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The natural history of the sleepy lizard (*Tiliqua rugosa*) – insight from chance observations and long-term research on a common Australian skink species

Natural history is the basis for the understanding of the biology of a species and its ecological roles (Bury, 2006, Lindenmayer et al., 2012). The development of an understanding of the natural history of a species often require long-term research, since aspects such as longevity, are usually difficult to determine otherwise (Fitch, 2006). In addition, many ecological processes, like succession and the associated community changes, usually take place at a pace that cannot be observed over a relatively short period of time, making long-term data collection invaluable (Fitch, 2006). In spite of this, the current trend among most academic institutions is to favour biochemical and/or molecular studies, which produce results relatively quickly, over long-term natural history or ecological research (Greene and Losos, 1988, Pianka, 2001, Tewksbury et al., 2014). This is a result of pressures that these institutions face for obtaining funding and other support, coupled with a lack of appreciation of natural history and ecological studies and decrease in interest in the natural environment among members of the general public (Greene, 1994, Mccallum and Bury, 2013). To enable long-term research, ecologists and other natural historians, therefore often have to run short-term projects, with more immediate outputs, in order to find a balance between meeting the demands of producing timely results and obtaining the necessary information that only long-term research can provide. This requires a genuine interest in the study subjects and a degree of resourcefulness. A successful strategy is to use a long term system as a scaffold to ‘hang’ individual projects from. The research on *Tiliqua rugosa* (Gray, 1825), mostly done in South Australia by the late Professor Michael Bull and his collaborators, is a clear illustration of how chance observations and short-term studies can be incorporated with long-term data collection for the unravelling of the ecology of a species. Herein we summarise the natural

history findings from this impressive long-term data collection which started in the late 1970's and from 1982 was continuous around road transects surrounding Bunday Bore Station (33°54'S; 139°20'E) in the Mid North region of South Australia. We incorporate these data with chance observations and other research to provide a comprehensive overview of what is known about the natural history of *T. rugosa*.

Distribution and Habitat

The sleepy lizard (*Tiliqua rugosa*, formerly classified as *Trachydosaurus rugosus*) is a relatively large (total length ca. 40 cm) skink species (Cogger, 2014, Gray, 1825, Shea, 1990, Bull and Pamula, 1996), endemic to the semi-arid parts of southern Australia, from Western Australia eastwards to southern Queensland (Cogger, 2014, Parsons et al., 2015). It is a habitat generalist and can inhabit arid *Acacia* scrublands, chenopod shrublands, coastal heaths, dry sclerophyll forests, eucalypt scrublands, gibber plains, mallee scrublands, spinifex-dominated sandy deserts and woodlands (Cogger, 2014). This species however, favours fairly open habitats dominated by shrubs, as opposed to habitats with dense tree canopy cover (Henle, 1990, Bull, 1995). Within these habitats these lizards establish home ranges that, depending on the season and/or climate, vary in size from about three to nine hectares (Satrawaha and Bull, 1981, Dubas and Bull, 1992, Kerr and Bull, 2006a, Bull et al., 2017). This home range size is relatively small compared to those of similar-sized carnivorous lizards, and is possibly due to its omnivorous diet (Satrawaha and Bull, 1981). The initial studies into the home ranges of sleepy lizards found that the home ranges of individuals overlap and are spatially and temporally stable over consecutive years (Bull, 1978, Bull, 1987, Bull and Freake, 1999). It was also found that the size of the home range of each lizard is not influenced by food availability (Dubas and Bull, 1991, Dubas and Bull, 1992) but rather by access to water (Kearney et al., 2018), since during periods of drought

lizards have smaller home ranges (Kerr and Bull, 2006a) and lizards with access to water tend to maintain larger home ranges (Leu and Bull, 2016). The analyses of data gathered over consecutive years indicates though that there is a subtle, but crucial association between spatial food resources and refuges, which influences the patterns in which sleepy lizards utilize their home ranges (Leu et al., 2010a, Malishev et al., 2017).

Sleepy lizards are ectotherms and prefer a body temperature of about 33° to 35°C (Bennett and John-Alder, 1986, Firth and Belan, 1998, Licht et al., 1966, MacMillen et al., 1989, Warburg, 1965), which they maintain through basking or seeking shelter when thermal conditions become unfavourable, so it is not surprising that their activity patterns are influenced by the time of year and the time of day. Studies into their activity patterns have determined that the lizards are primarily active during the warmer mid part of the day (i.e. unimodal) on days of mild temperature, usually during the late winter to spring period, to being active mainly during the cooler morning and afternoon periods (i.e. bimodal) on hot days, primarily during the late spring to summer period (Firth and Belan, 1998, Kerr and Bull, 2006b). However, it should also be noted that there are inter-sexual differences in activity patterns. Data collected over multiple years indicates that male sleepy lizards are more active than the females prior to mating as a result of remaining active later in the day than the females and traveling greater distances (Bull et al., 1991, Kerr and Bull, 2006b), likely to forage or even for opportunities of extra-pair mating (Leu et al., 2011b). After mating, the activity of the males decrease, most likely as a result of more effective foraging in conjunction with reduced energetic demands associated with reproduction (Leu et al., 2011b). The females, on the other hand, need to thermoregulate and meet the energetic demands of the developing embryos, so do not reduce their activity to the same extent as the males and likely only become inactive when weather conditions become unsuitable for activity (Bull et al., 1991, Fergusson and Algar, 1986, Leu et al., 2011b).

When prevailing temperatures are unfavourable sleepy lizards usually seek shelter in the burrows of other animals (Kerr et al., 2003). At other times of inactivity, the lizards usually make use of shrubs, hollow logs, or man-made objects such as sheets of corrugated iron as refuges (Henle, 1990, Kerr et al., 2003, Lancaster et al., 2012). Studies into the utilization of refuges found that sleepy lizards make use of numerous refuges within their home ranges (Leu et al., 2010b, Leu et al., 2011a) and that they do not select the refuges at random, but rather select refuges and positions within them depending on their thermal requirements (Auburn et al., 2009, Kerr and Bull, 2004b, Kerr et al., 2003).

The multiple-year study into the home ranges of sleepy lizards have also found that males usually occupy larger home ranges than those of females (Godfrey et al., 2013, Spiegel et al., 2018), and that both sexes do not make constant use of their entire home-ranges. Instead they utilise exclusive core areas, which usually overlap with that of their paired partner, which was proposed as suggestive of intra-sexual territoriality (Kerr and Bull, 2006a). Unlike other species in the sub-family Egerniinae, sleepy lizards do not make use of scat piling to indicate occupancy of their home ranges, but rather likely employ other forms of scent-marking (Fenner et al., 2015, Leu et al., 2016). The periphery of their home ranges (i.e. the part of their ranges outside of the core areas) overlap with those of neighbours and earlier studies suggested that although neighbours may periodically utilise the same refuges within these periphery areas they usually do so asynchronously, which was interpreted as a form of avoidance behaviour (Spiegel et al., 2015). However, more recent analysis of the available data, incorporating lizard movements, social networks (i.e. which individuals interact with each other and how often), and personality (i.e. the aggressiveness and boldness of individuals) suggest intra-sexual interactions in the peripheral areas are more likely a form of excluding behaviour since they take place relatively far from the centre of exclusive core areas and were at least in some cases motivated by agonistic behaviour (Spiegel et al., 2018),

thereby supports earlier assumptions of intra-sexual territoriality.

Diet and feeding behaviour

The diet of a species is a crucial component of its natural history because in addition to growth and maintenance, the food sexually mature lizards consume provides energy for reproduction (Derickson, 1976, Storer et al., 1979). *Tiliqua rugosa* has conical teeth that tend to be relatively larger along the middle of the jaw, compared to the other teeth (Greer, 1989, Shea, 1990) This is believed to be an evolutionary adaptation for an omnivorous diet (Estes and Williams, 1984). Although sleepy lizards are omnivores that will opportunistically feed on invertebrates and even carrion (See appendix 1), they primarily feed on plant material (See appendix 2), and even have specific adaptations, such as cecal ridges in the colon, which are adaptations associated with herbivorous lizards (Herrel, 2007). From long-term data collection it has been determined that *T. rugosa* mainly feed on the dominant available food (i.e. being opportunistic), so their diets tend to vary seasonally, and they favour a varied diet and thus consume different food items each day (Dubas and Bull, 1991). They also do not usually consume all the available food, but feed for a short while, and then move several metres to feed in a different locality, even when food is still available in the initial locality (Dubas and Bull, 1991, Dubas and Bull, 1992, Henle, 1990). Even though this may suggest that a large part of each day should be allocated to feeding, through the long-term studies into the foraging behaviour and activity patterns of *T. rugosa* it has been determined that irrespective of the gender or the time of year, these lizards spend about the same amount of time foraging, which constitutes only a small part (on average < 12 minutes) of each day (Dubas and Bull, 1991).

Considering the extensive distribution of *T. rugosa*, and the fact that it is an opportunistic omnivorous species, it is unlikely that its diet would be the same throughout its range.

Additional dietary studies and observations are therefore required from throughout the distribution range of this species to elucidate a comprehensive understanding of its diet, and how environmental change (due to climate change and/or anthropogenic habitat disturbances) may influence it or may already be having an impact on it. In addition to that, studies are also needed to determine if there are changes in the diet of different age classes, and if so, to what extent.

Reproduction

Tiliqua rugosa is viviparous, and produce one to three neonates, which are born in late autumn after a gestation period of ca. five months (Bull et al., 1993b, Munns, 2013). There is no direct parental care, but through long-term research it has been determined that the female can recognize her offspring via chemical signals and they are tolerated and remain within the mother's home range in their first year, after which they disperse (Bull et al., 1994, Main and Bull, 1996, Bull and Baghurst, 1998). *Tiliqua rugosa* young grow fairly rapidly (Bull, 1987). They reaching sexual maturity within three to four years (Bull, 1987), which is longer than most skink species listed in Greer (1989). However, species such as *Egernia cunninghami* and *Egernia rugosa*, which are related to *T. rugosa*, can take up to 5 years to reach sexual maturity but have life spans that are almost half of that of sleepy lizards (Chapple, 2003, Peck et al., 2016). The age at which sleepy lizards reach sexual maturity is therefore quick for such a long-lived species. Mortality rates are high among juveniles, most likely as a result of predation, parasitism and unfavourable environmental conditions, so only a few survive to adulthood (e.g. ca. 4% at the site near Mt. Mary), but adults have lower mortality rates and are estimated to live for ca. 50 years (Bull, 1995, Jones et al., 2016).

Prior to the long-term research into the natural history of *T. rugosa* it was noted that in spring these lizards walk in tandem, and it was assumed that the male was attending and guarding

the female (Bull, 1987), however the long-term data collection revealed that this simple explanation was an understatement of a behaviour that is extremely rare in lizards. Sleepy lizards are usually solitary, but during the mating season (September to December) they form pairs (Bull, 1988). The onset of the pairing period is determined by warm temperatures, but mating takes place in late October to early November, so the pairing period may vary (Bull and Burzacott, 2002, Brooker, 2016). Although some extra-pair fertilization may take place (Bull et al., 1998), the majority of sleepy lizard pairs are both socially and genetically monogamous (Leu et al., 2015). These pair bonds can be extremely stable, lasting multiple (e.g. one pair was recorded for 27 consecutive years in 2012) mating seasons (Leu et al., 2015), and can be so strong that males will remain with their partners even after the female died (Sharrad et al., 1995, How and Bull, 1998, Kerr and Bull, 2001). The partners are not constantly together during the pairing period, and separations, which may range in time from a few hours to several days, may take place (Bull, 1988, How and Bull, 2002, Leu et al., 2011b). It has been noted that male and female *T. rugosa* exhibit various personalities (i.e. behavioural types) and that aggressive males have weaker pairing bonds with females than do less aggressive males (Godfrey et al., 2012). By observing individuals over consecutive weeks, it was found that partners usually search for each other to re-establish the bonds and the reunion intensity increases later in the pairing period prior to the short period when females are receptive (Bull, 1988, Bull et al., 1993a, How and Bull, 2002, Leu et al., 2011b). Although both genders may re-establish the bond, it is more frequently initiated by the males (Leu et al., 2011b).

Mate-guarding either entails a male guarding a female against rival males because he is unable to defend the female's home range (Cuadrado, 2001), or in the case of non-territorial species, to ensure paternity (Marco and Pérez-Mellado, 1999). Earlier studies into the reason for the pairing behaviour of sleepy lizards disproved mate-guarding as an explanation (How

and Bull, 2002). Priming, a form of female coercion in which the female can only become receptive after repeated courtship, was proposed as a likely alternative explanation (How and Bull, 2002). An evaluation of data from multiple years supports the assumption that it is a form of female coercion (Bull, 2000). The female benefits energetically since there are indications that the males will defend the female from rival males (Bull and Pamula, 1996, Kerr and Bull, 2002, Murray and Bull, 2004) and act as a sentinel for potential threats (Bull and Pamula, 1998), both which permits the attended female to feed more effectively. Males benefit genetically from the pairing because males that remain monogamous and attend their regular partner usually father all her offspring (Bull et al., 1998).

Mating takes place in late October to early November, and familiar pairs tend to mate sooner than unfamiliar pairs (Leu et al., 2015), after which the pair separates (Bull and Burzacott, 2002), but remain in social contact by occupying overlapping core areas of their home ranges and sharing refuges (Leu et al., 2011b).

Competition

Members of a particular species compete with other individuals of the same species (intra-species competition) as well as with those of other species (inter-species competition) for resources within an ecosystem. Inter-species competition can have significant influences on populations and communities (Sih et al., 1985). Considering the spatial use of shelters by sleepy lizards and the fact that they are primarily herbivorous, makes competition among them and a variety of other taxa likely. However, this aspect of the natural history of sleepy lizards has received relatively little attention. Climate profiles suggest that *T. rugosa* and *Tiliqua scincoides* have very similar temperature requirements but the former is more adapted for drier conditions (Hancock and Thompson, 1997). A study that examined the resource partitioning by *T. rugosa* and two other congeneric blue-tongue species, *Tiliqua nigrolutea*

and *T. scincoides*, at a locality in Cape Jaffa in South Australia found that there are substantial overlaps among the species with regards to their utilisation of heat, space, cover, time and food resources (Yeatman, 1988). Still, it was noted that sleepy lizards consume more plant material than the other two blue-tongue species, and that *T. rugosa* more frequently utilise open habitats than *T. nigrolutea* and *T. scincoides* do (Yeatman, 1988). Another study compared the thermal ecology and diet of several xerophilous lizards, and found that the surface activity of *T. rugosa* is more restricted by temperature extremes than *Pogona vitticeps* is, and that the former are more generalists in what they eat than the latter are (MacMillen et al., 1989).

Sleepy lizards tend to flourish in some urban localities, such as in Perth, while in others their occurrence is very limited, even when related blue-tongue species do occur. The role that competition and habitat requirements plays in the distribution of sleepy lizards require further study.

Predators

As in competition, predation can have significant influences on communities and therefore ecosystems (Sih et al., 1985). Known and possible predators of sleepy lizards include aboriginal people, dingos (*Canis lupus dingo*), feral cats (*Felis catus*), foxes (*Vulpes vulpes*), carpet pythons (*Morelia spilota*), dugites (*Pseudonaja affinis*), peninsula brown snakes (*Pseudonaja inframacula*), western brown snakes (*Pseudonaja nuchalis*), common brown snakes (*Pseudonaja textilis*), and wedge-tailed eagles (*Aquila audax*) (Shine, 1989, Roberts and Mirtschin, 1991, Bull and Pamula, 1998, Metcalfe and Driver, 2008, Norval et al., 2018). However, the impact of these predators on sleepy lizard populations has not been studied.

Parasites and Pathogens

The long-term research on *T. rugosa* in South Australia did not start out as an investigation into the natural history of these lizards, but rather as studies into explaining the parapatric boundaries of the reptile ticks, *Amblyomma albolimbatum*, *Amblyomma limbatum* and *Bothriocroton hydrosauri*, that often infest them. All three species parasitize a variety of reptile hosts, but are most commonly found on *T. rugosa* (Andrews and Petney, 1981, Sharrad and King, 1981). In addition to these ticks *T. rugosa* has been reported as a host of a variety of other parasites (See appendix 3), some of which have only been recorded from *T. rugosa*, while others are known to parasitize a variety of hosts.

Parasites can negatively influence host survival and or fecundity and therefore directly or indirectly play important roles in host population dynamics (Scott and Dobson, 1989, Tompkins and Begon, 1999, Valkiūnas, 2001). Long-term research on the ticks *A. limbatum* and *B. hydrosauri* and their infestation of sleepy lizards initially suggested that tick infestation intensity (i.e. the number of ticks that infest the host) do not adversely affect survival, growth or reproduction in *T. rugosa* (Bull and Burzacott, 1993), but the ticks reduce the running speed of juvenile lizards and decrease the general activity levels and the distances that sub-adult and adult lizards travel each day (Main and Bull, 2000). Subsequent analysis of the long-term collected data found that infestation by *B. hydrosauri* reduces lizard survival (Jones et al., 2016). Through experimental increases of tick infestation it was also found that high tick loads have a negative influence on the retention of long-term partnerships in *T. rugosa*, most likely by impeding the activity and endurance of the male and thus his ability to attend the female (Bull and Burzacott, 2006). The ticks were also identified as vectors for the haemogregarine blood parasite, *Hemolivia mariae* (Smallridge and Bull, 1999), which also inhibits the activity of infected lizards (Bouma et al., 2007), which has been suggested to negatively impact the survival of juvenile lizards (Jones et al., 2016).

The long-term research into the social networks of sleepy lizards at the site near Mt. Mary

also provided some insight into the transmission of pathogens. It was determined that the asynchronous use of refuges aligns with the life history traits of the tick *A. limbatum* and therefore facilitates the transmission of the tick through the sleepy lizard population (Leu et al., 2010b), and that personalities of the lizards, their social networks, and movement ecology, determined the infestation intensity by the tick *B. hydrosauri*, which is dispersed by the movements of sleepy lizards (Bull, 1978, Sih et al., 2018).

Studies were not only limited to sleepy lizards and their ticks. It was also determined that the sleepy lizards in this population are often infected with up to three of the *Salmonella enterica* subspecies (*Salmonella enterica* subsp. *diarizonae*, *S. enterica* subsp. *enterica*, *S. enterica* subsp. *houtenae*, and *S. enterica* subsp. *salamae*) known to infect these lizards in this locality (Bull et al., 2012). Additionally the physical characteristics of their home ranges and their social networks were found to influence which *S. enterica* subspecies they were infected with (Parsons et al., 2015, Bull et al., 2012).

Apart from the results of these studies little is known about the influences of the various parasites on *T. rugosa*. As illustrated by the recently identified nidovirus, which causes a respiratory disease in these lizards, and often results in mortality if left untreated (O’Dea et al., 2016), our understanding of the parasites and pathogens in sleepy lizards is incomplete and warrant additional empirical investigations.

Conservation

Sleepy lizards are often attracted to roads by roadside vegetation and puddles that form on road surfaces during rains (e.g. Sadleir, 1958). Due to their slow movement and tendency to stop moving when approached, they are often killed by passing vehicles (Henle, 1990, Bull, 1995, Sharrad et al., 1995, Brooker, 2016). Eliminating this cause of mortality is likely impossible. A more realistic approach would be to determine which areas have higher

numbers of lizards and to take intervention measures in these localities. Investigations into the feasibility of intervention measures such as the construction of fauna underpasses (e.g. Chambers and Bencini, 2015) and/or the erection of signs, appealing to drivers to be mindful of lizards crossing the roads (as done for other wildlife), in combination with low barriers, in areas where lizards and other wildlife frequently cross roads are warranted. Studies should also look into the effectiveness of other possible intervention measures, such as the creation of drinking puddles and feeding and basking areas away from roads, which will attract lizards away from roads.

Other anthropogenic activities, such as the erection of fences, can also cause mortality in sleepy lizard populations (e.g. Waite, 1925, How and Bull, 1998, Ferronato et al., 2014). Possible changes in such structures, to minimize mortality in non-target species should be explored.

Urban development causes habitat destruction, one of the most serious threats to wildlife. *Tiliqua rugosa* is a fairly common species throughout its range in suitable habitats, and since this species can be human-commensal under some conditions it can even sometimes occur in suburban areas (Shea, 1998). Its abundance and current conservation status does not mean that conservation actions are not necessary. Actions should be taken before a species becomes threatened, not when it is endangered. There is therefore a need to determine under what conditions this species can persist in suburban areas. Such information could aid in designing urban and suburban developments that are more lizard-friendly, which could lessen the impact of anthropogenic activities on this and other related species.

Conclusion

Tiliqua rugosa has been studied more extensively than most lizard species in Australia, but the impressive body of information that this work has produced still does not provide a

complete understanding of its natural history and ecology. Most of the studies on this species were conducted in South Australia, and more specifically near Mt. Mary in the Mid North of South Australia. The species *T. rugosa* consists of four subspecies, *Tiliqua rugosa asper* Gray 1845 (eastern Australia), *Tiliqua rugosa konowi* Mertens 1958 (Rottnest Island, Western Australia), *Tiliqua rugosa rugosa* Gray 1825 (south-western Australia), and *Tiliqua rugosa palarra* Shea 2000 (mid-west coast of Western Australia), and most of what is known of this species is from the long-term research on the subspecies *T. r. rugosa* from a relatively small part of its distribution range. As indicated throughout this review, various aspects of the natural history warrant additional long and short-term empirical studies to fill the gaps in our understanding of the ecology of this species throughout its distribution range. In localities other than the site near Mt. Mary, the methodology of past studies can be replicated for comparison purposes. Such information would highlight likely regional variations in the ecology of sleepy lizards, which could be crucial for possible management and conservation actions.

The species also provides an excellent model to examine major evolutionary innovations such as the evolution of monogamy, viviparity and adaptations to differing environmental conditions. The solid foundation laid down by the late Michael Bull will undoubtedly be used as a platform for exploring these innovations using new genomic, statistical and other similarly powerful techniques. A truly lasting legacy.

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Appendix 1. Reported non-plant dietary items of *Tiliqua rugosa* (* – non-native species; WA – Western Australia; NSW – New South Wales; V – Victoria; SA – South Australia).

Family	Species	Locality	Reference
Cyanobacteria			
Nostocaceae	<i>Nostoc commune</i>	SA	Kerr and Bull (2004a)
Fungi			
	Unspecified	WA, SA	Longley (1944), Peters (1973), Yeatman (1988), Shea (1989)
Molluscs			
Hygromiidae	<i>Ceruella virgate</i> *	SA	Yeatman (1988), Satrawaha and Bull (1981)
Helicidae	<i>Theba pisana</i> *	SA	Dubas and Bull (1991)
	Unspecified snails	WA	Yeatman (1988), Shea (1989)
Arthropods			
Acrididae	<i>Chortoicetes terminifera</i>	SA	Dubas and Bull (1991)
Acrididae	Unspecified grasshopper	WA	Chapman and Dell (1980), Dell and Chapman (1979)
Carabidae	<i>Calosoma schayeri</i>	WA	Chapman and Dell (1980)
Carabidae	<i>Promecoderus</i> sp.	WA	Shea (1989)
Carabidae	Unspecified ground beetle	SA	Yeatman (1988)
Curculionidae	Unspecified weevil	WA, SA	Dell and Chapman (1979), Yeatman (1988)
Ixodidae	Unspecified tick	SA	Yeatman (1988)

Scarabaeidae	<i>Onthophagus duboulayi</i>	WA	Shea (1989)
Scarabaeidae	Unspecified (Melolonthinae)	WA	Shea (1989)
Scarabaeidae	Unspecified scarab beetle	SA	Yeatman (1988)
Tenebrionidae	Unspecified piedish beetles	WA	Henle, 1990 Shea (1989)
	Unspecified arachnid	WA	Shea (1989)
	Unspecified beetles	SA	Satrawaha and Bull (1981), Yeatman (1988)
	Unspecified bugs	WA	Chapman and Dell (1980)
	Unspecified crustacean	WA	Shea (1989)
	Unspecified dipteran (pupae)	WA	Shea (1989)
	Unspecified dragonfly	WA	Chapman and Dell (1980)
	Unspecified insect larva	WA	Shea (1989)
	Unspecified lepidopteran larva	WA	Yeatman (1988), Shea (1989)
	Unspecified millipede	WA	Shea (1989)
	Unspecified roach	WA	Yeatman (1988), Shea (1989)
	Unspecified spider	SA	Yeatman (1988)
Vertebrates			
Muridae	<i>Mus</i> sp.	SA	Yeatman (1988)
Myobatrachidae	<i>Heleioporus psammophilus</i>	WA	Brooker (2016)
Scincidae	Unspecified	SA	Dubas and Bull (1991)
Unspecified	Nestling birds	SA	Dubas and Bull (1991)
Other			
	Lizard scales (dermatophagy)	SA	Yeatman (1988)

Unspecified invertebrates	SA	Dubas and Bull (1991)
Rabbit bones	WA	Dell and Chapman (1979)
Rabbit scats	SA	Dubas and Bull (1991)
Carrion	SA	Satrawaha and Bull (1981)
Carrion (mammalian caudal vertebrae)	WA	Shea (1989)
Carrion (<i>Macropus</i> sp.)	SA	Dubas and Bull (1991)
Carrion (<i>Macropus fuliginosus</i>)	SA	Norval et al. (2018)
Carrion (<i>Oryctolagus cuniculus</i>)	V	Simpson (1973)
Carrion (<i>Pogona barbata</i>)	V	Simpson (1973)
Carrion (<i>Varanus</i> sp.)	NSW	Henle (1990)

Appendix 2. Reported plant-based dietary items of *Tiliqua rugosa* (* – non-native species; WA – Western Australia; NSW – New South Wales; V – Victoria; SA – South Australia).

Family	Species	Notes	Locality	Reference
Aizoaceae	<i>Mesembryanthemum crystallinum</i> *	fruit	WA	Tubb (1938)
Aizoaceae	<i>Tetragonia implexicoma</i>	fruit	SA	Yeatman (1988), Dubas and Bull (1991)
Amaranthaceae	<i>Chenopodium baccatum</i>	fruit	SA	Dubas and Bull (1991)
Anacardiaceae	<i>Schinus molle</i> *	fruit	SA	Norval et al. (2018)
Asparagaceae	<i>Acanthocarpus preissii</i>	fruit	WA	Peters (1973), Shea (1989)
Asparagaceae	<i>Asparagus asparagoides</i> *	fruit	SA	Yeatman (1988)
Asphodelaceae	<i>Dianella</i> sp.	fruit	SA	Yeatman (1988)
Asteraceae	<i>Angianthus tomentosus</i>	flowers	SA	Dubas and Bull (1991)
Asteraceae	<i>Arctotheca calendula</i> *	flowers	SA, V	Dubas and Bull (1991), Mattingley (1909)
Asteraceae	<i>Craspedia</i> sp.		NSW	Henle (1990)
Asteraceae	<i>Pallenis spinosa</i> *	flowers	SA	Dubas and Bull (1991)
Asteraceae	<i>Polycalymma stuartii</i>		NSW	Henle (1990)
Asteraceae	<i>Reichardia tingitana</i> *	flowers	SA	Dubas and Bull (1991)

Asteraceae	<i>Senecio lautus</i>	flowers	SA	Yeatman (1988)
Asteraceae	<i>Vittadinia gracilis</i>	leaves	SA	Norval et al. (2018)
Boraginaceae	<i>Echium plantagineum</i> *		NSW	Henle (1990)
Brassicaceae	<i>Brassica tournefortii</i> *	leaves	NSW	Henle (1990)
Brassicaceae	<i>Cakile</i> sp. *	leaves	SA	Yeatman (1988)
Brassicaceae	<i>Cakile maritima</i> *	flowers and leaves	SA	Dubas and Bull (1991)
Brassicaceae	<i>Carrichtera annua</i>	flowers, leaves and fruit	SA	Spiegel et al. (2015)
Chenopodiaceae	<i>Enchylaena tomentosa</i>	fruit	SA, NSW	Dubas and Bull (1991), Henle (1990)
Convolvulaceae	<i>Convolvulus remotus</i>	flowers and leaves	SA	Norval et al. (2018)
Dioscoreaceae	<i>Dioscorea hastifolia</i>	leaves	WA	Brooker (2016)
Ericaceae	<i>Astroloma macrocalyx</i>	fruit	WA	Keighery (1984)
Ericaceae	<i>Leucopogon parviflorus</i>	fruit	SA	Yeatman (1988)
Euphorbiaceae	<i>Euphorbia paralias</i> *	flowers	SA	Dubas and Bull (1991)
Fabaceae	<i>Medicago minima</i> *	flowers and leaves	SA	Norval et al. (2018)
Fabaceae	<i>Medicago</i> sp. *	flowers and leaves	SA	Dubas and Bull (1991)

Goodeniaceae	<i>Goodenia pinnatifida</i>	flowers	SA	Dubas and Bull (1991)
Iridaceae	<i>Moraea setifolia</i> *	flowers	SA	Dubas and Bull (1991)
Iridaceae	<i>Patersonia</i> sp.	flower	WA	Shugg (1983)
Lamiaceae	<i>Salvia verbenaca</i> *	flowers and leaves	SA	Norval et al. (2018)
Lamiaceae	<i>Teucrium sessiliflorum</i>	flowers	SA	Dubas and Bull (1991)
Malvaceae	<i>Sida intricata</i>	leaves	SA	Norval et al. (2018)
Nitrariaceae	<i>Nitraria billardierei</i>	fruit	SA	Dubas and Bull (1991)
Orchidaceae	<i>Dipodium punctatum</i>	flowers	V	Turner and Doery (1981)
Oxalidaceae	<i>Oxalis corniculata</i> *	leaves	SA	Dubas and Bull (1991)
Phormiaceae	<i>Dianella revoluta</i>	fruit	SA	Dubas and Bull (1991)
Plantaginaceae	<i>Plantago drummondii</i>		NSW	Henle (1990)
Plumbaginaceae	<i>Limonium ramosissimum</i> *	flowers	SA	Dubas and Bull (1991)
Polygonaceae	<i>Muehlenbeckia</i> sp.	fruit	SA	Yeatman (1988)
Primulaceae	<i>Anagallis arvensis</i> *	flowers	SA	Dubas and Bull (1991)
Scrophulariaceae	<i>Eremophila glabra</i>	flowers	SA	Dubas and Bull (1991)
Scrophulariaceae	<i>Eremophila longifolia</i>	flowers	SA	Norval et al. (2018)

Scrophulariaceae	<i>Myoporum insulare</i>	fruit	WA	Tubb (1938)
Scrophulariaceae	<i>Myoporum platycarpum</i>	flowers	SA	Norval et al. (2018)
Solanaceae	<i>Lycium ferocissimum</i> *	flowers and fruit	SA	Dubas and Bull (1991), Satrawaha and Bull (1981), Cole (1930)
Solanaceae	<i>Solanum nigrum</i> *		NSW	Henle (1990)

Appendix 3. Organisms that have been reported as parasites of *Tiliqua rugosa*.

Class	Species	Reference
Gammaproteobacteria	<i>Escherichia coli</i>	Gordon and Cowling (2003)
	<i>Salmonella enterica</i>	Bull et al. (2012)
Ciliata	<i>Nyctotherus trachysauri</i>	Johnston (1932)
Coccidia	<i>Eimeria</i> sp.	O'Donoghue (1998)
	<i>Eimeria tiliquae</i>	Yang et al. (2013)
	<i>Hemolivia mariae</i>	Smallridge and Bull (2000)
	<i>Schellackia</i> sp.	O'Donoghue (1998)
Flagellata	<i>Bodo</i> sp.	Johnston (1932)
	<i>Copromonas</i> sp.	Johnston (1932)
	<i>Trichomastix</i> or	Johnston (1932)
	<i>Trichomonas</i> sp.	
Sarcodina	<i>Endamoeba</i> sp.	Johnston (1932)
Cestoda	<i>Oochoristica trachysauri</i>	MacCallum (1921)
Nematoda	<i>Abbreviata antarctica</i>	Jones (1992)
	<i>Oxyuris</i> sp.	Thapar (1925)
	<i>Thelandros trachysauri</i>	Johnston and Mawson (1947)
	<i>Veversia tuberculata</i>	von Linstow (1904)
Trematoda	<i>Brachylaima cribbi</i>	Butcher and Grove (2005)
	<i>Microphallus</i> sp.	Angel and Mawson (1968)
	<i>Paradistomum crucifer</i>	MacCallum (1921)
Arachnida	<i>Amblyomma albolimbatum</i>	Neumann (1907)

<i>Amblyomma limbatum</i>	Sharrad and King (1981)
<i>Amblyomma moreliae</i>	Roberts (1964)
<i>Amblyomma triguttatum</i> <i>triguttatum</i>	Petney et al. (2008)
<i>Amblyomma vikirri</i>	Keirans et al. (1996)
<i>Bothriocroton hydrosauri</i>	Ferguson (1925)
<i>Ornithodoros gurneyi</i>	Sharrad and King (1981)
