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SHORT COMMUNICATION

Do displays and badges function in establishing the social structure of male toad-headed lizards, *Phrynocephalus vlangalii*?

Yin Qi · Hongfu Wan · Haijun Gu · Yuezhao Wang

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Abstract This study addresses several basic questions relating to the roles of badges and displays in establishing social structure in male *Phrynocephalus vlangalii*. Significant differences in body mass and condition were found between resident and floater males of *P. vlangalii*, and resident males engaged in tail curling and agonistic interactions more frequently than floater males. Frequency of tail curling was correlated negatively with body mass in floater males, but was not correlated with body mass and condition in resident males. Relative tail-tip badge size, relative belly patch size and relative tail length could significantly predict an individual's body mass, and body condition was positively correlated with relative tail length, suggesting that resident males may establish their social dominance by communicating their body mass and condition through frequent tail curling.

Keywords Display · Badge · Tail curling · Lizard · Resident · Floater

Y. Qi · H. Wan · H. Gu · Y. Wang (✉)
Chengdu Institute of Biology, Chinese Academy of Sciences, No.9, Section 4, Renmin-Nan Road, 610041 Chengdu, China
e-mail: arcib@cib.ac.cn

Y. Qi · H. Wan
Graduate University of Chinese Academy of Sciences, 100049 Beijing, China

H. Gu
Sichuan Provincial Forestry Department, 610081 Chengdu, China

Introduction

Badges and elaborate displays are thought to signal individual quality in many lizard species (Hover and Jenssen 1976; Jenssen 1977; Zucker 1989; Sinervo and Lively 1996). Badges are generally color patches that are known to be correlated with individual aggression, social status and bite force (Zucker 1989; Thompson and Moore 1991; Carpenter 1995; Zucker and Murray 1996; Vanhooydonck et al. 2005). In contrast, displays are behaviors that consist of variable body movements, such as the raising and lowering of the head and dewlap in the green anole *Anolis carolinensis* (Carpenter 1967; Jenssen 1977). Display behaviors are also known to predict an individual lizard's aggressiveness and performance capacity (Hover and Jenssen 1976; Brandt 2003; Orrell and Jenssen 2003; Perry et al. 2004; Osborne 2005). Individuals exhibiting different social statuses are expected to develop differences in their display behaviors and badges (Zucker 1989; Andersson et al. 2002; Lopez et al. 2004; McElroy et al. 2007).

Resident and floater tactics are common and widespread among vertebrates, especially in males (Waltz 1982; Dominey 1984; Morrison et al. 2002; Aragon et al. 2004). Individuals who take up resident tactics are generally considered to be dominant in social conditions, and they defend either a territory or a group of females. In contrast, subordinate individuals employ nonagonistic tactics, such as floater, sneaker or satellite tactics (Waltz 1982; Dominey 1984; Zug et al. 2001). Residents and floaters are believed to exhibit differences in their badges and display behaviors, because these traits are correlated with individual social status (Zucker 1989; Andersson et al. 2002; Lopez et al. 2004; McElroy et al. 2007). However, few studies have sought to specifically investigate the roles of badges and displays in the establishment of such social structures.

The Qinghai toad-headed lizard *Phrynocephalus vlangalii* is particularly well suited for studying the roles of badges and display behaviors in establishing social structure. They have strikingly complex tail curling, tail wagging and push-up behaviors and possess a prominent ventral side black tail-tip badge and belly patch (Fig. 1; Zhao 1999). Field observations showed that males slowly curl their tails while guarding their territories, and the rates and intensities of the tail curling, tail wagging and push-ups increase as an intruder approaches (Yin Qi, personal observation). In a previous study of the spatial behavior of *P. vlangalii*, Wang et al. (2004) found that two types of male territorial behavior existed. Some individuals were consistently observed in small areas (residents), while others were observed only occasionally and did not occupy distinct areas (floaters). Residents defended certain areas and drove off conspecific males by frequently displaying toward and chasing other males. Floaters did not defend territories and were infrequently observed in the same area after their initial capture.

The present study addresses the following four basic questions relating to the roles of badges and displays in establishing social structure in male *P. vlangalii*. (1) Do resident and floater males differ in body mass, body condition and sizes of tail-tip badge and belly patch? (2) Do resident and floater males differ in their display behaviors, such as frequency of tail curling (FTC), frequency of tail wagging (FTW), and frequency of pushup (FUP), and in their experiences in agonistic interactions? (3) Are the frequencies of display behaviors (FTC, FTW and FUP) correlated with body mass and condition? (4) Are the sizes of the relative tail-tip badge and belly patch and the relative tail length correlated with individual body mass and condition?

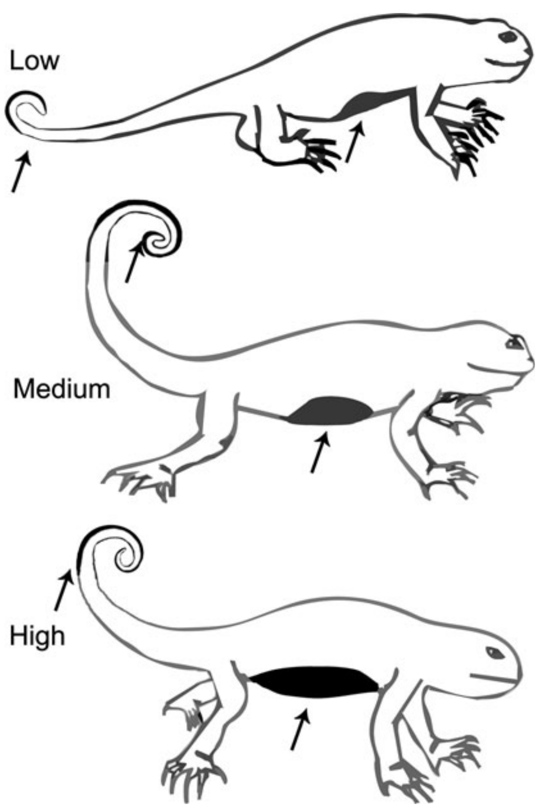

Fig. 1 Intensity of tail displays by the toad-headed lizard (*Phrynocephalus vlangalii*) from slight tail-tip elevation (*low*) to tightly spiraled display (*medium*) and wagging (*high*). The tail-tip badge and belly patch (indicated by *arrows*) are shown during display

Materials and methods

Study site

Field work was conducted during the reproductive period of *P. vlangalii* from May to June in 2009 near the Xiaman Conservation Station in the Zoige (Ruoergai) Wetland Nature Reserve in southwestern China (33°43′ 25.0″ N, 102°29′ 04.0″ E; elevation 3464 m above sea level). In this area, *P. vlangalii* occupies large sparsely vegetated sand dunes, and is isolated within a wetland ecosystem. The vegetation on and around these sand dunes is predominantly composed of three grass species (*Kobresia humilis*, *K. prattii* and *Elymus natans*) and a shrub (*Salix sclerophylla*). A 50 m × 40 m plot was set up and divided into 20 quadrats, each of size 10 m × 10 m, thus forming a grid on the field (Aragon et al. 2001). This plot allowed us to discriminate resident from floater male lizards by monitoring their activity closely (Rose 1982).

Captures and morphological measurements

All animals observed on the plot were caught by noosing or in pitfall traps. Immediately after capturing the animal, we measured a series of morphological traits. Body mass, which has been found to be an important determinant of dominance rank in a variety of taxa (Jenssen 1977; Lawrence 1987; Zucker and Murray 1996; Emlen 1997), was measured with a Pesola spring scale to the nearest 0.1 g. The following morphological characters were measured using digital calipers to the nearest 0.1 mm: snout-vent length (SVL), distance from the snout to the vent; tail length, distance from the vent to the tail-tip; belly length, distance from the posterior base of the forelimb to the anterior base of the hindlimb (Zhang et al. 2005). We removed the influence of body size on tail length by regressing it against SVL and using the residuals as relative tail length in further analyses. Tail length and belly length were measured because they were likely correlated with sizes of tail-tip badge and belly patch. Body condition was estimated using the residuals from the regression of log body mass on log SVL (Green 2001).

Each lizard was marked by toe clipping and given a unique color code on its dorsum using acrylic paint. The paint allowed us to monitor lizards from a distance of more than 4 m with the aid of 10×35 binoculars without disturbing the natural behavior of the animals. Toe clipping was used for permanent marking because this method has been shown to have no effect on lizard behavior or fitness in other species (Morrison et al. 2002). All lizards were released at their capture sites within 5 min. The sexual maturity of each lizard was estimated from its SVL, and only mature adult males and females (SVL > 51 mm, for adult males and females) were included in our study (Wu et al. 2002). Sex was determined by checking for the presence of hemipenal bulges.

Belly patch and tail-tip badge size

Belly patch and tail-tip badge were quantified as in Meyers et al. (2006). A digital photograph was taken as the animal was pressed against a piece of glass exposing both the belly and tail-tip. Digital photographs were then imported into Image J (W.S. Rasband, Image J, US NIH, Bethesda, MD, USA, http://rsb.info.nih.gov/ij/, 1997–2007), and the two badges were digitized using the Polygon Selection tool. Sizes were calculated by using the Analyze function (Abramoff et al. 2004). Both belly patch and tail-tip badge were visible as continuous black patches, so all selections and analyses were performed by one experienced investigator in order to reduce spurious variability. Relative belly patch size was calculated as the residual of belly patch size against SVL, and relative tail-tip badge size was calculated as the residual of tail-tip badge size against tail length.

Displays and behavior types

A combination of focal and behavioral sampling was used to monitor lizard activity and to quantify their display behaviors. Two time periods were chosen to conduct our censuses each day, a morning session (0900–1230 h) and an afternoon session (1230–1630 h). During the censuses, the position of each sighted lizard on our grid was recorded in *x*- and *y*-coordinates. If the lizard remained undisturbed, the individual was monitored continuously with binoculars for 10 min as it moved throughout the environment. The 10-min session was divided into 30-s sample intervals by an electronic metronome. Occurrences of tail curling, tail wagging, and pushup behaviors were recorded for the instant of each sample point (Fig. 1). Tail curling was defined as slight elevation of the tail-tip to full curling with the distal part of the tail held vertically in a circle or spiral and with the tail-tip badge visible to the observer; tail wagging was defined as the tail being elevated and undulated from side to side; pushup was defined as the four legs being raised and the back arched with belly patches visible to the observer. When possible, the number of agonistic interactions—including chasing and fighting between males, a male and a female, and a male and a juvenile—for focal lizards was also recorded. Sampling was conducted for 10 min because this is the accepted protocol for studies of field display behavior in lizards (Perry et al. 2004; McElroy et al. 2007). Sample intervals of 30 s are also recommended for studies involving field behavior measurements (Martin and Bateson 1986). The FTC was defined as the proportion of 20 instantaneous samples during which tail curling occurred; the FTW was defined as the proportion of 20 instantaneous samples during which tail wagging occurred; and FUP behavior was defined as the proportion of 20 instantaneous samples during which pushup behaviors occurred (Carpenter 1967; Martin and Bateson 1986). We quantified only tail curling, tail wagging and pushup behaviors because the tail-tip badge and belly patch became visible during these displays and were possibly correlated with individual quality (Jenssen 1977; Cooper 2001). During behavioral observations, the investigator minimized any disturbance of the focal lizard by maintaining a distance of >5 m and relying on the use of binoculars. A maximum of two independent sightings for an individual were scored per day. All fieldwork was carried out on sunny days with an air temperature range of 20–26°C.

Male lizards were characterized as residents or floaters based on the number of sightings observed and their residency on the study plot (Morrison et al. 2002; Aragon et al. 2004). Residents were defined as individuals with more than three sightings in different days and a residency of at least 15 days. All other individuals were defined as floaters (Morrison et al. 2002; Aragon et al. 2004). Residency was calculated as the number of days separating the first and last sightings of each lizard. These methods have been used successfully in a number of other studies on lizards (Aragon et al. 2001; Morrison et al. 2002; Stapley and Keogh 2005), and are generally considered reliable and accurately depict the behavioral types of individuals. Ten males were recaptured in 2009 from the 32 males marked in the same plot in 2008. All but two of these males were categorized as residents using the above criteria, suggesting that the classification method for residents and floaters did indeed reflect the male's natural condition.

Data analysis

Data were analyzed using SAS 9.0/STAT (SAS Institute Inc., Cary, NC, USA). Prior to data analysis, normality and homogeneity were systematically checked for each variable using the Kolmogorov–Smirnov and Hartley tests, respectively. When necessary, variables were log transformed to meet the requirements of parametric tests. Nonparametric tests were used only when data did not meet the assumptions of parametric tests even after the appropriate transformations. The significance level was defined as 0.05. Descriptive statistics were given as mean ± SE.

To test whether resident and floater males differ in body mass, body condition, relative tail-tip badge size, relative belly patch size and relative tail length, a one-way MANOVA was used with behavior type (resident or floater) as the main factor and body mass, body condition, relative tail-tip badge size, relative belly patch size and relative tail length as response variables. A Wilcoxon two-sample test was used to compare display behaviors (FTC, FTW and FUP) between residents and floaters. The chi-squared (χ^2) test was used to compare the number of individuals that show agonistic behavior between residents and floaters.

To examine whether relative tail-tip badge size, relative belly patch size and relative tail length predicted body mass and condition, multiple linear regression was used with body mass or condition as dependent variables and relative tail-tip badge size, relative belly patch size and relative tail length as independent variables. We investigated both full regression models and reduced models generated by a stepwise selection procedure with $P < 0.05$ to enter a variable. Spearman's rank correlation was used to test the relationships among body mass, body condition, FTC, FTW and FUP within resident and floater males separately.

Results

A total of 37 males were captured in May of 2009, among which 26 were classified as residents and 11 were classified as floaters. All measurement data are presented in Table 1. Residents and floaters differed significantly in body mass (whole model: Wilks' $\lambda = 0.83$, $F_{5,30} = 3.57$, $P = 0.04$; $F_{1,34} = 4.92$, $P = 0.03$) and body condition ($F_{1,34} = 5.27$, $P = 0.02$), but differences in relative tail-tip badge size ($F_{1,34} = 0.1$, $P = 0.75$), relative belly patch size ($F_{1,34} = 2.18$, $P = 0.15$) and relative tail length ($F_{1,34} = 0.99$, $P = 0.33$) were not significant.

Display behaviors of 31 males (23 residents, 8 floaters) were measured in the field, and all of them occurred during agonistic interactions (male–male, male–female, male–juvenile). In general, FTC was higher than FTW and FUP. FTC was significantly higher in residents than in floaters ($Z = -1.7$, $n_1 = 23$, $n_2 = 8$, $P = 0.04$), while FTW ($Z = -0.82$, $n_1 = 23$, $n_2 = 8$, $P = 0.21$) and FUP ($Z = -0.86$, $n_1 = 23$, $n_2 = 8$, $P = 0.19$) were not significantly different (Table 1; Fig. 2). Residents were observed to engage in agonistic interactions more frequently than floaters ($\chi^2 = 7.35$, $df = 1$, $P = 0.007$).

For floaters, FTC was significantly and negatively correlated with body mass ($r = -0.91$, $P = 0.002$, $n = 8$), but was not significantly correlated with body condition ($r = -0.12$, $P = 0.77$, $n = 8$). Similar to FTC, FTW was significantly and negatively correlated with body mass ($r = -0.74$, $P = 0.03$, $n = 8$), but was not significantly correlated with body condition ($r = 0.3$, $P = 0.48$, $n = 8$). FUP was not significantly correlated with either body mass ($r = -0.42$, $P = 0.3$, $n = 8$) or body condition ($r = -0.22$, $P = 0.6$, $n = 8$). For residents, none of FTC, FTW or FUP was significantly correlated with body mass ($r = 0.15$, $P = 0.5$; $r = 0.18$, $P = 0.42$; $r = -0.03$, $P = 0.9$, respectively; $n = 23$) or body condition ($r = 0.05$, $P = 0.82$; $r = 0.28$, $P = 0.19$; $r = 0.06$, $P = 0.77$, respectively; $n = 23$).

Table 1 Comparison of body mass, body condition, display behaviors (FTC, FTW and FUP), and sizes of tail-tip badge and belly patch between resident and floater male toad-headed lizards (*Phrynocephalus vlangalii*) in the Xiaman population

	Resident	Floater
Number of individuals	26	11
Number of sightings (time)	8.5 ± 0.85	3.0 ± 0.79
Residency (day)	18.4 ± 0.54	5.3 ± 1.31
Mean body mass (g)	7.6 ± 0.17	6.8 ± 0.36
Body condition [log (mass)/log (SVL)]	0.03 ± 0.01	−0.03 ± 0.01
Frequency of tail curling (FTC)	0.4 ± 0.05	0.2 ± 0.07
Frequency of tail wagging (FTW)	0.1 ± 0.02	0.1 ± 0.05
Frequency of pushup (FUP)	0.1 ± 0.01	0.04 ± 0.02
Relative tail length	3.32 ± 0.59	2 ± 1.26
Relative tail-tip badge size	1.65 ± 0.54	1.33 ± 0.61
Relative belly patch size	0.21 ± 0.01	0.2 ± 0.02

Values shown are mean ± SE

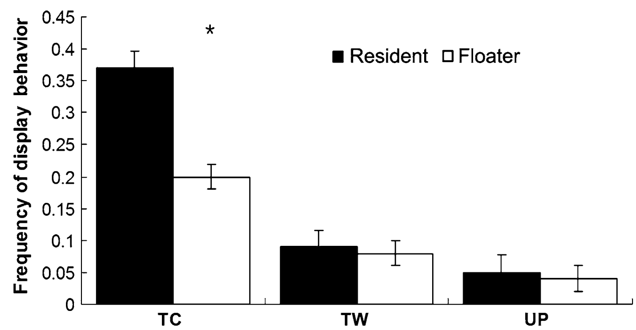

Fig. 2 Bar graphs showing mean ± SE of average frequency of tail curling (*TC*) and tail wagging (*TW*) and pushup behavior (*UP*) per 10 min for male resident and floater toad-headed lizards (*Phrynocephalus vlangalii*). *Asterisk* indicates significant difference between residents ($n = 23$) and floaters ($n = 8$)

Full models for the two multiple regression analyses testing the effects of relative tail-tip badge size, relative belly patch size and relative tail length on body mass and body condition were significant (body mass: $R^2 = 0.49$, $F_{3,33} = 10.44$, $P < 0.0001$; body condition: $R^2 = 0.29$, $F_{3,33} = 4.5$, $P = 0.009$). Partial regressions of body mass against relative tail-tip badge size, relative belly patch size and relative tail length were also significant ($\beta = 30.78$, $P < 0.0001$; $\beta = -0.37$, $P = 0.01$; $\beta = 0.26$, $P = 0.003$, respectively). Nevertheless, partial regression of body condition was only significant against relative tail length ($\beta = 0.01$, $P = 0.003$). The stepwise selection procedure concurred with the full models and found that both body mass ($r = 0.68$, $F_{1,35} = 30.44$, $P < 0.0001$) and body condition ($r = 0.48$, $F_{1,35} = 10.71$, $P = 0.002$) were positively related to relative tail length.

Discussion

Our results showed that resident male *P. vlangalii* had larger body masses and better body conditions than males adopting floater tactics. Previous studies have demonstrated that body mass is an important determinant of dominance rank in a variety of taxa (Jenssen 1977; Lawrence 1987; Carpenter 1995; Zucker and Murray 1996). Body condition, which represents an index of the relative amount of fat stored and an estimate of individual physical condition, has also been suggested to be critical for maintaining dominance in vertebrates (Green 2001; Judge and Brooks 2001; Jenssen et al. 2005). Occupying a territory provides a male with resources, such as mates, food or basking sites (Martins 1994; Haenel et al. 2003); however, territorial behavior comes at a cost and also involves intense contests among conspecifics. Therefore, natural and sexual selection may favor heavier males in better condition adopting resident tactics, while poor quality males adopt floater tactics (Waltz 1982; Gross 1996).

Displays are important visual signals (Kim 1995; Zug et al. 2001; Brandt 2003), and are known to predict a lizard's aggression, endurance and performance capacity (Hover and Jenssen 1976; Brandt 2003; Orrell and Jenssen 2003; Perry et al. 2004; Osborne 2005). Such signals allow a rival male or female to identify the quality of a dominant individual without having to engage in physical combat (Osborne 2005). Specific display behaviors may transmit information about an individual's aggressiveness to conspecifics and thereby influence the outcome of dominance interactions (Hover and Jenssen 1976; Orrell and Jenssen 2003; Osborne 2005). Our results showed that resident males of *P. vlangalii* engaged in tail curling and agonistic interactions more frequently than floater males. Therefore, we suggest that resident males may maintain their social dominance to some degree by communicating their body mass and body condition to intruders through frequent tail curling, and thereby may reduce the cost of engaging in physical combat. However, we found no relationships between FTC and body mass or body condition in resident males. The lack of correlation between tail curling intensity and body condition is conceivable, as condition represents the level of fat storage, whereas tail curling intensity depends on energy stores that are immediately accessible (Green 2001; Osborne 2005). Nevertheless, the lack of correlation between tail curling intensity and body mass is surprising, because many previous studies have suggested that displays are energetically costly and should be correlated with body mass (Vehrencamp et al. 1989; Ros et al. 1997). Actually, studies on tree lizards *Urosaurus ornatus* and brown anoles *Anolis sagrei* found a positive correlation between body mass and display intensity (Tokarz 1985; McElroy et al. 2007). We suggest that tail curling in *P. vlangalii* may convey other information such as residency in a certain area or burrow quality to conspecifics. Many studies on lizards have shown that residency, reflected in occupancy of territory, could confer advantages to individual lizards during contests, with residents winning more encounters than floaters (Cooper and Vitt 1987; Olsson 1992; Aragon et al. 2006). More research is needed to test this hypothesis.

Badges are known to be correlated with individual aggression, social status and bite force in lizards (Zucker 1989; Thompson and Moore 1991; Carpenter 1995; Zucker and Murray 1996; Vanhooydonck et al. 2005). Our results are consistent with this theory. The relative tail-tip badge size, relative belly patch size and relative tail length of *P. vlangalii* significantly predicted body mass, and body condition was positively correlated with relative tail length. The tail-tip badge or tail, which becomes obvious during tail curling, likely signals information concerning body mass and condition in male *P. vlangalii* during their social dominance contests. Previous works studying male northern cardinals *Cardinalis cardinalis* suggested that redness of breast plumage positively predicts individual body mass, while bill color signals individual body condition (Moller and Pomiankowski 1993; Jawor and Breitwisch 2004). Many studies on lizards have also suggested that badge variations are correlated with individual social status (Zucker 1989; Sinervo and Lively 1996; Aragon et al. 2004). For example, throat colors among male *Uta stansburiana* are correlated with aggressiveness and territoriality. Orange-throated males are most aggressive and defend large territories, blue-throated males are less aggressive and defend smaller territories, and yellow-throated males do not defend a territory but adopt "sneaking" tactics (Sinervo and Lively 1996). Furthermore, strong selection pressures, such as increased predation risk and conspecific contests, imply that badges would be most beneficial for fitness if they appear on structures that are normally out of sight but become visible during display (Jenssen 1977; Zug et al. 2001). This may explain why the black tail-tip badge and belly patch are on the ventral side only and are shown during tail display in *P. vlangalii* (Fig. 1). Similar quality-related concealed badges have been found in the throat colors (fight ability) of the Augrabies flat lizard *Platysaurus broadleyi* and the belly patch size (aggression) of the tawny dragon *Ctenophorus decresii* (Osborne 2005; Whiting et al. 2006).

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