</td>
<td>−0.023</td>
<td>0.028</td>
</tr>
<tr>
<td>P-value</td>
<td><strong>0.001</strong></td>
<td><strong>0.003</strong></td>
<td>0.645</td>
<td><strong>0.025</strong></td>
</tr>
<tr>
<td>Stability between networks</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
</tr>
</tbody>
</table>
Figure 1. Social networks of Otago skinks at Ōrokonui Ecosanctuary. a) represents 19 skinks during summer. b) represents 32 skinks during autumn/winter and c) represents 32 skinks during winter/spring. The number in each square/circle represents the skink ID. Adult females are represented by white circles, and adult males as white squares. Subadults are represented by grey squares and juveniles are represented by grey circles. The sexes of the subadults and juveniles were unknown. The black lines between individuals on the networks illustrate the interactions between the skinks, and the thickness of each edge is indicative of the strength of associations (measured using a simple ratio index; SRI).

Figure 2. Comparison between the interaction strengths (SRI) observed between the different time periods for Otago skinks at Ōrokonui Ecosanctuary. The figures represent the comparison of interaction strengths (SRI) between all pairs of skinks (n = 32) in a) summer versus autumn/winter, b) autumn/winter versus winter/spring, c) autumn/winter versus winter/spring for juveniles only (n = 13 skinks), and d) autumn/winter versus winter/spring for adults and sub-adults only (n = 19 skinks). Each point on the graph represents a pair of lizards. The coordinate pair (0,0) indicates pairs of skinks that were never seen interacting in either season.
This stability appears to be mainly driven by the continuity of interactions formed by a small number of adult and subadult skinks through time. Additionally, a large number of skink pairs were consistently found to not interact across seasons. The interactions and the interaction strengths formed between juvenile skinks, on the other hand, showed a substantial reduction between autumn/winter and winter/spring. Since their initial release into the enclosure in spring 2013 (Bogisch et al. 2016), the adult skinks would have had time to familiarize with their environment and neighbours. As a result, this may have increased their awareness of who to associate with (and not associate with), therefore reducing stress and unwanted encounters with unfamiliar individuals (Godfrey et al. 2013).

The social network obtained in autumn/winter featured a cluster of juvenile skinks, with more than half of the interactions being made up juvenile–juvenile interactions. Of the 15 juveniles in the enclosure, two were born the previous season and had been present during sample collection in November 2017. The remaining 13 juvenile skinks were therefore likely to have been born between February and March 2018, similar to when parturition takes place in the wild (Cree & Hare 2016). In captivity, clutch (litter) sizes of Otago skinks have been reported to reach up to five to six juveniles (Collen et al. 2009). Hence, given their numbers, it is likely that the aggregated individuals observed in autumn/winter were from different clutches, and from multiple mothers. However, due to the lack of genetic information obtained, the relatedness between juveniles and the adult females could not be determined. The aggregations of juveniles observed in this study suggest that age may be important in explaining the aggregation patterns of Otago skinks. Aggregations of juveniles have been observed in various lizard species such as green iguanas (Iguana iguana) (Burghardt et al. 1977), thick-tailed geckos (Nephrurus milii) (Kearney et al. 2001), and other skinks such as the black rock skink (Egernia saxatilis) (O’Connor & Shine 2003). One plausible explanation for the clustering of juveniles could be attributed to group protection (Boykin & Zucker 1993). As juvenile skinks are especially vulnerable to danger such as predation from larger adult skinks in the population (Bogisch et al. 2016; Elangovan et al. 2019), it may be advantageous for them to aggregate into a group for increased protection (Boykin & Zucker 1993). In addition, as this species is active throughout the year, it is also possible that the aggregation of juveniles may be a consequence of shared use of overnight shelters, which could provide a thermoregulatory advantage in terms of reduced cooling rates (Rabosky et al. 2012).

Another explanation for the clustering of juvenile Otago skinks may be attributed to parental care. Among the other interaction types, the second most common interaction type observed in the population at Ōrokonui Ecosanctuary was between adult females and juveniles, followed by adult males and juveniles. The juveniles clustered in the enclosure were often seen associating with one adult male and one adult female. Parental care occurs in situations where the costs of parental expenditure are outweighed by fitness benefits for the offspring (Langkilde et al. 2007). Contrary to the situation in mammals and birds, however, parental care in lizards typically involves the offspring not being fed, but instead, protected (Somma 2003). One plausible pre-condition for the evolution of parental care in Otago skinks is viviparity. The live bearing of young in lizards has been found to increase parent-offspring interactions (Klug et al. 2012) and has been a crucial exaptation for the formation and stabilisation of kin-based sociality (Halliwell et al. 2017b). Increased physical interactions between parents, neonates and their siblings are made possible by viviparity and the subsequent lack of dispersal by offspring, and this could bring about family-based social structure (Shine 1988). This can then provide juveniles with protection against aggression from conspecifics and potential infanticide through added vigilance and defence from the parents (Langkilde et al. 2007). Females experiencing their postpartum period have previously been documented as having increased levels of aggression, especially when their young are at risk (O’Connor & Shine 2004). In addition to protection, offspring care could also provide neonates with better access to foraging, basking, and retreat sites (Bull & Baghurst 1998). Associations between parents and offspring have also been found to facilitate behavioural plasticity in offspring as demonstrated in Liopholis whitti (Munch et al. 2018).

In winter/spring, juvenile skinks, albeit still connected, were not heavily clustered in the network as they previously were in autumn/winter. The decrease in the number of interactions and the interaction strengths between juveniles could be attributed to dispersal, where juveniles might be emigrating away from their natal site or being chased away by territorial adults (Wolf 1994). In other skink species, juveniles have frequently been observed in groups consisting of either one or no parents, suggesting that with age, juveniles tend to disperse into social groups where they are less likely to be related to each other (Chapple & Keogh 2006). The dispersal of juvenile Otago skinks could be influenced by density and this may be important for a captive environment where there are high densities of skinks, such as the enclosure at Ōrokonui Ecosanctuary (Lena et al. 1995).

In the Ōrokonui population, we observed a reduction in the percentage of male–female interactions from summer to autumn/winter, followed by a slight increase in winter/spring. Mating in Otago skinks typically occurs in early autumn (Cree & Hare 2016) and observations for the autumn/winter season had begun on 17 April, during the mid-autumn period. Hence, it is possible that the mating period was completed before observations for the autumn/winter season had even commenced, resulting in the decrease in male–female interactions observed from summer to autumn/winter. It is also possible that males become more cryptic from summer to autumn/winter, whereas females continue to bask frequently in order to maintain optimal developmental temperatures for their offspring. The increase in male–female interactions from autumn/winter to winter/spring may be attributed to a secondary mating season in spring, a behaviour that has previously been observed in Oligosoma ornatum (Porter 1987). The increased proportion of male–female interactions during summer, prior to mating, could be a result of pair bonding during the pre-mating period. Extended associations during the pre-mating season have been observed in the sleepy lizard Tiliqua rugosa, where male–female pairs are found to frequently associate for approximately 8 weeks prior to mating (Bull et al. 1998). Thus, in our research, it is plausible that the high proportion of male–female interactions amongst Otago skinks may reflect pre-mating associations.

This study adds to our existing knowledge on the sociality of Otago skinks. Social behaviour had previously been observed in Otago skinks (Coddington & Cree 1997; Germano 2007), but little was known about the stability and structure of social interactions in these lizards. This study involves the longest duration over which sociality has been observed in Otago skinks; we documented interactions over an 11-month period, providing evidence towards the presence
of sustained relationships and group living in this species. This study has also observed group sizes of up to 8, and this is larger than previous recordings of 2 to 4. However, habitats and population densities can potentially affect the social behaviour of reptiles (Halliwell et al. 2017a). Therefore, it is important to acknowledge the artificial situation at Ōrokonui Ecosanctuary, where individuals are potentially forced into closer interactions, as opposed to the interactions formed within wild populations at lower density.

In general, skinks have been found to be socially competent and adaptable to novel social environments (Riley et al. 2018). At Ōrokonui, the overall stability observed within the Otago skink population is biologically representative of particular pairs of individuals having sustained relationships that last beyond the mating period, as well as pairs of individuals that never interacted with each other, despite their close spatial proximity. Identifying the presence of social stability within a captive population of Otago skinks could potentially be a first step towards incorporating considerations of their social organisation into their conservation management. Applied to a conservation translocation scenario in the wild, our work suggests that incorporating an understanding of sociality into capture procedures may minimise disruption to social structures and ultimately improve outcomes of translocation (Collen et al. 2009). Our research paves the way for taking an experimental approach in future translocations to determine if social structure does indeed affect translocation outcomes.

Author contributions

VE, SSG, JM & AC contributed to the study design. VE and LB collected the field data. VE and SSG conducted the statistical analysis, and all authors contributed to writing and editing the manuscript.

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