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Association networks reveal social organization in the sleepy lizard

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We investigated the social organization of the Australian sleepy lizard, *Tiliqua rugosa*, by describing the social network of a local population. We attached activity meters and GPS recorders to 21 neighbouring lizards in a semiarid site in South Australia, and monitored their location every 10 min over 3 months (September–December 2007). From over 5000 sets of synchronized location records we calculated distances between all possible dyads of active lizards, and constructed binary social networks based on close associations between individuals. We compared empirical networks with a null model network for spatially structured populations that assumed random movement within lizard home ranges. We showed significantly lower network degree (i.e. fewer cases of individuals associating) in the observed network than in the null model, and deduced avoidance between some individuals. We found the predominant form of social organization was pair living, and, contrary to previous reports, we found pair associations persisted after mating had finished. Thus, the network analysis revealed a cryptic social organization, which cannot be explained by either biparental care or mate guarding, but may instead relate to refuge site distributions, enhanced vigilance or efficient location of mates in subsequent seasons.

Most animal species show some form of social behaviour (Bried et al. 2003; O'Connor & Shine 2003; Croft et al. 2004; Whitehouse & Lubin 2005; Boomsma & Franks 2006; Smith et al. 2008), and there is increasing interest in how populations are divided into social units, that is, sets of individuals that interact more frequently among each other than with members of other social units (Struhsaker 1969). The description of social network structure within a population can help address this question. The socioecological model (Crook 1965; Trivers 1972; Emlen & Oring 1977) has provided a theoretical framework that suggests how the formation and structure of the social unit in a species is determined by the distribution of risks and environmental resources in time and space, and by strategies that maximize individual reproductive success. Investigations of the socioecological model have rarely focused on reptiles. Historically, most lizard species were considered to be solitary, and to have a polygynous mating system (Bull 2000; Chapple 2003). This perception is changing and lizards are beginning to be recognized as complementary model organisms (Fox et al. 2003; O'Connor & Shine 2003; Stow & Sunnucks 2004; Chapple & Keogh 2006; While et al. 2009a, b). Furthermore, studies of lizards will contribute to a broader understanding of the evolution of social behaviour as lizards have unique selection pressures. For example, neither biparental care, which selects for social associations in many bird species (Mock & Fujioka 1990; Kokko 1999), nor infanticide risk, a strong selection pressure in primates (van Schaik & Kappeler 1997), is common in lizards (although infanticide in lizards is occasionally reported, Lanham & Bull 2000; O'Connor & Shine 2004). Instead, mate guarding (Olsson & Shine 1998; Cuadrado 2001; Murray & Bull 2004), enhanced vigilance (Lanham & Bull 2004) and resource distribution (Duffield & Bull 2002; Nieuwoudt et al. 2003; O'Connor & Shine 2003) may select for social associations in lizards.

Kappeler & van Schaik (2002) defined three logically distinct components of a social unit: social organization, social structure and mating system. We investigated the social organization, which describes the size and composition (with respect to sex, age and kinship) of a social unit as well as the distribution of its members in space and over time. While there are some contingencies among the three components of a social unit, there is also room for independent variation. Social units in which one male and one female are associated are particularly interesting in this respect because

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they provide an opportunity to study the dynamics of intersexual conflict (Chapman et al. 2003). As a result of this conflict, a monogamous mating system does not necessarily imply a pair-living social organization and vice versa. For example, the gidgee skink, *Egernia stokesii*, is a group living but monogamous skink (Gardner et al. 2002), whereas the fat-tailed dwarf lemur, *Cheirogaleus medius*, is pair living but has a polygynandrous mating system (Fietz et al. 2000). Pair living is the most common type of social organization in birds, because biparental care is possible and adaptive, but pairs are rare among other vertebrates (Reichard & Boesch 2003). Pair living in mammals, reptiles, amphibians and fish without biparental care therefore constitutes one of the most intriguing problems in socioecology. Two main hypotheses are used to explain pair living in the absence of biparental care (Stow & Sunnucks 2004). One is that males adopt pair living when they are unable to maintain access to multiple females, because of their distribution in time and space (Emlen & Oring 1977). Then males secure access to the single female through territoriality or direct mate guarding (Cuadrado 2001). The other is that females adopt pair living when they benefit from male presence, for example through enhanced vigilance (Bull & Pamula 1998) or reduced harassment by other males (Censky 1997).

Previous studies have suggested that the Australian sleepy lizard, *Tiliqua rugosa*, lives in pairs for extended periods before but not after mating (Bull 1988; Bull et al. 1998; Kerr & Bull 2006a). In this study we explored the social association patterns in a sleepy lizard population during both the pre- and postmating periods and described the social organization. Sleepy lizards establish long-term stable home ranges with minimal positional shift between years (Bull & Freake 1999). Although there is extensive home range overlap with neighbouring lizards of both sexes, home range core areas only overlap on average with one other individual, usually of the opposite sex (Kerr & Bull 2006a). This spatial arrangement, in particular the exclusive core home ranges, suggests that social interaction predominantly occurs between one male and one female, that is sleepy lizards have a pair-living social organization. But, spatial overlap of the home ranges of a male and a female does not necessarily imply their regular direct association because individuals may still actively avoid each other within their home ranges. However, pair living was further supported by reports from previous random encounter studies of close associations of male–female pairs over 8 weeks in spring before lizards mate, but also of pairs appearing to separate after mating (Bull 1988; Bull et al. 1998). In both the pre- and postmating periods, male and female individuals are often also encountered alone (Bull 1988; Bull et al. 1998). Additionally, after mating, groups of more than two lizards are sometimes found sharing key refuge sites that provide cool, deep shelter during the hot and dry austral summer (Kerr & Bull 2006a). These observations suggest a complexity of sleepy lizard social behaviour that remains to be discovered.

To investigate the social organization of the sleepy lizard we continuously monitored social associations among a large sample of neighbouring individuals over a period of 3 months. We used a network approach to analyse this detailed data set, which allowed a much more detailed evaluation of the social association patterns than more traditional approaches. In particular, it allowed us to investigate the association patterns of our study population as an entity (Krause et al. 2007), while taking into account that interacting individuals in a study population are not truly independent from one another (Croft et al. 2008). We described the social network in a population of sleepy lizards and compared it to a novel null model network for spatially structured populations. We addressed three questions: (1) are sleepy lizard social association patterns nonrandom, (2) is there a consistent pattern of more regular social associations that illuminates an underlying social organization, and (3) do social association patterns change over time?

METHODS

Study Site and Animals

This study took place in a 700 × 1000 m site near Bundey Bore Station, in the mid-north of South Australia (33°54′16″S, 139°20′43″E). The area is characterized by homogeneous chenopod shrubland, dominated by bluebush, *Maireana sedifolia*, and has an annual average rainfall of 238 mm (1925–2006). The sleepy lizard is a large (adults: snout–vent length ≥ 28 cm), long-lived (20–50 years, Bull 1995) scincid lizard endemic to Australia. In the study area it is most active during spring and early summer (mid-September to mid-December, Bull 1987; Firth & Belan 1998), the time when we conducted our study. Mating occurs during a short 2-week period, usually in late October or early November (Bull 1988). Previous studies have separated the activity period into an 8-week premating season (mid-September to mid-November), when individuals can be found in pairs during random encounter observations, and a postmating season (mid-November to mid-December), when lizards are rarely encountered in pairs (Bull 1988; Bull et al. 1998). Lizard activity at the study site is infrequent by late December (Kerr & Bull 2006b), when the annual plants that they feed on have usually dried out.

GPS Tagging of Study Animals

The lizards were treated using procedures formally approved by the Flinders University Animal Welfare Committee in compliance with the Australian Code of Practice for the Use of Animals for Scientific Purposes and conducted under the Department of Environment and Heritage Permit to Undertake Scientific Research.

In August 2007 we captured all of the 21 adult lizards (10 males, 11 females) that occupied neighbouring home ranges in the study site. We attached a 37 g unit to the tail of each lizard which included a data logger, a GPS device and a radiotransmitter, and which represented 4.9% of an average 750 g lizard, 6.7% of the lightest lizard. Lizards were caught by hand and units attached using surgical adhesive tape. The use of adhesive tape is a well-established method to attach radiotransmitters to the tail of the sleepy lizard, and we have never observed any skin irritation or other adverse effect on lizard health or behaviour. The methods have been observed and approved by a veterinarian member of the Flinders University Animal Welfare Committee. Lizards could be located and individually recognized by their unique radiotransmitter frequency. Between 15 September and 15 December, the data loggers recorded body temperature, and the number of steps taken every 2 min of every day (Kerr et al. 2004), plus a GPS location every 10 min if the lizard had moved in that period. We synchronized the data-recording process among all GPS devices, so that all locations were recorded at exactly the same time. Once every 2 weeks we recaptured each lizard to download the data and to replace the battery. Handling time (less than 60 min) was excluded from the data set. Over the study period we used 22 GPS devices, to allow for occasional service requirements. After the study we removed the units and released all lizards. We did not detect any damage or irritation of the skin where the units were attached and lizards naturally shed their skin in the following months. We believe that the GPS devices did not adversely affect lizard behaviour, because movement activity appeared similar to that of untagged lizards and mating behaviour of similarly tagged lizards has been regularly observed (How 2001; Kerr et al. 2004; Michniewicz 2004; S. Godfrey, personal communication).