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# Eastern water dragons modify their social tactics with respect to the location within their home range



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Keywords: eastern water dragon home range reptile social avoidance social behaviour social plasticity social preference Animals may modify their behaviour towards conspecifics to manage social conflict that arises due to group living. Given that social conflict is likely to vary through space, we would expect individuals to adjust their social behaviour, accordingly, across their home range. This, however, remains to be explicitly investigated. Here, we used a longitudinal behavioural data set on eastern water dragons, *Intellagama lesueurii*, a social reptile, to investigate the extent to which social tactics (individual patterns of long-term social preferences and avoidances) vary across individuals' home ranges. We found that expression of both social tactics increased within the core home range, which also coincided with increased population density and frequency of agonistic displays. Furthermore, we found that the magnitude of this spatial behavioural shift was sex dependent, with females exhibiting a greater increase in both social tactics than males. Together, our results illustrate that dragons modify their social tactics across space, highlighting the importance of accounting for the spatial dimension when studying social behaviour. Our observations further suggest that spatial social plasticity may be key to balancing costs associated with increased social conflict. We encourage new studies to test this link, which may provide important insight into the adaptive significance of spatial social plasticity.

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Animals should modify their behaviour towards conspecifics to adequately manage social conflict associated with group living (Oliveira, 2009; Schradin et al., 2011; Taborsky & Oliveira, 2012; de Waal & Aureli, 2000; de Waal, 2000). Under natural conditions, however, the strength of social conflict often varies across the landscape, for instance due to spatial heterogeneity in the distribution and density of conspecifics, which, in turn, can often be concentrated around ecologically significant resources (Rubenstein, 1981; Svanbäck & Bolnick, 2007). As a result, we would expect individuals to adjust their social behaviour, accordingly, across their home range (i.e. the area occupied by individuals in their regular activities, to be distinguished from territory or area actively defended by individuals, Burt, 1943). Indeed, studies have demonstrated that individuals may adjust territorial behaviours, such as patrolling, agonistic displays, territory marking or territorial calls, based on their spatial positioning (Mayade, Cammaerts, & Suzzoni, 1993; Mertl-Millhollen, 1988; Olsen, Downs, Tucker, & Trost, 2011).

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Group living often generates strong social conflict due to, for instance, increased resource competition, aggression and sexual harassment (Clutton-Brock & Huchard, 2013; Pusey & Packer, 1997; Rubenstein, 2012; Smuts & Smuts, 1993). Here, individuals can negotiate potential conflict by adjusting their social behaviour according to the environment they experience (i.e. exhibiting plasticity in social behaviour, Lewis, 2008; Noë, 2001; Oh & Badyaev, 2010; Oliveira, 2009; Taborsky & Oliveira, 2012). Examples of this include female horses, Equus ferus, forming long-lasting associations to manage harassment from males (Cameron, Setsaas, & Linklater, 2009), or male house finches, Carpodacus mexicanus, changing their social group and spatial range based on the attractiveness of opponents (Oh & Badyaev, 2010). The ability of individuals to optimally adjust their social behaviour may become particularly important when they encounter elevated levels of social conflict, for instance, under high population density. This is evident in the striped mouse, Rhabdomys pumilio, which, when living under high population densities, exhibits philopatry and group living during the breeding season to avoid competition with unfamiliar neighbours (Schoepf & Schradin, 2012). Also, studies in primates show that short-term increases in population density





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reduce the rate of social interactions to minimize the risk of aggressive conflicts (Aureli & de Waal, 1997; Judge & de Waal, 1993). When exposed to prolonged periods of high density, however, primates have also exhibited increased tendencies towards postconflict reconciliation and play behaviours (Cordoni & Palagi, 2007; Tacconi & Palagi, 2009). Together, these studies show that individuals may manage social conflict by opting to associate with or socially tolerate certain conspecifics, while simultaneously avoiding others (Cameron et al., 2009; Connor, Smolker, & Richards, 1992; Schülke, Bhagavatula, Vigilant, & Ostner, 2010; de Waal, 2000). The adoption of either may depend on their associated costs and benefits, which, in turn, may vary with respect to the social system and the current environment (e.g. population density or levels of resource competition).

Population density is tightly linked to resource distribution, as conspecifics are often concentrated around discrete resource patches, increasing competition and the potential for conflict (Aureli et al., 2008; Clutton-Brock & Huchard, 2013; West-Eberhard, 1979). This may extend to the scale of an individual's home range, where the heterogeneous distribution of resources may lead to spatial variation in density of conspecifics. As a result, individuals are most likely to experience differing degrees of resource competition and social conflict across their home range. In species with extensive home range overlap, for instance, the risk of resource competition may be highest within an individual's core home range, as this generally contains the most intensely used resources (e.g. sleeping sites, refuges and reliable food sources, Burt, 1943: Kaufmann, 1961). Here, under scenarios where there is a high risk of social conflict, we would expect a shift in the costs and benefits of socializing. On the one hand, the costs of socializing may increase due to potential aggression and related injuries (Calhoun, 1962). On the other, competition may also increase the benefits of cooperation, for instance in resource acquisition or defence (Clutton-Brock, 2009; Port, Schülke, & Ostner, 2017). Therefore, we would expect to see individuals adjusting their social behaviour with respect to spatial changes in the costs and benefits of socializing (Aureli et al., 2008). This would lead to spatial variation in the expression of social behaviour, a concept yet to be extensively studied.

Here, we used a longitudinal behavioural data set on eastern water dragons, Intellagama lesueurii (hereafter referred to as dragons), a social reptile (Strickland & Frère, 2017; Strickland, Gardiner, Schultz, & Frere, 2014; Strickland et al., 2017), to explore the extent to which individual patterns of long-term social preferences and avoidances (hereafter referred to as preferences and avoidances or social tactics) vary across space (i.e. the position of the animal relative to the centroid of its home range). Our studied population inhabits a curated inner-city park in Brisbane, Australia. The landscape of this 16 ha park is highly heterogeneous and includes a variety of themed gardens and recreational areas (e.g. rainforest, arid features, large flower displays and playgrounds, Gardiner, Doran, Strickland, Carpenter-Bundhoo, & Frère, 2014). The density of resident dragons (approximately 336 adult individuals, Strickland et al., 2014) is similarly heterogeneous, with high population densities occurring in certain types of habitat, such as those with complex vegetation and water features, and results in extensive home range overlap among individuals (Gardiner et al., 2014). This pattern suggests that dragon home ranges will contain high levels of spatial heterogeneity in the distribution of resources and conspecifics. As such, we would expect that this would require dragons to modify the type of social tactics (preferences and avoidances) they foster depending on their spatial position within their home range. In the current study, we explored whether and how individuals exhibit spatial variation in their social tactics. We further tested for sex-biased variation, given differences in life histories. Here, male dragons are territorial and compete aggressively with other males over females (Baird, Baird, & Shine, 2012), while females' challenges include resource acquisition (e.g. food, refuge, suitable nesting sites) and managing male sexual harassment. Because competition over food and safety has been shown to result in increased expression of social tactics (Hirsch, 2011; Vogel & Janson, 2007), we would expect female dragons to exhibit a greater extent of preferences and avoidances than males. Moreover, previous studies in this species have shown similar sex differences, with females showing stronger associations than males (Strickland et al., 2014).

## METHODS

#### Study Species, Site and Data Collection

The eastern water dragon is a semiaquatic, arboreal agamid lizard native to Australia that is distributed across the east coast from central New South Wales to northern Queensland. It is a longlived reptile (up to 15 years) that displays male-biased sexual dimorphism, with males being significantly larger, having bigger heads and jaws and presenting red ventral coloration (Baird, Baird, & Shine, 2013; Cuervo & Shine, 2007; Thompson, 1993). Males can grow over 1 m long, with snout-to-vent lengths (SVL) up to over 30 cm and body weights reaching 1 kg, being the largest agamid lizard in Australia (Thompson, 1993; Wilson & Swan, 2003). Dragons are omnivorous and generalists, with a broad diet including insects, small animals and plant materials, such as flowers, fruits and seeds, even extending their diet to include anthropogenic food sources. The males exhibit alternative mating strategies, which are plastic, showing various degrees of dominance and territoriality (Baird et al., 2012). Dragons exhibit a defined social structure, showing preferences for specific individuals within their range, in some cases even when there is little spatial overlap (Strickland et al., 2014). Also, individuals selectively and actively avoid other individuals, even when there is substantial home range overlap (Strickland et al., 2014, 2017). Dragon males in this population have an average (±SD) home range size of  $4270 \pm 2248.4 \text{ m}^2$ , whereas females' home ranges average  $2778 \pm 1126.7 \text{ m}^2$ . Individual home ranges overlap extensively (each home range overlaps on average with those of  $128 \pm 44$ conspecifics), with some individuals sharing their entire (100%) home range with others.

We used data collected as a part of an ongoing longitudinal study of dragons at the Roma Street Parkland (RSP), Brisbane, Australia (27°27′46′S, 153°1′11′E; for more information on the study site and population see Strickland et al. (2014) and Gardiner et al. (2014)). Behavioural surveys were conducted following a fixed transect that covers approximately 85% of the population. Surveys were carried out twice daily (between 0730 and 1030 hours and between 1300 and 1500 hours) between August and April, when dragons are most active. For each individual sighted we noted the sex (based on morphological differences, Baird et al., 2013; Cuervo & Shine, 2007; Thompson, 1993) and GPS location (using a GARMIN eTrex10 handheld device), and made observations of agonistic behaviour typical of agamid lizards (e.g. head bobbing, tail slaps, forelimb waving, push-ups, Baird et al., 2012; Carpenter, Badham, & Kimble, 1970; Osborne, 2005; Perry, LeVering, Girard, & Garland, 2004; Pratt, Alberts, Fulton-Medler, & Phillips, 1992). A profile image of each animal's head was also captured (using a Canon EOS 600 digital camera), to enable individual identification using the software I3S Manta (Van Tienhoven, Den Hartog, Reijns, & Peddemors, 2007), which relies on unique scale patterns and coloration (Gardiner et al., 2014). The software compares individual pictures to an existing database and outputs the 50 closest matches, Download English Version:

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