



The social life of eastern water dragons: sex differences, spatial overlap and genetic relatedness



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Understanding the ways individuals socialize with each other and how they differ temporally, spatially and phylogenetically is key to unravelling the evolutionary processes that shape social evolution. Our current knowledge of social evolution in vertebrates, however, has primarily come from bird and mammalian studies. Despite being largely understudied, reptiles remain an important piece of the puzzle in our study of social evolution; they represent a major class of vertebrates and, similar to mammals and birds, many are gregarious. Increasing our understanding of sociality in reptiles is important given that it would allow for comparisons across phylogenetically distinct vertebrate classes. In this study, we investigated the social structure of the eastern water dragon, *Intellagama lesueurii*, and found that males and females showed both preference and avoidance for members of either sex. Furthermore, we found sex differences in the extent of individual sociability: females generally formed stronger associations with one another than any other sex class (e.g. male–male, male–female). Although association patterns correlated to some extent with home range overlap, we found no evidence of a correlation with kinship. Overall, our study presents additional evidence that sociality can evolve outside the realm of kin selection.

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Group living, defined here as a set of conspecifics aggregating and interacting with each other more than expected by chance (Wilson, 1975), is a fundamental component of sociality. Individuals can benefit from living in groups and associating with conspecifics via enhanced foraging efficiency (Brown, 1988; Canonge, Deneubourg, & Sempo, 2011), reduced predation risk (Sorato, Gullet, Griffith, & Russell, 2012; Sridhar, Beauchamp, & Shanker, 2009) and increased fitness benefits, by either increased offspring survival (McGuire, Getz, & Oli, 2002) or increased reproductive success (Silk, 2007). Living within a group may also incur costs, such as increased competition for resources (Clutton-Brock & Huchard, 2013) and increased risk of transmission of disease (Godfrey, Bull, James, & Murray, 2009). This implies that individuals face a cost–benefit trade-off when living within a group, and it is thought that sociality may evolve when the net benefits of living in a group outweigh the costs (Alexander, 1974). But before we can begin to understand what the cost–benefit trade-offs of group living within a population may be, we must first endeavour to understand and characterize its social structure. This is particularly

important given that the extent of the cost–benefit trade-off for an individual may depend on the type of its interactions (e.g. random versus nonrandom, loose versus stable association, kin versus nonkin, within versus between the sexes, etc.).

The majority of empirical studies investigating sociality to date have focused on birds and mammals. From these studies, we have discovered that social systems are incredibly variable both within and across species, and yet, similarities can be found across taxa. For instance, birds have been documented to live in cooperatively breeding social systems, for example the superb fairy-wren, *Malurus cyaneus* (Dunn, Cockburn, & Mulder, 1995). Birds have also been found to live in groups with dominance hierarchies such as in house sparrows, *Passer domesticus* (Buchanan, Evans, & Goldsmith, 2003). Similarly, mammals have been shown to live in cooperatively breeding social systems (e.g. banded mongoose, *Mungos mungo*; Cant, 2000) and social dominance hierarchies (e.g. mountain gorillas, *Gorilla beringei beringei*; Robbins, 1999). In addition, mammals have been documented living in both fission–fusion social systems (e.g. Bechstein's bats, *Myotis bechsteinii*; Kerth, Perony, & Schweitzer, 2011: chimpanzees, *Pan troglodytes troglodytes*; Le Hellaye, Goossens, Jamart, & Curtis, 2010) and stable social groups (e.g. female chacma baboons, *Papio hamadryas ursinus*; Silk et al., 2010). From this body of work, we have gained a

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greater understanding of the factors that drive social evolution such as, but not limited to, predation risk (Dunbar, 1988; Van Schaik & van Hooft, 1983), inbreeding avoidance (Perrin & Mazalov, 2000), competition for resources (Clutton-Brock & Harvey, 1977; Krebs & Davies, 1993) and kin selection (Hamilton, 1964). But we are yet to unravel the extent to which these factors influence sociality in reptiles.

In contrast to birds and mammals, reptiles have largely been ignored in the study of social evolution (Doody, Burghardt, & Dinets, 2013). Reptiles do, however, remain an important piece of the puzzle when it comes to our understanding of social evolution: they represent a distinct phylogenetic lineage (O'Connor & Shine, 2003; While, Uller, & Wapstra, 2009), and, similar to mammals and birds, many are gregarious. A growing body of work over the last decade has shown that a variety of reptile species are social (reviewed in Doody et al., 2013). This has been particularly apparent within the scaled reptile order (Squamata) in which social organization includes social pair bonds and stable family groups (e.g. sleepy lizard, *Tiliqua rugosa*; Leu, Bashford, Kappeler, & Bull, 2010; black rock skink, *Egernia saxatilis*; O'Connor & Shine, 2003; gidgee skink, *Egernia stokesii*; Duffield & Bull, 2002). Social grouping in reptiles is not unique to skinks and lizards. Snakes also display what has been coined cryptic social behaviour, whereby individuals are found preferentially aggregating with one another. For example, juvenile and pregnant female rattlesnakes, *Crotalus horridus*, commonly aggregate preferentially with kin (Clark, Brown, Stechert, & Greene, 2012) and turtle-headed sea snakes, *Emydocephalus annulatus*, are found ranging with the same individuals in subsequent years (Shine, Shine, Shine, & Shine, 2005). Together, these results demonstrate that some reptile species do, in fact, exhibit complex social systems, and may provide valuable empirical systems with which to further our understanding of social evolution in vertebrates by allowing factors influencing sociality to be compared between all major vertebrate classes. Such comparisons are important in the development of social evolution theory because they would enable us to gain greater insights into the ecology of sociality across species.

The eastern water dragon, *Intellagama lesueurii*, is a semi-aquatic, arboreal agamid lizard native to Australia. It is long lived (Thompson, 1993) and displays male-biased sexual dimorphism. Males display plasticity in their mating strategies, switching between two tactics involving either aggressively defending a territory or assuming satellite subordinate behaviour (Baird, Baird, & Shine, 2012). Eastern water dragons occur at high density along freshwater shorelines (Thompson, 1993) and anecdotal and observational evidence suggests that they are social, with females interacting with territorial males more than with satellite males (Baird et al., 2012). No studies to date, however, have investigated whether or not eastern water dragons exhibit evidence of social structure. It has been suggested that to describe a population as socially structured, individuals within that population must exhibit nonrandom patterns in their affiliative associations with one another (Croft, James, & Krause, 2008; Whitehead, 1997; Whitehead, Bejder, & Ottensmeyer, 2005). That is, individuals exhibit preferences and avoidance for one another. Here, we combined behavioural and genetic data to investigate whether a population of eastern water dragons at the Roma Street Parkland, located within the central business district of Brisbane, Australia, exhibit nonrandom patterns in their affiliative associations. In particular, we tested for sex differences in patterns of association and spatial overlap. We then used genetic data to investigate whether individuals preferentially associate with kin. Associations between individuals can be challenging to observe and record in the wild, and, as such, we used spatial proximity as a proxy for associations between eastern water dragons. This methodology

was suggested by Whitehead (1997) and has been used in many mammalian studies to assess group and dyad membership in order to characterize social structure (e.g. giraffes, *Giraffa camelopardalis*; Carter, Seddon, Frère, Carter, & Goldizen, 2012; bottlenose dolphins, *Tursiops aduncus*; Frère et al., 2010; Spix's disc-winged bats, *Thyroptera tricolor*; Vonhof, Whitehead, & Fenton, 2004).

METHODS

Study Population

We used data collected as part of an ongoing behavioural and genetic study of eastern water dragons at Roma Street Parkland (RSP) in Brisbane, Australia (27°27'46"S, 153°1'11"E). RSP is a highly curated city park which covers an area of 16 ha and comprises a range of discrete habitats including an arid zone, densely planted ornamental flower garden, wetland zone and tropical bromeliad gardens. Its diverse vegetation and available water bodies has accommodated a large population of eastern water dragons estimated at 586 individuals (Gardiner, Doran, Strickland, Carpenter-Bundhoo, & Frère, 2014). Located in the heart of Brisbane's Central Business District, the Parkland is semienclosed by busy roads, residential and commercial buildings as well as a train line. This may deter easy immigration to or emigration from the park for individual eastern water dragons (see Figure 1 in Gardiner et al., 2014).

Surveys

Surveys were conducted following a transect line through the RSP averaging once a week during the field season (September–March) when eastern water dragons are most active, starting January 2011 and finishing January 2013. Eastern water dragons are present in 60% of the park, and transects covered approximately 85% of this area (see map in the Supplementary material). For each individual that we encountered, we collected the following information: its sex, GPS location and a photo of its profile. Sex was assigned based on morphological differences; males are considerably larger, with heavyset jaws, and sport distinctive red chests whereas females are generally smaller and lack the red coloration. One individual's sex could not be determined, so it was classed as unknown. GPS coordinates of an animal's location were collected using a GARMIN eTrex10 GPS device (Garmin Ltd. Eastern Creek, Australia). The photographs of an individual's head profile were taken using a Canon EOS 600 digital camera for photo identification.

Individual Identification

Photographic ID was possible using scale patterns, coloration and scars on the animals' profiles as distinguishing features. Individual ID was determined using the I³S Manta (Spot Shape, Reijns, Rotterdam, Netherlands) software package which was initially designed for the individual identification of manta rays, *Manta birostris* (Van Tienhoven, Den Harthog, Reijns, & Peddemors, 2007). This software allows users to mark three reference points on each image; we used ear, nose and eye of each individual. Unique scale patterns around each animal's ear are marked with a series of ellipses to generate an electronic 'fingerprint' for each image. The software then generates a list of the 50 closest matches against a database of known individuals. The identity of individuals is then confirmed manually by comparing the profile of the unknown individual to the 50 closest matches. Ambiguous identifications and poor quality photographs were discarded. I³S manta returned the correct identification within the first five matches in

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