ORIGINAL ARTICLE



The driving forces behind female-female aggression and its fitness consequence in an Asian agamid lizard

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Received: 20 December 2018 / Revised: 18 April 2019 / Accepted: 29 April 2019 © Springer-Verlag GmbH Germany, part of Springer Nature 2019

Abstract

Female-female aggression and its effect on fitness are poorly understood compared to male-male aggression. We quantified female-female aggression in the viviparous toad-headed agama, Phrynocephalus vlangalii, and tested the mate limitation and resource competition hypotheses, to explain the driving forces behind heightened female-female aggression. We established populations in outdoor enclosures and separately manipulated mate and food availability while quantifying aggressive interactions between known females. Female mass and offspring quantity and quality were monitored for 2 years and used as an index of female fitness. Interestingly, female-female aggression was highest outside the mating season, when females were pregnant. Also, male availability did not significantly influence female-female aggression. Consequently, we found no evidence in support of the mate limitation hypothesis. Female-female aggression, however, was greatest during periods of low-food availability. Greater food availability did have positive fitness consequence for females: high-food treatment females were more likely to gain mass and give birth than females from the low-food treatment, and offspring from high-food treatment females were more likely to survive the first winter. However, we did have an effect of year: female mass was negatively associated with female-female aggression in year 1 but positively associated in year 2, although the association was not significant. The same pattern appeared in the association between offspring sprint speed and female-female aggression: higher levels of female-female aggression in year 1 were associated with slower offspring, while in year 2, higher female-female aggression was associated with faster offspring. Overall, our results demonstrate a link between female-female aggression and competition for resource (food) and highlight the potential importance of female aggressive behavior as a mechanism that influences female fitness.

Significance statement

Male-male contest competition has been a cornerstone of sexual selection theory for decades because dominant males can control more space and access to females. Conversely, female aggression is poorly understood and sometimes considered a paradox, especially in species lacking parental care. We tested whether female-female aggression in the viviparous lizard *P. vlangalii* is best explained by competition for males (mate limitation hypothesis) or competition over food (food limitation hypothesis). Interestingly, female aggression peaks after mating, while females are still pregnant. Heightened aggression at this time supports the food limitation hypothesis because any advantage females have in terms of access to resources will benefit offspring born into her home range. Likewise, access to additional food resources may improve female survival and future reproductive investment through greater energy storage.

Keywords Female-female aggression · Fitness · Mate limitation · Resource competition · Reptile · Phrynocephalus vlangalii

Communicated by S. J. Downes

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00265-019-2686-8) contains supplementary material, which is available to authorized users.

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Introduction

Female-female aggression has garnered great attention in the last decade (Gill et al. 2007; Clutton-Brock 2009; While et al. 2009), and this represents a dramatic shift from male-biased theoretical paradigms (Rosvall 2011; Tobias et al. 2012; Rosvall 2013b; Stockley and Campbell 2013). There are several fundamental issues associated with female-female aggression (Rosvall 2011; Tobias et al. 2012; Stockley and Campbell 2013). A key question is whether exaggerated female traits and behaviors, such as female-female aggression, are byproducts of genetic correlations with males (Lande 1980) or are a consequence of direct selection on females themselves (Stockley and Campbell 2013). Males and females share the vast majority of their genomes, and traits that are advantageous to males are frequently expressed in females too (Ellegren and Parsch 2007; Forstmeier et al. 2011). Nevertheless, other evidence suggests that female-female aggression evolved from direct selection on females themselves, which likely functions in competition over reproductive and social benefits (Tobias et al. 2012; Stockley and Campbell 2013). Due to different constraints on reproductive rate between the sexes and gamete investment, competition for mates is most likely restricted to males, while female intrasexual competition is more likely linked to fecundity-related resources (Bateman 1948; Trivers 1972). To address these issues, many evolutionary biologists advocate that research should focus on identifying the fitness component and targets of selection that are critical for female survival and reproduction (e.g., mate identity, parental care, food) (Tobias et al. 2012; Stockley and Campbell 2013). Additionally, most current knowledge of female aggression is largely derived from studies of mammals and birds. In order to better understand the selective pressures driving the evolution of female aggression, we need data from disparate taxa with different evolutionary history.

Several non-mutually exclusive hypotheses have been proposed to explain the evolution of female-female aggression. The parental investment-guarding hypothesis suggests that females compete for the availability of male parental care investment (Yasukawa and Searcy 1982; Sandell and Smith 1997). On the other hand, while the mate defense hypothesis proposes that females compete for the maintenance of monogamy, more aggressive females are more likely to be monogamously mated and therefore may receive more direct benefits from their mates than under polygyny (Sandell and Smith 1997; Sandell 1998). These two hypotheses overlap because female benefits from monogamy are mostly through male assistance in offspring care. The mate limitation hypothesis posits that females compete for mates when fewer males are present. This hypothesis is most applicable to species with relative reversed sex roles, female-biased sex ratios, or otherwise when there is a shortage of high quality males (Forsgren et al. 2004; Lewis and Rooney 2004; Bebié and Mcelligott 2006; Huchard and Cowlishaw 2011). For example, in the tidewater goby (*Eucyclogobius newberryi*), females compete aggressively for access to limited numbers of territorial males (Swenson 1997). Lastly, the resource competition hypothesis states that females compete for critical resources (food, burrow, and nesting sites), which likely influence female reproductive success and fitness. For example, female tree swallows (*Tachycineta bicolor*) compete for limited nesting sites (Rosvall 2008), while female burying beetles (*Nicrophorus vespilloides*) compete for limited carcasses where they lay their eggs (Eggert et al. 2008).

However, heightened aggression in females may adversely impact parental care, reproduction, and slow offspring development (Gebhardt-Henrich and Richner 1998). In particular, females engaged in frequent female-female aggression may have to reduce their investment in offspring production and hatching (Seebacher et al. 2013), reduce the time and energy in parental care (O'Neal et al. 2008; Stockley and Campbell 2013), reduce their facial attractiveness to conspecific males (Fisher 2004), and lose social opportunities for resource benefits (Rosvall 2008). Therefore, females are predicted to tradeoff aggression with reproductive investment. Aggression may intensify at specific reproductive stages or in particular social contexts when competition for mates or critical resources is acute (Gill et al. 2007; Huchard and Cowlishaw 2011; Seebacher et al. 2013). For example, female buff-breasted wrens (Thryothorus leucotis) respond more aggressively to intrusions by females or pairs compared with that of males, and their aggressive response largely depends on season. Also, female intrusions elicit strong aggressive response during pre-breeding, whereas responses to pair intrusions are more intense during breeding seasons (Gill et al. 2007).

The Qinghai toad-headed agama (Phrynocephalus vlangalii) is an excellent model system for studying femalefemale aggression. Both females and males have high levels of aggression during and outside the mating season (Qi et al. 2011). Furthermore, the sex ratio in natural population is female-biased during the mating season (Wu et al. 2002), which suggests that mate availability for females is likely limited. In addition, as a high elevation species, food may represent a limited resource for P. vlangalii, and hypoxia and low temperatures likely restrict their activity period and foraging time; therefore, both males and females of P. vlangalii defend territories around burrows beyond the breeding season. Also, offspring share burrows with adults at the time of birth (Qi et al. 2012). Furthermore, as a capital breeder, P. vlangalii has a simple placenta, which may mobilize resources gained by females into energy and nutrients needed for the offspring (Thompson and Speake 2006; Wu et al. 2015). A high proportion (ca. 67%) of females give birth synchronously in late August and early September, while others do not reproduce at all, and sexual maturity is reached by age 2 (Wu et al. 2015). Hence, any trait that affects an individual's access to resources may be linked to reproductive success and thus be under selection.

We experimentally examined the potential causes of female-female aggression by manipulating sex ratios and food availability in populations of *P. vlangalii* maintained in seminatural enclosures over a 2-year period. Specifically, two hypotheses proposed to explain variation in female-female aggression were tested. We first tested the mate limitation hypothesis which predicts that female-female aggression increases when potential mates are limited. We then tested the resource competition hypothesis, which predicts that females become more aggressive when food is limited and that greater access to food would translate into fitness through nutrition provision at a critical breeding stage.

Methods

Study site

We conducted our experiments at the Xiaman Conservation Station in the Zoige Wetland Nature Reserve $(33.71389^{\circ} \text{ N}, 102.48543^{\circ} \text{ E}, elevation = 3475 \text{ m a.s.l.})$, northeast Sichuan Province, China. Twelve enclosures $(5 \times 5 \times 1.5 \text{ m})$ were constructed with bricks (Appendix S1). The enclosures are located 2 km from the natural population, where all lizards were collected, and therefore they experienced the same environmental conditions as wild lizards. To simulate the natural habitat of these lizards, we filled each enclosure with sand (0.5 m deep) from the wild and planted grass randomly to attract insects for foraging lizards while also providing structural habitat. To provide additional habitat, ten bricks were randomly arranged in each enclosure. All enclosures were covered with a net to exclude avian predators. The enclosures were set up to be as similar as possible.

Mate limitation hypothesis

During the active season (May to September) in 2012, we tested the mate limitation hypothesis by manipulating mate availability while holding population density and resource availability constant. A total of ten lizards were released into each enclosure, which is similar to their natural population density (3000 lizards/ha) (Wu et al. 2005). We established the following sex ratio treatments: male-biased (MB, male/female = 6:4), female-biased (FB, male/female = 4:6), and equal sex ratio (MF, male/female = 5:5). We acknowledge that one constraint to this study design is that females in the female-biased treatment likely had greater opportunity to express female-female aggression compared to those in the male-biased treatment (Rosvall 2011), although one similar study had shown that female-female aggression largely depends on

male availability rather than population density (Kvarnemo et al. 1995). The treatments were randomly assigned to each enclosure, with four replicates per treatment. A total of 120 adult lizards (60 males and 60 females) were caught by noosing from six different field sites separated by at least 500 m from each other. This was necessary to ensure lizards randomized to each treatment were not familiar with each other. All lizards were individually marked using PIT tags (HT157, Guangzhou HongTeng Barcode Technology Co., Ltd., China). The snout-vent length (SVL) and body mass were measured for each lizard, and sex could be determined by checking for a hemipenis bulge and tail-tip color in this species. To facilitate individual identification during observation, we marked each female on their dorsum using non-toxic acrylic paint. All above procedures were carried out within 1 h after capture. After 24 h, lizards were released to their assigned enclosure, and supplementary food was provided every 2 days for each enclosure to maintain their body condition.

Resource competition hypothesis

During the active season (May to September) in 2013, we manipulated food availability while holding population density and sex ratio constant to test the resource competition hypothesis. The sex ratio was maintained at male/female = 4:6, being similar to natural populations (Wu et al. 2002). Two food treatments, a high-food availability (HFA) and a lowfood availability (LFA), were randomly assigned to the 12 enclosures, with six replicates per treatment. For HFA, 30 mealworms were provided to each enclosure every 2 days; for LFA, ten mealworms were provided to each enclosure every 2 days. A total of 120 lizards (48 males and 72 females, a proportion of them were survivors from mate limitation hypothesis experiment and others were newly collected using noosing), were randomly divided into 12 groups and assigned to each treatment. To reduce the effect of historical interactions, we avoided releasing familiar lizards into the same enclosure. All lizards were processed in the same way as for the mate limitation experiment.

Measurement of female-female aggression

During testing of both hypotheses, behavioral measurements commenced after a 3-day acclimation period. We used ad libitum sampling (Martin and Bateson 2007) during a 25min observation period during which we used binoculars to systematically scan the enclosure from one side to the other and recorded any aggressive interactions by females. We used ad libitum sampling because we were only interested in female-female aggressive interactions. We defined aggressive interaction as either a tail display (tail coil, Peters et al. 2016), chasing, or biting/fighting, because all those behaviors happened concomitantly during agonistic interactions in *P. vlangalii* (Peters et al. 2016). For each interaction, we identified the contest initiator and rival and recorded the specific behaviors displayed by each individual. Finally, we calculated the total number of aggressive interactions a female engaged in with different rivals during the entire season and used this as measurement of female-female aggression. It was not possible to record data blindly because our study involved known animals in the field, from obvious treatments. When weather permitted, we visually scanned all 12 enclosures once daily during 09:30–16:00 h. Occasionally, we were only able to scan six enclosures within a day due to bad weather, and the other six enclosures were scanned first the next day. To avoid bias due to the time of scanning, the 12 enclosures were randomly sampled by the same person (YW).

Index of fitness

To examine the fitness consequence of female-female aggression, we measured female and offspring quality for 2 years after the resource competition experiment in 2013 (year 1) and 2014 (year 2). We measured female post-parturition mass (female mass hereafter), female birth probability (whether or not a female gave birth), offspring litter size, body condition of offspring at birth, offspring sprint speed, offspring growth rate, and offspring overwinter survival. To facilitate data collection, all pregnant females were caught and kept in plastic tubs ($60 \times 45 \times 34$ cm) separately in late August 2013 to ensure the measurement of all offspring and in order to correctly assign them to their mother. To simulate the natural habitat of these lizards, we filled each tub with sand (10 cm deep) from the field. Water and food were provided ad libitum. We measured the female mass after they gave birth. Mass was measured to the nearest 0.01 g using a digital balance. We treated whether or not a female gave birth as a binomial variable (1 =giving birth, 0 = not giving birth). Offspring mass and SVL were measured using similar methods after 24-h birth period. Offspring body condition at birth was calculated using the residuals from a regression of log body mass against log SVL (Haenel and John-Alder 2002).

Offspring sprint speed was measured and calculated using similar methods as Qi et al. (2014). In brief, we enticed the lizards to sprint down a 1.5-m racetrack by lightly touching them with an artist's paint brush on the base of their tail, and all runs were recorded using a high-speed digital camera (Panasonic HDC-HS80). Each offspring's sprint speed was measured once/day over three consecutive days. The maximum sprint speed was used in analysis because lizards' performance can be variable due to motivation and other factors (Losos et al. 2002). We then marked offspring using toe-clipping and released into the mother's home enclosure together with their mother. Ten mealworms were provided every 2 days to maintain their body condition. We noosed all offspring and measured their SVL again after the first month and offspring growth rate was computed using the formula: $(SVL_{t2} - SVL_{t1}) / (\Delta t)$, where SVL_{t2} is the SVL at recapture, SVL_{t1} is the SVL at birth, and Δt is the number of days between birth and recaptures (Mangiamele et al. 2016). For ectotherms in high elevation areas, surviving their first winter is a key component of their life history (Wu et al. 2015). In *P. vlangalii*, the hibernation period starts in late October and lasts for approximately 6 months until early April (Wu et al. 2015). We measured offspring survival after hibernation and calculated the offspring overwinter survival as the ratio of the number of offspring still alive after hibernation, against litter size.

To examine the consequence of female-female aggression on long-term fitness, we kept females and offspring in the same enclosure after hibernation for another 3 months. Ten mealworms were provided to each enclosure every 2 days to compensate the effect due to food shortage. All fitness variables were measured again in late August in 2014.

Statistical analysis

In the mate limitation experiment, we examined the relationships between female-female aggression, sex ratio treatment, and season using a generalized linear mixed model (GLMM) in the "lme4" package (Bates et al. 2015) using R version 3.12 (R Development Core Team 2011). We considered sex ratio treatment and season as fixed effects, with enclosure as a random effect, and assumed a Poisson error distribution. Due to the overdispersion of the data (response variance being greater than the mean in the Poisson error distribution), we included the observation level (sequence of observation) as another random effect following Elston et al. (2001). We also included female SVL as a covariate because the body size has been shown to link with aggression in many animals (Whiting et al. 2006; McGinley and Taylor 2016).

In the resource competition experiment, we also examined the relationships between female-female aggression, food availability, and season using GLMM in the "Ime4" package (Bates et al. 2015). The food availability and season were considered as fixed effects, with female SVL as a covariate, and the enclosure and observation-level as random effects, while assuming a Poisson error distribution.

We examined the relationships between female fitness, food availability treatment, and female-female aggression using GLMM or a linear mixed model (LMM). Fitness measurements collected in 2013 and 2014 were pooled, and the year was included as a fixed effect. Enclosure was regarded as a random effect in all models. For models of offspring body condition at birth, offspring sprint speed, and growth rate, female identity was included as a random effect to account for the potential effect of similar genetic background. A Gaussian error distribution was assumed in models of female mass, offspring body condition at birth, offspring sprint speed, offspring growth rate, and offspring overwinter survival. A Poisson error distribution was assumed in the model of offspring litter size, while a binomial error distribution was assumed in the model of female birth probability. In addition, we considered the interaction between year and female-female aggression because the effect of female-female aggression was likely different between years. The interaction between year and female-female aggression was significant in the female mass and offspring sprint speed models (P < 0.05); therefore, we reran those models separately for each year.

We checked and validated each model using the residual distribution. Model residuals in female mass, offspring body condition at birth, and offspring growth rate were normally distributed; however, there were two highly influential points in the offspring growth rate model. Excluding these two points did not change the estimates significantly. We present estimates from the final full model regardless of significance, because these parameters directly related to our predictions. To visualize how our fitness changed with respect to female-female aggression, we calculated the predicted values and 95% confidence intervals based on the fixed effects by the method outlined here: http://bbolker.github.io/mixedmodels-misc/glmmFAQ.html (last accessed 24 January 2019). All analysis was carried out using R version 3.12 (R Development Core Team 2011).

Results

Mate limitation hypothesis

We scanned each enclosure on 43 occasions (=days) during the breeding season and recorded 248 female-female aggressive interactions. Female-female aggression as a function of sex ratio treatment and season is presented in Fig. 1a, b. The GLMM model suggested that female-female aggression was not significantly different among sex ratios (Fig. 1a and Table 1). However, we found significant seasonal variation in female-female aggression, with female-female aggression in the post-mating season (when females were still pregnant) being greater than in the mating season (Fig. 1b and Table 1).

Resource competition hypothesis

We conducted 27 visual scans (=days) per enclosure during the breeding season and recorded 238 female-female aggressive interactions. Variation in female-female aggression as a function of food availability treatment and season is presented in Fig. 1c, d. The female-female aggression in the HFA treatment was significantly lower than in the LFA treatment

Fig. 1 Comparison of femalefemale aggression under different **a** sex ratio treatments. **b** season in mate limitation experiment, and under different c food treatments and **d** season in food competition experiment. Values shown are means ± 1 SE. FB, female-biased sex ratio; MB, male-biased sex ratio; MF, equal sex ratio; InSeason, during mating season (May to June); OutSeason, outside the mating season (July to September). The asterisk represents significant effects with p < 0.001



 Table 1
 Summary of generalized

 linear mixed models (GLMM)
 examining the variation of

 female-female aggression in mate
 limitation and food competition

 experiments
 experiments

Hypotheses	Parameter	Estimate	SE	z	Р
Mate limitation $(n = 65)$	Intercept	0.22	0.28	0.79	0.43
Random = enclosure + obs.	Treatment (MB vs FB)	0.29	0.32	0.89	0.37
	Treatment (MF vs FB)	0.29	0.27	1.06	0.29
	Treatment (MB vs MF)	-0.002	0.32	-0.007	0.99
	Season (OutSeason vs InSeason)	0.95	0.24	4.02	< 0.001
	Standardized SVL	-0.08	0.08	-0.97	0.33
Food competition $(n = 73)$	Intercept	-0.51	0.30	-1.70	0.09
Random = enclosure + obs.	Treatment (LFA vs HFA)	1.08	0.31	3.51	< 0.001
	Season (OutSeason vs InSeason)	0.90	0.20	4.52	< 0.001
	Standardized SVL	0.09	0.09	0.92	0.36

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Bold values indicate significant effect. Continuous variables have been standardized (mean = 0, SD = 1)

obs. observational level, *MB* male-biased sex ratio, *FB* female-biased sex ratio, *MF* equal sex ratio, *InSeason* mating season from May to June, *OutSeason* outside the mating season from July to September, *LFA* low-food availability treatment, *HFA* high-food availability treatment

(Fig. 1c and Table 1). In addition, female-female aggression in the post-mating season was significantly greater than in the mating season (Fig. 1d and Table 1).

Consequences of food availability on fitness

Mean value of female mass, probability of females giving birth, and mean value of offspring overwinter survival under different food availability are presented in Fig. 2a–c. We found a significant and positive effect of food availability on female mass, with female mass in the high-food availability treatment being larger than in low-food availability (Fig. 2a and Table 2). Fifty of 62 females (80.7%) gave birth in the HFA treatment group, while 34 of 55 females (61.8%) gave birth in the LFA treatment group. The probability of female birth was significantly increased by food availability (Fig. 2b and Table 2). We also found a significant and positive effect of food availability on offspring overwinter survival, offspring in the HFA treatment group had higher overwinter survival than in the LFA treatment group (Fig. 2c and Table 2).

Consequences of female-female aggression on fitness

Female mass and offspring sprint speed are presented in Fig. 3 as a function of female-female aggression. Female-female aggression had a significant impact on female mass, but the effects varied between years: high levels of female-female aggression non-significantly reduced female mass in year 1 but non-significantly increased female mass in year 2 (Table 2 and Fig. 3a). Similarly, female-female aggression had a significant impact on offspring sprint speed, and the effect was different between years: high levels of female-female aggression non-significantly reduced offspring sprint speed in year 1 but significantly increased offspring sprint speed in year 2 (Table 3 and Fig. 3b).

Discussion

Food, not mate availability, appears to drive female-female aggression in P. vlangalii. This is inferred from the following evidence: (1) females were more aggressive under low levels of food availability (Fig. 1c); (2) female-female aggression showed a strong seasonal pattern where the highest level of aggression was recorded after the mating period, when females were already pregnant (Fig. 1b, d); and (3) femalefemale aggression is not explained by competition over available males and indeed manipulating male availability did not significantly influence female aggression (Fig. 1a). Our findings are consistent with the resource competition hypothesis and preclude the effect of mate availability on female-female aggression. Food availability as a determining factor of female aggression has been found in many mammalian species, whose aggression peaks during pregnancy and lactation, thereby ensuring sufficient food and space for their offspring (Stockley and Bro-Jørgensen 2011; Clutton-Brock and Huchard 2013). Similarly, in birds, female aggression varies with season and context according to when females most likely experience resource constraints (Gill et al. 2007; Cain and Langmore 2015).

High-food intake has clear fitness benefit, assuming high availability translates into high-food intake. Females from high-food treatment group were more likely to increase their mass and give birth (19% more) compared with those from low-food treatment group, and females that experienced the high-food treatment tended to have offspring with high overwinter survival. Interestingly, females were also more aggressive after the mating period once they were already pregnant. This behavior on its own suggests that female aggression may play an important role in resource acquisition at a critical time during allocation to developing embryos.



Fig. 2 Comparison in a female mass, b proportion of females giving birth, and c mean value of offspring overwinter survival between food treatments. HFA, high-food availability treatment; LFA, low-food availability treatment. The asterisk represents significant effects with p < 0.05

The fitness consequence of female aggression in *P. vlangalii* is complex. If we simply consider the relationship between food availability and reproduction, the greatest effect of increasing food availability was the larger female mass, higher proportion (19% more) of females that reproduced and higher offspring overwinter survival. This relationship did not hold true when considering the influence of aggression: more aggressive females were not more likely to reproduce and give birth to offspring with higher overwinter survival. One direct impact of aggression for females was to significantly increase female mass and offspring sprint speed, but these effects are variable with time: high levels of femalefemale aggression likely have detrimental impact on female mass and offspring sprint speed in the first year, whereas in the second year, high aggression would favor female mass and offspring sprint speed (Fig. 3). This is very different to the hypothesis that female-female aggression has direct consequence on fitness (Tobias et al. 2012; Stockley and Campbell 2013). For example, in the Carolina dark-eyed junco (Junco hyemalis), more aggressive females are more competitive and are also more likely to construct a successful nest (Cain and Ketterson 2012). A similar outcome for aggressive females has been found in the White's skink (Liopholis whitii), in which higher survival rates of juveniles have also been attributed to increased female-female aggression during the breeding season and postpartum periods (Sinn et al. 2008).

The complex relationship between female-female aggression and fitness in P. vlangalii is likely due to the costs of female aggression and female energy allocation. In many territorial species, residents may pay an energetic cost in controlling (and acquiring) a territory through a loss in body condition (Whiting et al. 2006). It appears that in P. vlangalii, there may be an initial cost in securing resources and excluding other females as well as their offspring, which later results in energetic benefits presumably through reduced competition. Given that all females were introduced into their enclosures at the same time, it is likely that they would be establishing dominance with individuals they would be encountering for the first time and competing for space. During this time, they might have higher aggression levels, and consequently, more aggressive females likely allocate more energy to maintain their social dominance and elevated testosterone levels (Gill et al. 2007; Sandell 2007), which has been documented to slow the development of offspring and reduce offspring survival in many birds (Clotfelter et al. 2004; O'Neal et al. 2008; Rosvall 2013a). Nevertheless, in year 2, when female aggression was lower, food resources gained from female-female

 Table 2
 Generalized linear mixed
 or linear mixed models examining the variation in female mass, female birth probability and litter size against food availability treatment, female-female aggression, year, and interaction between female-female aggression and year

		Beha	Behav Ecol Sociobiol		:73
Models	Estimate	SE	df	T/Z	P
Female mass ($n = 100$, random = en	nclosure)				
~ treatment + year + female aggres	sion + year × fem	ale aggression	l		
Intercept	5.58	0.30	95.00	18.71	< 0.0001
Treatment (HFA)	1.02	0.34	95.00	2.99	0.004
Year (1)	1.85	0.27	95.00	6.77	< 0.0001
Female aggression	0.91	0.37	95.00	2.45	0.02
Year (1) \times female aggression	- 0.99	0.37	95.00	-2.68	0.01
Year 1					
Intercept	7.94	0.26	10.26	30.74	< 0.0001
Female aggression	-0.28	0.23	29.78	-1.20	0.24
Year 2					
Intercept	6.17	0.14	8.22	45.72	< 0.0001
Female aggression	0.21	0.13	17.61	1.60	0.13
Female birth probability ($n = 117$, r	random = enclosur	e)			
\sim treatment + year + female aggres	sion + year \times fem	ale aggression	L		
Intercept	1.01	0.45		2.24	0.03
Treatment (HFA)	1.08	0.51		2.12	0.03
Year (1)	-0.88	0.48		-1.83	0.07
Female aggression	-0.39	0.37		-1.05	0.29
Year (1) \times female aggression	0.91	0.51		1.79	0.07
Litter size $(n = 84, \text{ random} = \text{enclose})$	sure)				
\sim treatment + year + female aggres	sion + year \times fem	ale aggression	L		
Intercept	1.01	0.15		6.58	< 0.0001
Treatment (HFA)	0.23	0.19		1.21	0.23
Year (1)	-0.38	0.14		-2.75	0.01
Female aggression	0.10	0.18		0.57	0.57
Year (1) \times female aggression	-0.05	0.18		-0.28	0.78

Bold values indicate significant effects

LFA low-food availability treatment, HFA high-food availability treatment





Fig. 3 Relationships between a predicted female mass and female-female aggression and **b** predicted offspring sprint speed and female-female aggression. The solid line represents predicted values for the first year,

while the dashed line represents predicted values for the second year. The dotted lines represent lower and upper 95% confidence interval. Model predictions are based on models in Table 2

Table 3Linear mixed modelexamining the variation inoffspring body condition,offspring sprint speed, offspringgrowth rate, offspring overwintersurvival against food availabilitytreatment, year, female-femaleaggression, and interactionbetween female-femaleaggression and year

Models	Estimate	SE	df	T/Z	Р
Offspring body condition $(n = 206,$	random = enclos	ure + female	identity)		i
\sim treatment + year + female aggres	sion + year \times fem	ale aggressio	n		
Intercept	-0.05	0.01	19.78	- 5.44	< 0.0001
Treatment (HFA)	0.01	0.01	18.02	0.77	0.45
Year (1)	0.03	0.01	175.20	6.03	< 0.0001
Female aggression	-0.00	0.01	71.65	-0.60	0.55
Year (1) \times female aggression	0.00	0.01	172.80	0.09	0.93
Offspring sprint speed ($n = 133$, ran	ndom = enclosure	+ female ide	ntity)		
\sim treatment + year + female aggres	sion + year \times fem	ale aggressio	n		
Intercept	0.31	0.03	48.07	10.65	< 0.0001
Treatment (HFA)	0.01	0.03	23.83	0.21	0.83
Year (1)	0.04	0.02	127.02	1.55	0.13
Female aggression	0.06	0.03	69.57	2.32	0.02
Year (1) \times female aggression	-0.08	0.03	120.33	- 3.03	0.003
Year 1					
Intercept	0.35	0.02	10.88	15.13	< 0.0001
Female aggression	-0.02	0.02	44.30	- 1.11	0.27
Year 2					
Intercept	0.30	0.02	27.30	16.91	< 0.0001
Female aggression	0.04	0.02	22.80	2.23	0.04
Offspring growth rate ($n = 133$, ran	dom = enclosure	+ female ider	tity)		
\sim treatment + year + female aggres	sion + year × fem	ale aggressio	n		
Intercept	0.05	0.01	13.29	9.69	< 0.0001
Treatment (HFA)	-0.01	0.01	9.54	- 1.03	0.33
Year (1)	-0.00	0.00	117.17	-1.33	0.19
Female aggression	-0.00	0.00	105.38	-0.52	0.61
Year (1) \times female aggression	-0.00	0.00	124.69	- 1.39	0.17
Offspring overwinter survival $(n = 1)$	84, random = enc	losure)			
\sim treatment + year + female aggres	sion + year × fem	ale aggressio	n		
Intercept	0.49	0.07	79.00	7.25	< 0.0001
Treatment (HFA)	0.32	0.06	79.00	5.20	< 0.0001
Year (1)	0.05	0.08	79.00	0.64	0.52
Female aggression	-0.15	0.08	79.00	-1.77	0.08
Year (1) \times female aggression	0.12	0.08	79.00	1.50	0.14

Bold values indicate significant effects

LFA low-food availability treatment, HFA high-food availability treatment

aggression most likely translated into fitness benefits through increased female mass and offspring sprint speed, although the former increase was not significant.

Alternatively, age-dependent changes in aggression and the likelihood of winning a contest might also mediate the complex relationship between female-female aggression and fitness in *P. vlangalii*. Old females that are aggressive may suffer fewer fitness costs than aggressive young females, because older females are more likely to win contests (Cooper et al. 2015). The year-to-year variation in female-female aggression and fitness is potentially due to age effects if the females in year 2 are older than those in year 1. We think this possibility

is low, because females were randomly caught in the field and were randomly allocated to each enclosure at the start of the experiment.

Conclusions

We provide evidence that female-female aggression in *P. vlangalii* is driven by food availability rather than mate availability. High-food availability significantly increased female mass and the likelihood that a female gave birth, and females experiencing higher food treatments tend to have

offspring with higher overwinter survival. Also, we detect a year effect of female-female aggression and its effect on female mass and offspring sprint speed. Compared to male aggression, female-female aggression is a much understudied phenomenon. Our study demonstrates that female-female aggression may play a more significant role in the fitness of species lacking parental care than previously believed.

Acknowledgments We are grateful to Er Ga and Cuo ke for logistical assistance in Zoige. Thanks to Xintao Deng for assistance with data collection in the field and Daniel Noble for advice on statistical methods. We thank two anonymous reviewers for their constructive comments that improved this manuscript.

Funding This project was supported by grants from the National Natural Science Foundation of China to YQ (grant numbers 31201723, 31572273, 31872233) and to YW (grant number 31801980).

Data availability The datasets generated during and/or analyzed during the current study are available on Figshare https://doi.org/10.6084/m9. figshare.7375829.v1.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval We obtained the appropriate permissions for conducting the study at the Xiaman Conservation Station in the Zoige Wetland Nature Reserve from the Forestry Department of the Sichuan Provincial Government and the Management Office of the Zoige Nature Reserve. Handing of lizards followed approved protocols from the Experimental Animal Ethics Committee of the Chengdu Institute of Biology, Chinese Academy of Sciences (protocol number 2017005). We also adhered to the ABS/ASAB "Guidelines for the treatment of animals in behavioral research and teaching."

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