

## Aspects of the ecology and behaviour of the Seychelles theraphosid *Nesiergus insulanus* (Arachnida: Araneae: Theraphosidae)

Gregory Canning<sup>1\*</sup>, Brian Kevin Reilly<sup>1</sup> and Ansie S. Dippenaar-Schoeman<sup>2</sup>

<sup>1</sup>Department of Nature Conservation, Tshwane University of Technology, P. Bag X680, Pretoria 0001, South Africa: gregcan@absamail.co.za, reillybk@tut.ac.za

<sup>2</sup>Agricultural Research Council, Plant Protection Research Institute, P. Bag X134, Queenswood, 0121 Pretoria, South Africa & Department of Entomology and Zoology, University of Pretoria, 0001, Pretoria, South Africa: dippenaar@arc.agric.za

\*Corresponding author

### ABSTRACT

Aspects of the ecology and life history of the little known theraphosid *Nesiergus insulanus* are determined on Frégate Island in the Seychelles archipelago. The general behaviour of this species is revealed to be comparable to that of other theraphosids, with field and captive observations establishing that they are a generalist and opportunistic species. The defensive behaviour of the species is determined to be based primarily on the avoidance of conflict situations, with overt aggressive behaviour seldom displayed. Although the opportunistic existence that this species has developed is probably obligatory due to their sedentary lifestyle and limited availability of resources, this behaviour nonetheless allows the species to occupy diverse habitats and exploit niches unavailable to more specialized species.

KEY WORDS: Behaviour, ecology, generalist, opportunistic, exploit, aggressive.

### INTRODUCTION

The ecological importance of spiders is well recognized in almost every terrestrial and semi-terrestrial habitat on Earth. As all spiders are predators, they benefit humankind by playing an important role in controlling pests in agricultural and other ecosystems as well as by feeding on economically important pest species such as cockroaches and mosquitoes (Mansour *et al.* 1980). Spiders are a significant source of food for other species such as birds, lizards and other invertebrates, and are of particular importance for birds in winter when other prey may be less available (Peterson *et al.* 1989). Their silk is essential in the construction of birds' nests with at least 24 families of passerines using it in nest construction (Hansel 1993). Ground-dwelling spiders transfer energy from below-ground detritus food webs to above-ground terrestrial food webs (Johnston 2000), and spiders are also seen as having a high bio-indicative value as they are strongly associated with biotopes (Whitmore *et al.* 2002).

The Theraphosidae (Mygalomorphae) have a pantropical distribution with 120 genera and over 900 species described (World Spider Catalog 2014). They are considered to be one of the more primitive spider groups (Dippenaar-Schoeman 2002) and tend to be large, sedentary animals that seldom leave the burrows they inhabit (Coddington 2005). *Nesiergus insulanus* Simon, 1903 is a relatively small theraphosid, reaching a maximum size of approximately 27 mm in length. It is a member of the subfamily Ischnocolinae, and appears to be endemic to the Seychelles archipelago, with little known of its ecology and status. Published reports consist of nothing more than taxonomic descriptions and brief observations of their natural history (Simon 1903; Guadanucci & Gallon 2008; Saaristo 2010; Canning *et al.* 2014). This dearth of knowledge is not restricted to this species and there is a general lack of baseline information on most spider groups (Dippenaar-Schoeman *et al.* 2005). A better understanding and more

meaningful knowledge on the life history and ecology of the species is required in order to establish the significance of the species in the community.

Despite the biology of theraphosids remaining poorly known (Costa & Pérez-Miles 2002; Marshall & West 2008), an increasing amount of research is currently being carried out and a significant number of papers have recently been published on theraphosid behaviour (Pérez-Miles *et al.* 2005; Bertani *et al.* 2008; Dor *et al.* 2011; Ferretti *et al.* 2012).

Before the importance of *N. insulanus* in the island community is established, more information on their ecology, life history and distribution is required. The research carried out by the authors is an attempt to further our knowledge and understanding of this species. Moreover, a thorough understanding of theraphosid biology and ecology is necessary from a conservation standpoint, as natural populations are being threatened by habitat disturbances and captures for pet commerce (Costa & Pérez-Miles 2002). The loss of habitat is of particular concern in the Seychelles, where the limited habitat availability has undergone severe environmental degradation and where numerous severe environmental threats further imperil the biodiversity of the islands.

#### MATERIAL AND METHODS

##### *Study site*

Frégate Island (04°35'19"S 55°56'55"E) covers an area of 219 hectares and is located 55 kilometres east of Mahé (Merton *et al.* 2002) in the granitic Seychelles archipelago. It is the most isolated of the granitic islands (Ferguson & Pearce-Kelly 2004) and overlies oceanic basalt. Phosphatised granite and phosphate-cemented sandstone are associated with guano deposits on the plateau, with the highest point being Mont Signal 125 m above sea level. The low-lying areas of the island were marshy in the past and were characterized by sediments of fine clay and quartz (Braithwaite 1984). However, these marshy areas have been replaced, to the detriment of many species, by cultivated fields, gardens and a marina development.

In 1787 Frégate was described as consisting of scrub and low trees (Fauvel 1909), and was assumed to be similar to other granitic islands of the Seychelles. Continuous human settlement is thought to have commenced in the early nineteenth century, with the clearance of native *Pisonia grandis* woodland commencing in the late 1800s to make way for plantations (Robertson & Todd 1983). During the 1900s the island was cleared further for a *Cocos nucifera* plantation and *Vanilla planifolia* was established on stakes of *Pterocarpus indicus*, with these stakes growing to form one of the major habitat types on the island, replacing native forest (Gerlach 2005). *P. indicus* has since died out on the island as a result of an outbreak of Sandragon wilt disease, which was first noticed in 2001 (Boa & Kirkendall 2004) and which killed the last tree in 2004 (P.M. Goza pers. comm.). Whilst this area of the island has regenerated naturally with mostly native species, or been replanted with native species, the rest of the island is still predominantly covered in exotic and often invasive species. Cattle and pigs were kept on the island from at least the late 1990s (T.J. Mokoena pers. comm.) with introductions of the grasses *Panicum maximum* and *Cenchrus ciliaris* to provide grazing for the cattle. *P. maximum* has since established itself widely on the island and forms dense thickets in many areas of the island. Cattle and pigs have been removed, and although

these changes have affected the distribution of this and other species (Canning *et al.* 2014), Frégate has retained important faunal biodiversity and has been the subject of concerted conservation efforts that have included the eradication of cats in the 1990s, rats in 2000 (Millet *et al.* 2005) and the common myna *Acridotheres tristis* Linnaeus, 1766 in 2011 (Canning 2011).

### *Field methods*

Ecological data were collected both in the field and by observing spiders under captive conditions. Twenty females, including four mature specimens, were captured in the field and kept in a communal polystyrene box of dimensions 630×295×170 mm and with a layer of soil 80 mm deep. The top of the box was covered with a glass sheet to prevent escape and for observation purposes. Spiders were provided with fresh water daily and food once a week. Termites were fed to the spiders except when prey preferences were being determined. Two male spiders were housed in separate plastic containers of dimensions 185×140×84 mm.

Field sampling sites were determined by initially conducting a repeatable pilot study. The island (Fig. 1) was divided into habitat types based on the vegetation map of Henriette and Rocamora (2009) and was searched for the presence of burrows. Vegetation types are clearly distinguishable as a result of large-scale anthropogenically induced vegetation changes. Ground truthing determined the precise location of these various habitats. In each described habitat an extensive search was conducted between the beginning of February and the end of March 2010 on three separate occasions. Leaf litter was searched through, rocks and logs were overturned and replaced, and all other litter was searched to find burrows. This allowed for the determination of habitats in



Fig 1. Map of Frégate Island, sampling sites indicated by white dots (adapted from Google Earth, DigitalGlobe map data 2015).

which spiders occurred. After determining these habitats, the island was stratified into quadrats, each measuring 100×100 m and numbered. A random integer generator ([www.random.org](http://www.random.org)) was used to obtain random sample sites in each vegetation type in which spiders were present, ensuring that approximately 25% of the island was represented. 48 sites were generated by this method and all of these sites were sampled. Of these sites, 38 were found to support these spiders. The ecological requirements of the spiders in the habitats in which they occurred was determined and for this reason those habitat types that were found not to support the species in the pilot study were excluded from this process.

Ecological data were collected in the field at the 38 sample sites in which burrows occurred, in nine different habitat types, namely coconut-dominated woodland, *Ficus benghalensis*, mixed exotic woodland, native woodland, replanted native woodland, hotel area native planted, exotic scrub, grassland, and coconut woodland planted with natives. Visits to sampling sites were made on three separate occasions between May 2010 and July 2011.

#### *Diet and hunting techniques*

Diet was determined both in the field and under captive conditions. Areas surrounding burrow aggregations as well as exposed burrows and burrow entrances were searched for possible prey and for the remains of prey. Techniques of prey capture were determined under captive conditions. Prey was provided to the spiders in the evenings and at dusk when they would appear at the edge of their burrows. Their method of capture was observed and recorded. No prey capture was observed in the field. The captive population was offered a number of different orders of invertebrates on a weekly basis for a period of one month to determine preferences. Under captive conditions the invertebrates offered included prey from the following orders: Blattodea, Isoptera, Spirostreptida, Orthoptera, Isopoda, Heterobranchia and Hymenoptera.

Pitfall traps were set at 15 sites in the vicinity of burrow aggregations within sampled quadrats to capture potential prey species. Five different habitat types were chosen for their high spider densities and the total area covered by these habitat types. In each habitat type, three sites were randomly selected for trap placement for a period of three weeks during August 2011. Plastic flower pots of 75 mm depth and 90 mm diameter were used as traps. A total of 150 traps were set at all sample sites, with ten traps at each sample site. They were inserted into the ground, ensuring the lip was flush with the surface, in two rows 1 m apart. Traps were filled with approximately 100 ml of water mixed with liquid dishwashing soap. The contents of the traps were collected once a week and identified to order level where possible. Prey density for selected pitfall trap sites was compared with the density of burrows within those habitat types, and the correlations between these variables were measured using the Spearman Rank Higher Order ( $\rho$ ) Correlation Coefficient.

#### *Predators*

Predators of these spiders were determined by casual observations during field data collection and no experimentation was conducted to determine potential predators of the spider.

### *Defensive strategies*

Defensive strategies were observed primarily under captive conditions, although field observations were also recorded. Observed behaviour was recorded following direct threats to individuals. Under captive conditions spiders were subjected to threats in the form of blowing on the spider, as well as prodding. Forty female spiders and two male spiders were each individually placed in a cylindrical glass bottle of 69×95 mm. A plastic lid with a hole cut in the centre prevented escape. Spiders were blown on for a period of one minute and then subjected to gentle prodding with an ear bud for a period of up to three minutes. Blowing was in bursts of approximately one second interspersed by periods of approximately five seconds. Observations of reactions were recorded.

Size-biased agonistic behaviour has been reported in intraspecific interactions (Hodge 1987) and spiders were therefore categorized according to size to determine whether there is any difference in defensive behaviours based on size. Size ranges of the spiders were categorized as (A) individuals up to 8 mm, (B) individuals from 8–11 mm, (C) individuals from 12–15 mm and (D) individuals larger than 15 mm. Ten spiders for each size category were subject to the experimentation described above. The males were both mature adults larger than 15 mm. Intraspecific agonistic behaviour was not tested under field or captive conditions and the threats described above were used to simulate possible predatory threats. Chi square analysis determined statistical association in observed defensive behaviours.

### *Life cycle*

Reproductive behaviour was observed under captive conditions. Two males were captured when discovered wandering in January 2011 and the first individual captured was placed in a container for three days before being introduced to the larger container with mature females. After mating had taken place the male was returned to its original container and kept there. The mated female was removed from the communal container and placed in the same type of container that the male was placed in. The behaviour of both sexes post mating was recorded. The second captured male was introduced to the communal container in January with mature females and behaviour was observed and recorded. Spiderling emergence, behaviour and dispersal patterns were recorded under these captive conditions. Patterns of spiderling dispersal post emergence were determined by using a nearest neighbour analysis.

## RESULTS

### *Diet and hunting techniques*

The burrows of *N. insulanus* do not have silk mats or triggers to assist in the detection of prey and the primary method of hunting consisted of occupying the burrow entrance and waiting for prey, predominantly nocturnally. Prey passing by was captured and rapidly taken down the burrow. On occasion the spiders left the burrow completely to capture prey at short distances from the burrow entrance, although they remained within close proximity of the burrow entrance. Prey detected up to four centimetres from the burrow was attacked. Movement of the prey alerted the spider to its presence, whereafter the spider rushed from the burrow, gripped the prey in its fangs and immediately returned to the burrow. When there was abundant prey, they seized an individual prey

item, returned to the burrow and returned to the surface where they seized more prey and returned to the burrow. Under captive conditions spiders were observed catching a termite, holding it in their fangs and then catching another one and adding it to the one already captured, until they had caught up to three termites, before retreating into their burrow. Whilst most observations of spiders hunting took place at night and under captive conditions, they were on occasion observed sitting at their burrow entrances during daylight hours, during overcast and cool weather conditions. This was observed under captive conditions and in the field.

*N. insulanus* had no preference for any particular prey type offered and fed on all items presented to them. All individual prey that came within range of a waiting spider was attacked. Potential prey items found in the vicinity of burrows at sample sites included species from eight invertebrate orders, namely Araneae, Diptera, Hymenoptera, Hemiptera, Coleoptera, Blattodea, Spirostreptida and Orthoptera. Remains of spirostreptidans, blattodeans and coleopterans were found at the entrance to burrows and the remains of these orders, along with the remains of Scorpiones, were found in excavated burrows.

Pitfall traps captured individuals from at least 16 different identifiable invertebrate orders as well as vertebrates from two different orders. Invertebrates caught in the pitfall traps belonged to the following orders (frequency is given in parentheses): Araneae (6.14%), Diptera (flies 16.54%, mosquitoes 0.94%, hippoboscids 0.07%), Hymenoptera (ants 38.63%, wasps 1.22%), Lepidoptera (7.87%), Hemiptera (1.139%), Coleoptera (0.82%), Blattodea (0.74%) Isoptera (15.75%), Spirostreptida (0.19%), Orthoptera (2.28%), Siphonaptera (0.27%), Neuroptera (0.11%), Heterobranchia (0.98%), Ixodida (1.33%), Scolopendromorpha (0.11%), Ephemeroptera (0.03%), Isopoda (0.15%) and unidentified orders (4.52%). Two individuals from vertebrate orders were caught in the pitfall traps, one each from Squamata (Scincidae) and Gymnophiona (Caeciliidae).

Prey density for selected pitfall trap sites was compared to the density of burrows within those habitat types and the results indicate a modest correlation between these two variables when the data are combined across habitats ( $r=0.59$ ).

### *Predators*

As *N. insulanus* is an island and fossorial species, its predators are limited. A Seychelles magpie robin *Copsychus sechellarum* Newton, 1865 was observed moving leaf litter and exposing a burrow before catching a spider, which was then carried away to be fed to a chick. A Seychelles skink *Trachylepis seychellensis* (Duméril & Bibron, 1839) was also observed feeding on spiders after burrows had been exposed.

### *Defensive strategies*

The defensive strategies of these spiders focused on avoiding confrontation. Only on four occasions was overt aggression displayed, where the threat was physically attacked, and this was only observed in two individuals. A total of 11 different displays towards threats were observed with some variation between displays (Table 1). These displays may be divided into three main behaviour types: (1) *avoidance*, where the spider attempts to move away from the threat — the spider may also touch the threat in a non-aggressive manner; (2) *confrontation*, where the spider is actively aggressive towards the threat and includes threat displays — confrontational displays were rarely

TABLE 1

Descriptions of defensive behavioural displays of *Nesiergus insulanus* subjected to prodding and blowing. The three main defensive behaviours of avoidance, confrontation and immobility are further divided into subcategories of these displays.

<b>Avoidance</b>	
Running	Spider attempts to move away from threat by running.
Retreat	Spider backs away from threat slowly.
Protect and Retreat	Spider brings first two pairs of legs towards anterior cephalic region while the back two pairs of legs are maintained in extended position. At the same time the spider backs away slowly or rapidly from threat.
Touch	Spider pulls first two pairs of legs in towards lateral thoracic region, back two legs are placed in extended position, spider places from one leg to both front pairs gently on threat until threat level is intensified and then removes legs and slowly backs away.
<b>Confrontation</b>	
Raised Palps	Spider retracts first pair of legs, pedipalps are raised and brought slowly down towards threat.
Fang Display	Spider raises cephalothorax, pulls legs in, raises pedipalps, lifts chelicerae and exposes fangs.
Threat Approach	Spider rapidly and aggressively moves towards threat, raises either one or both pairs of front legs and pedipalps and places legs (one or both pairs) on threat.
Aggressive Bite	Spider aggressively attacks threat, places front pair of legs on threat, moves forward, rapidly bites threat and then backs away.
<b>Immobility</b>	
Body Cover	Spider folds all legs up and over the cephalothorax and abdomen and remains motionless (Fig. 2).
Motionless	Spider remains motionless in same position in which it was first observed, despite prodding.
Thanatosis	This behaviour was only observed in males after excessive harassment. After displaying for a period the spider suddenly becomes active and attempts to run away.

observed and were generally displayed immediately, with no stages leading up to an aggressive display; and (3) *immobility*, where the spider goes into a defensive posture and remains immobile — immobility included thanatosis.

Blowing initiated no response other than going into an immobile display where the spider brings all legs up and over the cephalothorax and abdomen, and remains motionless in this position. Prodding elicited displays that are described above (Table 1). Spiders moved between displays rapidly and each display generally lasted for short periods of only a few seconds at a time.

A chi-square test of observed defensive behaviours of 40 individual females indicated that there was no statistically significant association between observed frequencies of behaviour types between the different size categories ( $\chi^2 = 34.96$ ,  $df = 27$ ,  $p > 0.05$ ) (Table 2).

The frequency of confrontational behaviour increased with the size of the spider, and spiders in category D (> 15 mm) used confrontational behaviour in 24.6% of observed behaviours, compared with 9% for category A (< 8 mm), 6.7% for category B (8–11 mm) and 15% for category C (12–15 mm). Conversely, the frequency of avoidance behaviour decreased with an increase in the size of individual spiders, with 75.6% of observed

TABLE 2

Observed frequency of combined defensive behaviours per size category and gender. Categories A-D are represented by females. Chi square analysis indicates no statistically significant association between observed frequencies of behaviours between size categories ( $\chi^2=34.96$ ,  $df=27$ ,  $p>0.05$ ). Behaviours are divided into three main categories, which are in turn divided into subcategories. The behaviours with subcategories in parentheses are – Avoidance (running [A-Ru], retreat [A-Re], protect and retreat [A-PR], touch [A-T]); Confrontation (raised palps [C-RP], fang display [C-FD], threat approach [C-TA], aggressive bite [C-AB]) and Immobility (body cover [I-BC], motionless [I-Mo], thanatosis [I-Th]).

Size Categories	Behaviours and subcategories										
	A-Ru	A-Pr	A-T	A-Re	C-Rp	C-Fd	C-Ta	C-Ab	I-Bc	I-Mo	I-Th
A	11	7	3	4	3				5		
B	8	10	10	8	1	1	1		6		
C	9	6	8	11	4	1	3	1	13	4	
D	8	5	7	10	7	2	3	3	15	1	
Male	5								4		2

behaviours in category A involving avoidance, 80% in category B, 57% in category C and only 49% in category D (Fig. 3).

Males avoided threats by running away, folding their legs over their cephalothorax and abdomen or moving slowly away from threat. They also remained immobile and then suddenly darted off or displayed thanatosis.

### *Life cycle*

A single day after being introduced to the communal container, the male approached the burrow of a mature female at night. The female exited the burrow on approach of the male. Hereafter, display behaviour and mating were not observed as the female would retreat into the burrow and the male would retreat to the far side of the container at any disturbance from a light source or movement near the container. The following day the male was observed with leg number four on the right-hand side missing and on the side of the container furthest from the female. This male was then removed and placed in a separate container. A depression was excavated in which the male remained during the day, emerging at night to wander. During this period the male did not feed, despite being presented with food. This behaviour continued for five days, after which the male died.

The female completely closed the burrow and was removed from the communal container and placed alone in a different container, where she immediately excavated another burrow into which she retreated. The burrow was closed with silk and soil, and remained closed for 84 days, after which spiderlings emerged at night. Forty-six spiderlings emerged and immediately wandered between 3 cm from the maternal burrow and the edge of the container where they began constructing burrows. The spiderlings were measured and removed to the larger container where they dispersed randomly ( $R_n=1.02$ ) and constructed burrows over the entire area of the container. The size of the spiderlings varied between 4.74 mm and 5.17 mm, with a mean of 4.97 mm. The





Fig 2. Female *Nesiergus insulanus* with egg sac in burrow and displaying defensive behaviour type: immobility-body cover.

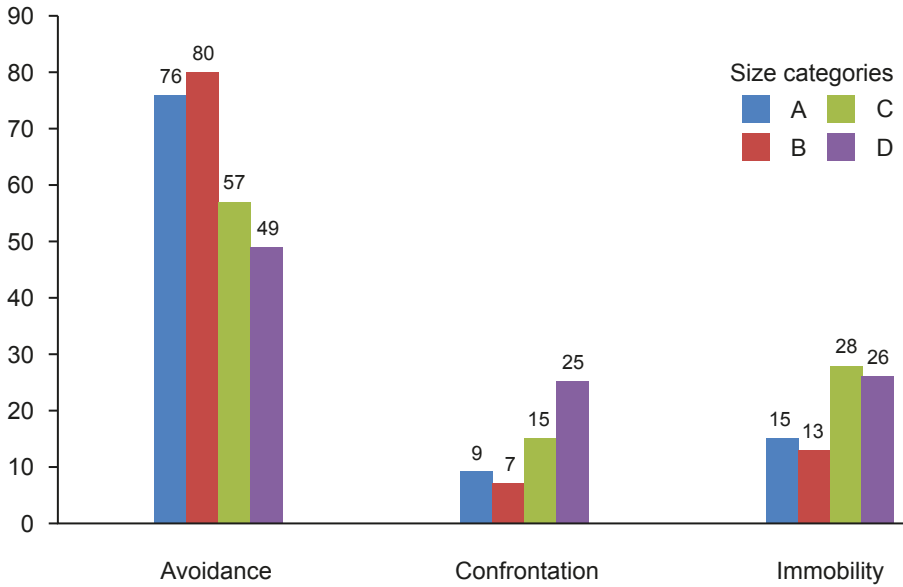


Fig 3. Graph depicting differences in the three primary defensive behaviours between size categories of *Nesiergus insulanus*. The frequency of confrontational behaviours can be seen to increase with the size category of the spider.

female was returned to the communal container, where she constructed a new burrow which remained open.

A second male was introduced to the communal container towards the end of January; however, this male did not approach any burrows or display any behaviour other than escape attempts. This male was removed after three days and returned to an individual container where it continued wandering at night. It too did not eat during this period. It was returned to the communal container after three days, but once again made no approach to any mature female burrows. It was returned to an individual container after three days and died four days thereafter.

#### DISCUSSION AND CONCLUSION

Questions on the ecology of this species have been answered and their general ecology and behaviour is established to be similar to the behaviour of other theraphosids. Their lack of preference for a specific prey item and their opportunistic burrowing behaviour allow them to colonize a wider range of habitats. Although this behaviour could be deemed an obligatory adaptation to their occurrence on small and isolated islands with limited resources, thus restricting their ability to occupy a more specialized niche, they may be considered a generalist and opportunistic species that is able to exploit resources unavailable to more specialized species.

The feeding behaviour of most mygalomorph spiders consists primarily of positioning themselves at the entrance of their retreat and waiting for prey to come within striking distance (Coyle 1986; Dippenaar-Schoeman 2002). Theraphosidae have been observed using this technique (De Wet & Dippenaar-Schoeman 1991), as well as the technique of waiting behind a slightly open trap door for prey to pass within striking distance (Dippenaar-Schoeman 2002). An early detection system of assemblages of silk threads, twigs, grass and other debris described by Main (1978) is also a method of prey capture used by theraphosids (Dippenaar-Schoeman 2002). The ambush method used by *N. insulanus* would expend the least amount of energy and reduces the probability of being detected by predators. Spiders exhibit very low resting metabolic rates and altered feeding behaviours as mechanisms to survive extended periods of limited food availability (Philip & Shillington 2010). This survival technique is important in sedentary species that rely on their prey to wander within striking distance, particularly in habitats of low prey densities. Individuals captured in pitfall traps do not all necessarily accurately reflect the actual prey of the spiders, but are merely potential prey items. Of the individuals represented from the 16 identifiable invertebrate orders caught in the pitfall traps, at least eight orders are known to be preyed on by the spiders as a result of experimentation with captive spiders and from remains found in burrows. A ninth order, Scorpiones, is also a known prey item from remains found in burrows.

A high proportion of burrows were found lying adjacent to rocks and rotting logs, which not only provides a degree of protection from the elements, but also acts as a natural channelling system for their invertebrate prey. The North American tarantula *Aphonopelma paloma* Prentice, 1992 has been found to prey on beetles, ants, spiders and scorpions (Prentice 1992), and various authors have recorded other species feeding on ants, beetles, cicadas, cockroaches, Orthoptera, termites, Lepidoptera, Hymenoptera (De Wet 1991; Coyle 1995; Paulsen 1999), arachnids (Paulsen 1999), millipedes and snails (Coyle 1995). Most arachnids, including the theraphosidae, are generalist predators

(Bradley 1993). Marshall & West (2008) described mygalomorphs as being sedentary to the point of being functionally sessile; this type of lifestyle implies that these spiders cannot afford to be selective in their prey selection, are opportunistic and need to be able to feed on any available prey. This includes juvenile millipedes that are known to possess toxins such as benzoquinones, phenols, hydrogen cyanide, quinazolinones, and alkaloids (Eisner *et al.* 1978). Although the feeding on millipedes is uncommon, other invertebrates are also able to feed on them successfully (Eisner *et al.* 1978). Spiders are able to deal with potentially toxic prey; orb-weaving spiders have been reported to encase bombardier beetles in silk, thus protecting themselves against the quinonoid spray ejected by these beetles (Eisner & Dean 1976).

As prey densities vary spatially and temporally, the mild correlation found between densities of spider burrows and potential prey densities may vary temporally. However, studies by Bradley (1993, 1996) established no seasonal correlations in prey availability and spider densities for *Misgolas rapax* Karsch, 1878 and *Argiope keyserlingi* Karsch, 1878. He also found a weak correlation between potential prey caught in pitfall traps and foraging phenology of the trapdoor spider *M. rapax*, and no correlation between spider densities and potential prey for *A. keyserlingi*. Riechert and Lockley (1984) also found no apparent density-dependant relationship between arachnids and their prey.

Predation of spiders by birds, lizards, wasps and others means that many have adapted strategies to prevent being preyed upon, and Rypstra (1984) showed that spiders in the tropics have a higher survival rate when protected from predation by birds. A number of insectivorous bird species occur on Frégate Island and the high density of lizards on the island would prove to be a threat to exposed spiders. Lizards have been found to have an impact on the density of web-building spiders on islands (Schroener & Toft 1982) and a sedentary, burrow-bound existence can be seen as a survival strategy against these predators, apart from the other advantages that residing in a burrow brings.

As an Old World theraphosid, these spiders have no urticating hairs as a means of defence (Pérez-Miles 1998) and their venom is assumed to be weak and not used for defensive purposes. Pérez-Miles *et al.* (2005) found that the defensive behaviours of the tarantulas *Eupalaestrus weijenberghi* Thorell, 1894 and *Acanthoscurria suina* Pocock, 1903 consisted of raising the cephalothorax, anterior legs and palps, and attempting to escape rapidly from the threat, as well as remaining immobile. They rarely attempted to bite and urticating hairs were only released if harassment of the spiders continued after other behaviours were displayed. These displays (other than the release of urticating hairs) are similar to those displayed by *N. insulanus* and they are common in the theraphosids (Pérez-Miles *et al.* 2005). Overtly aggressive behaviour raises the risk of injury or death to the spider, and displays, escape, or avoidance of the threat are thus the preferred options in defensive action. Riechert (1982) points out that spiders are able to recognise conspecifics as competitors rather than as predators, and in encounters typically use communication as an alternative to fighting. Intraspecific agonistic behaviour was not tested, although from casual observations these spiders are not aggressive towards one another and they ignore their neighbours, even under conditions of high density.

Aggressive female behaviour towards males during the reproductive process of spiders is recognized in many spider groups (Elgar 1992) and even though sexual cannibalism is generally rare in theraphosids (Jackson & Pollard 1990), and the rate among all spider groups may not be as high as generally considered (Jackson 1980), cannibalism by the

female after mating has been recorded for theraphosid species (Shillington & Verrell 1997). Aggressive attacks by the female towards the male have also been observed for *Brachypelma klaasi* Schmidt & Krause, 1994 (Yánñez *et al.* 1999). Despite no mating behaviour being observed, the loss of the male's limb under captive conditions when introduced to the female suggests aggressive behaviour on the part of the female.

With a better understanding of the life history and ecological requirements of *N. insulanus*, conservation efforts to ensure its survival may be successfully implemented. A number of studies have shown that spiders are a good indicator group (Allred & Gertsch 1976; Bonte *et al.* 2002; Samu & Szinetár 2002) and with a better understanding of the species' functioning in the community, their potential as an indicator species may be established.

#### ACKNOWLEDGEMENTS

Rick West is gratefully acknowledged for his encouragement and support, and his willingness to provide detailed information on subject matter. Permission granted by the Seychelles Department of Environment in the Ministry of Home Affairs, Environment, Transport and Energy to carry out the research as well as issuing of permits is sincerely appreciated. Suggestions from two anonymous reviewers were also greatly appreciated.

#### REFERENCES

- ALLRED, D.M. & GERTSCH, W.J. 1976: Spiders and scorpions from Northern Arizona and Southern Utah. *Journal of Arachnology* **3**: 87–99.
- BERTANI, R., FUKUSHIMA, C.S. & DA SILVA JR, P.I. 2008. Mating behavior of *Sickius longibulbi* (Araneae, Theraphosidae, Ischnocolinae), a spider that lacks spermathecae. *The Journal of Arachnology* **36**: 331–335.
- BOA, E. & KIRKENDALL, L. 2004. Sandragon Wilt Disease, Seychelles. *TCP Final Technical Report*.
- BONTE, D.L., BAERT, L. & MAELFAIT, J.P. 2002. Spider assemblage structure and stability in a heterogeneous coastal dune system (Belgium). *Journal of Arachnology* **30**: 331–343.
- BRADLEY, R.A. 1993. The influence of prey availability and habitat on activity patterns and abundance of *Argiope keyserlingi* (Araneae: Araneidae). *Journal of Arachnology* **21**: 91–106.
- 1996. Foraging activity and burrow distribution in the Sydney brown trapdoor spider (*Misgolas rapax* Karsch: Idiopidae). *Journal of Arachnology* **24**: 58–67.
- BRAITHWAITE, C.J.R. 1984. Geology of the Seychelles. In: , D.R., ed., *Biogeography and Ecology of the Seychelles*. The Hague: Dr. W. Junk Publishers, pp. 17–79.
- CANNING, G. 2011. Eradication of the invasive common myna, *Acridotheres tristis*, from Fregate Island, Seychelles. *Phelsuma* **19**: 43–53.
- CANNING, G., REILLY, B.K. & DIPPENAAR-SCHOEMAN, A.S. 2014. The distribution and population status of *Nesiergus insulanus* (Araneae: Theraphosidae: Ischnocolinae) on Frégate Island, Seychelles. *Arachnology* **16** (4): 116–121.
- CODDINGTON, J.A. 2005. Phylogeny and classification of spiders. In: Ubick, D., Paquin, P., Cushing, P.E. & Roth, V., eds. *Spiders of North America: an identification manual*. American Arachnological Society, pp. 18–24.
- COSTA, F.G. & PÉREZ-MILES, F. 2002. Reproductive biology of Uruguayan theraphosids (Araneae, Mygalomorphae). *The Journal of Arachnology* **30**: 571–587.
- COYLE, F.A. 1986. The role of silk in prey capture by non-araneomorph spiders. In: Shear, W.A., ed., *Spiders: webs, behaviour, and evolution*. California: Stanford University Press, pp. 269–305.
- 1995. A revision of the funnelweb mygalomorph spider subfamily Ischnothelinae (Araneae, Dipluridae). *Bulletin of the American Museum of Natural History* **226**: 1–133.
- DE WET, J.I. 1991. A revision of the genus *Ceratogyrus* Pocock (Araneae: Theraphosidae), M.Sc. thesis, Rand Afrikaans University.
- DE WET, J.I. & DIPPENAAR-SCHOEMAN, A.S. 1991. A revision of the genus *Ceratogyrus* Pocock (Araneae: Theraphosidae). *Koedoe* **34**: 39–68.
- DIPPENAAR-SCHOEMAN, A.S. 2002. *Baboon and Trapdoor Spiders of Southern Africa: An Identification Manual*. Pretoria: Agricultural Research Council.
- DIPPENAAR-SCHOEMAN, A.S., Van Der Walt, A.E., De Jager, M., LE ROUX, E. & VAN DEN BERG, A. 2005. The spiders of the Swartberg Nature Reserve in South Africa. (Arachnida: Araneae). *Koedoe* **48** (1): 77–86.

- DOR, A., CALMÉ, S. & HÉNAUT, Y. 2011. Predatory interactions between Centruroides scorpions and the tarantula *Brachypelma vagans*. *Journal of Arachnology* **39** (1): 201–204.
- EISNER, T. & DEAN, J. 1976. Ploy and counterploy in predator-prey interactions: orb-weaving spiders versus bombardier beetles. *Proceedings of the Natural Academy of Sciences of the United States of America* **73**: 1365–1367.
- EISNER, T., ALSOP, D., HICKS, K. & MEINWALD, J. 1978. Defensive secretions of millipedes. In: Bettini, S., ed., *Arthropod Venoms. Handbook of Experimental Pharmacology* **48**. Berlin: Springer, pp. 41–72.
- ELGAR, M. A. 1992. Sexual cannibalism in spiders and other invertebrates. In: Elgar, M.A. & Crespi, B.J., eds, *Cannibalism: Ecology and Evolution among Diverse Taxa*. Oxford: Oxford University Press, pp. 128–153.
- FAUVEL, A. 1909. *Unpublished documents on the history of the Seychelles anterior to 1810*. Mahé, Seychelles: Government Printing Office.
- FERGUSON, A. & PEARCE-KELLY, P. 2004. *Management Guidelines for the Welfare of Zoo Animals – The Frigate Island giant tenebrionid beetle (Polposipus herculeanus)*. London: The Federation of Zoological Gardens of Great Britain and Ireland.
- FERRETTI, N., POMPOZZI, G., COPPERI, S., PÉREZ-MILES, F. & GONZÁLEZ, A. 2012. Copulatory behavior of Microstigmatidae (Araneae: Mygalomorphae): a study with *Xenonemesia platensis* from Argentina. *Journal of Arachnology* **40** (2): 252–255.
- GERLACH, J. 2005. The impact of rodent eradication on the larger invertebrates of Frigate Island, Seychelles. *Phelsuma* **13**: 44–54.
- GUADANUCCI, J.P.L. & GALLON, R.C. 2008. A revision of the spider genera *Chaetopelma* Ausserer 1871 and *Nesiergus* Simon 1903 (Araneae, Theraphosidae, Ischnocolinae). *Zootaxa* **1753**: 34–48.
- HANSEL, M. 1993. Secondhand silk. *Natural History* **102**: 40–46.
- HENRIETTE, E. & ROCAMORA, G. 2009. Frigate Island Vegetation Map. Frigate Island Satellite imagery (1999) provided by Centre for GIS, MND, Government of Seychelles. Adapted from M. Hill 2001, Draft.
- HODGE, M.A. 1987. Agonistic interactions between female bowl and doily spiders (Araneae, Linyphiidae): owner biased outcomes. *Journal of Arachnology* **15**: 241–247.
- JACKSON, R.R. 1980. Cannibalism as a factor in the mating strategy of the jumping spider *Phidippus johnsoni* (Araneae, Salticidae). *Bulletin of the British Arachnological Society* **5**: 129–133.
- JACKSON, R.R. & POLLARD, S.D. 1990. Intraspecific interactions and the function of courtship in mygalomorph spiders: a study of *Porrhothele antipodiana* (Araneae: Hexathelidae) and a literature review. *New Zealand Journal of Zoology* **17**: 499–526.
- JOHNSTON, J.M. 2000. The contribution of microarthropods to aboveground food webs: A review and model of belowground transfer in a coniferous forest. *American Midland Naturalist* **143**: 226–238.
- MAIN, B.Y. 1978. Biology of the arid-adapted Australian trapdoor spider *Anidiops villosus* (Rainbow). *Bulletin of the British Arachnological Society* **4**: 161–175.
- MANSOUR, F., ROSEN, D., SCHULOV, A. & PLAUT, H.N. 1980. Evaluation of spiders as biological control agents of *Spodoptera littoralis* larvae on apple in Israel. *Acta Oecologica* **1**: 225–232.
- MARSHALL, S.D. & WEST, R. 2008. An ontogenetic shift in habitat use by the Neotropical tarantula *Ephobopus urinus* (Araneae, Theraphosidae, Aviculariinae). *Bulletin of the British Arachnological Society* **14** (6): 280–284.
- MERTON, D., CLIMO, G., LABOUDALLON, V., ROBERT, S. & MANDER, C. 2002. Alien mammal eradication and quarantine on inhabited islands in the Seychelles. In: Veitch, C.R. & Clout, M.N., eds, *Turning the tide: the eradication of invasive species*. IUCN SSC Invasive Species Specialist Group. Gland, Switzerland and Cambridge, U.K.: IUCN, p. 414.
- MILLET, J., CLIMO, G. & SHAH, N.J. 2005. Eradication of Common Mynah *Acridotheres tristis* population in the granitic Seychelles: Successes, failures and lessons learned. *Advances in vertebrate pest management* **3**: 169–183.
- PAULSEN, M. 1999. A *Harpactira* burrow reveals the secrets of its occupant. *Journal of the British Tarantula Society* **15**: 14–23.
- PÉREZ-MILES, F. 1998. Notes on the systematic of the little known theraphosid spider *Hemirrhagus cervinus*, with a description of a new type of urticating hair. *Journal of Arachnology* **26**: 120–123.
- PÉREZ-MILES, F., COSTA, F.G., TOSCANO-GADEA, C. & MIGNONE, A. 2005. Ecology and behaviour of the ‘road tarantulas’ *Eupalaestrus weijenberghi* and *Acanthoscurria suina* (Araneae, Theraphosidae) from Uruguay. *Journal of Natural History* **39** (6): 1–16.
- PETERSON, A.T., OSBORNE, D.R. & TAYLOR, D.H. 1989. Tree trunk arthropod faunas as food resources for birds. *Ohio Journal of Science* **89** (1): 23–25.
- PHILIP, B.N. & SHILLINGTON, C. 2010. The effect of prey availability on metabolism and activity in the tarantula *Phormictopus cancerides*. *Canadian Journal of Zoology* **88** (1): 90–98.
- PRENTICE, T.R., 1992. A new species of North American tarantula, *Aphonopelma paloma* (Araneae, Mygalomorphae, Theraphosidae). *Journal of Arachnology* **20**: 189–199.

- RIECHERT, S.E. 1982. Spider interaction strategies: Communication vs. coercion. *In*: Witt, P. N. & Rovner, J., eds, *Spider communication: mechanisms and ecological significance*. Princeton, NJ: Princeton University Press, pp. 281–313.
- RIECHERT, S.E. & LOCKLEY, T. 1984. Spiders as biological control agents. *Annual Review of Entomology* **29**: 299–320.
- ROBERTSON, S.A. & TODD, D.M. 1983. Vegetation of Frégate Island, Seychelles. *Atoll Research Bulletin* **273**: 39–64.
- RYPSTRA, A.L. 1984. A relative measure of predation on web-spiders in temperate and tropical forests. *Oikos* **43**: 129–132.
- SAARISTO, M.I. 2010. Araneae. *In*: Gerlach, J. & Marusik, Y., eds, *Arachnida and Myriapoda of the Seychelles islands*. Manchester, U.K.: Siri Scientific Press, pp. 8–306.
- SAMU, F. & SZINETÁR, C. 2002. On the nature of agrobiont spiders. *Journal of Arachnology* **30**: 389–402.
- SCHROENER, T.W. & TOFT, C.A. 1982. Spider populations: extraordinarily high densities on islands without top predators. *Science* **219**: 1353–1355.
- SHILLINGTON, C. & VERRELL, P. 1997. Sexual strategies of a North American ‘tarantula’ (Araneae: Theraphosidae). *Ethology* **103**: 588–598.
- SIMON, E. 1903. *Histoire naturelle des araignées*, Paris: Roret, volume 2 part 4, pp. 669–1080.
- WHITMORE, C., SLOTOW, R., CROUCH, T.E. & DIPPENAAR-SCHOEMAN, A.S. 2002. Diversity of spiders (Araneae) in a Savanna Reserve, Northern Province, South Africa. *Journal of Arachnology* **30**: 344–356.
- WORLD SPIDER CATALOG. 2014. Version 15. Natural History Museum Bern. (<http://wsc.nmbe.ch>; accessed 4/8/2014)
- YÁNĚZ, M., LOCHT, A. & MACÍAS-ORDÓÑEZ, R. 1999. Courtship and mating behavior of *Brachypelma klaasi* (Araneae, Theraphosidae). *Journal of Arachnology* **27**: 165–170.