Female–female aggression functions in mate defence in an Asian agamid lizard

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Female–female aggression and its functions are poorly understood compared with male–male aggression. Here, we examined the role of female–female aggression in mate defence in an Asian agamid lizard, Phrynocephalus vlangalii, in which male neighbours are valuable to females in both mating success and resource defence. We provided three social contexts by pairing a resident female with either a neighbour male, unfamiliar male or unfamiliar female, then introduced a tethered unknown female (intruder). We carried out our experiments during and outside the mating season to test the links between female–female aggression and mate defence. The aggressive responses of resident females in these different social contexts were compared by quantifying variation in their territorial displays. Resident females were faster to display to the intruder in the presence of a neighbour male compared with both the unfamiliar male and female. We also found that female lizards signalled faster in the presence of the neighbour male than the other contexts, but only during the mating season. To separate the effects of familiarity from those of sex, we carried out a second experiment in which we paired a resident female with a neighbour male or neighbour female, before introducing a tethered unfamiliar female. In this experiment, resident females responded sooner to intruder females when paired with the neighbour male, although signalling speeds were equivalent. Taken together, our results suggest female–female aggression is used for both resource and mate defence, and so might be under direct selection. Our study highlights that female aggression more broadly requires further work.

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Although reported in many taxonomic groups, the potential functions of female–female aggression are poorly understood compared to male–male aggression (Clutton-Brock & Huchard, 2013; Lea & Ryan, 2015; Mobley & Green, 2013; Rosvall, 2011). A key question is whether exaggerated female traits and behaviour, including female–female aggression, are by-products of genetic correlations with males (Lande, 1980), or a consequence of direct selection on females themselves (Stockley & Campbell, 2013). Males and females share most of their genome, and traits that are advantageous to males are frequently expressed in females as well (Forstmeier, Martin, Bolund, Schielzeth, & Kempenaers, 2011; Lande, 1980). A comparative study of testosterone levels in birds demonstrates that direct selection on males probably affects female trait expression indirectly; hence female birds in which males have higher testosterone levels also have higher testosterone levels (Møller, Garamszegi, Gil, Hurtrezboussès, & Eens, 2005; Rosvall, 2013). However, growing evidence suggests that female–female aggression has important consequences for female intrasexual competition and evolves from direct selection on females (Cain & Ketterson, 2012; Rosvall, 2011; Stockley & Bro-Jørgensen, 2011; Stockley & Campbell, 2013). For example, in the Carolina dark-eyed junco, Junco hyemalis, larger females are more aggressive and competitive, and are also more likely to breed successfully (Cain & Ketterson, 2012). A similar outcome for aggressive females has also been found in the White's skink, Egernia whitii (Sinn, While, & Wapstra, 2008).

Several nonmutually exclusive hypotheses have been proposed to explain the function of female–female aggression (Rosvall, 2011; Stockley & Bro-Jørgensen, 2011). The resource competition hypothesis predicts that female–female aggression facilitates the acquisition of critical resources (e.g. food and space). Support for this hypothesis comes from mammalian species, with female aggression peaking during pregnancy and lactation, thereby ensuring sufficient food and space for their offspring (Boness,

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Anderson, & Cox, 1982; Robinson & Kruuk, 2007). Similarly, in birds, female aggression varies with season and context according to when females are most likely to experience resource constraints (Cain & Langmore, 2015; Gill, Alfson, & Hau, 2007), to ensure high nest success (Cain & Ketterson, 2012). In contrast, the offspring defence hypothesis proposes that female–female aggression in mammals contributes to protecting offspring from infanticide, thereby ensuring their survival (Christenson & Le Boeuf, 1978; Wolff & Peterson, 1998). Higher survival rates of juvenile White's skink have also been attributed to increased female–female aggression during the breeding season and postpartum periods (Sinn et al., 2008), suggesting that offspring defence explanations are taxonomically widespread.

The mate competition hypothesis predicts female–female aggression functions in obtaining mates (Mobley & Green, 2013; Rosvall, 2011). Classical sexual selection theory asserts that females increase their fitness mainly through resource competition; however, many recent studies have suggested that females, like males, may improve fitness through competition for mates and mate defence associated with paternity, parental care or critical resources (Andersson & Iwasa, 1996; Rosvall, 2011; Stockley & Bro-Jørgensen, 2011). For example, female starlings, *Sturnus vulgaris*, use aggressive behaviour to repel additional females, thereby ensuring parental care from nearby males (Pärn, Lindström, Sandell, & Amundsen, 2008; Sandell & Smith, 1997). Similarly, female topi antelopes, *Damaliscus lunatus*, compete with conspecific females for exclusive access to the best males (Bro-Jørgensen, 2002). Owing to the potential adverse impact, aggression levels among females are likely to vary seasonally and become particularly intense when competition for mates or critical resources is high (Gill et al., 2007; Huchard & Cowlishaw, 2011).

The Qinghai toad-headed agama, *Phrynocephalus vlangalii*, from high elevation areas on the Tibetan Plateau of northwestern China, provides an excellent system for studies on female aggression. This lizard is found in high densities around sand dunes, where male and female lizards occupy small home ranges centred on a burrow. Female home ranges are generally smaller than those of males, and are more likely to overlap with males than with other females (Qi, Noble, Fu, & Whiting, 2012). However, the sex ratio in this species is female biased during the mating season, leaving many females without male neighbours (Wu et al., 2002). Burrows are vital resources to both sexes as they are necessary for avoiding predators during spring and summer, and for escaping harsh winter conditions (Peters, Ramos, Hernandez, Wu, & Qi, 2016). In addition, males have been observed helping neighbour females in territory defence and repelling floater males, which seek forced mating opportunities (Qi, Li, Suo, Li, & Wang, 2011, Qi, Wan, Gu, & Wang, 2011). Occasionally, several females may even form a coalition to repel male intruders (Qi, Li, et al., 2011, Qi, Wan, et al., 2011). Perhaps most interestingly, female–female aggressive interactions are very common both in and outside the mating season, and in a previous study, female–female aggression after the mating season was shown to play an important role in food competition and has important consequences for offspring fitness (Qi et al., 2012; Wu, 2016). However, how female–female aggression functions during the mating season, and whether it plays a role in mate defence, is still unclear.

The objective of the present study was to examine whether female–female aggression functions in mate defence as well as in the defence of resources (i.e. burrows). To assess variation in female aggressive behaviour, we quantified variation in tail displays by female *P. vlangalii*, which are a key component of burrow defence, as a function of the social context. In experiment 1, we compared female–female aggression towards an unfamiliar female intruder

in three social contexts with a resident female paired with either a neighbour male, unfamiliar male or unfamiliar female (Fig. 1). To elucidate the links between female–female aggression and mate defence, we carried out trials during and outside the mating season. In accordance with the resource competition hypothesis, and our previous work on the effect of social context on tail displays in *P. vlangalii* (Peters et al., 2016), we predicted that females would perform tail displays to intruders regardless of social context. Furthermore, we hypothesized that resident females in a female-biased system should value neighbour males highly and predicted that they would exhibit increased aggression when the social companion was a neighbour male, and the aggression level would be notably different between social contexts during the mating season (May–June; Wu, Fu, Yue, & Qi, 2015). The choice of social contexts in experiment 1 was chosen specifically to reflect natural populations in which female territories are more likely to overlap with male than female territories. The unfamiliar male and female social contexts allowed us to examine the effect of sex, while keeping familiarity constant (both unfamiliar). However, the design confounds familiarity and sex and so differences in resident female behaviour in the presence of neighbour males would be ambiguous. Consequently, in experiment 2 we compared female burrow defence in the presence of neighbour male and neighbour female social companions in the mating season. We predicted that female–female aggression should be higher under the neighbour male social context than in the neighbour female social context in line with the mate defence hypothesis.

METHODS

Study Site

We conducted our experiments at Xiaman Conservation Station in the Zoige Wetland Nature Reserve (33.71389°N, 102.48543°E, elevation 3475 m above sea level), in the northeast of Sichuan Province, China. In Zoige, *P. vlangalii* mainly reside in sand dunes and dig burrows near vegetation, with a population density of approximately 3000 lizards/ha (Wu et al., 2002). The vegetation is predominantly composed of *Dracocephalum heterophyllum* and *Carex aridula*, occasionally alongside *Astragalus sutchuenensis*, *Anaphalis lacteal*, *Vicia cracca*, *Morina kokonorica*, *Oxytropis glabra*, *Linum stelleroides* and *Clematis tangutica*. The climate in this area is characterized by a short spring and summer (4 months, from April to July) and a long autumn and winter (8 months, from August to March of the following year).

Experiment 1

Design and procedure

To ascertain whether female–female aggression functions in mate defence, we quantified variation in aggressive signalling of 59 resident females in different social contexts in a repeated measures design (May–August 2015). We introduced a female intruder to a resident female in the presence of one of three social companions (Fig. 1): neighbour male, unfamiliar male or unfamiliar female. A neighbour male was defined as the nearest male whose burrow was within 2 m of the resident female, while both unfamiliar male and female were from a different site, more than 3 km from the focal site, to reduce the likelihood of previous interactions between lizards. We paired resident lizards with intruders of similar snout–vent length (SVL) and mass (within 0.3 mm and 1 g, respectively). Social companions were kept 0.5 m from the focal lizard using a transparent plastic terrarium (30 × 30 cm and 30 cm high; Fig. 1). This has not been trialled before in lizards but similar methods with birds have changed females' responses towards