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## Body Size Affects the Predatory Interactions between Introduced American Bullfrogs (*Rana catesbeiana*) and Native Anurans in China: An Experimental Study

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ABSTRACT.—Introduced American Bullfrogs (Rana catesbeiana) have established breeding populations in several provinces in China since their introduction in 1959. Although Bullfrogs are viewed as a potentially important predator of Chinese native anurans, their impacts in the field are difficult to quantify. We used two experiments to examine factors likely to mediate Bullfrog predation on native anurans. First, we examined effects of Bullfrog size and sex on daily consumption of a common Chinese native (Rana limnocharis). Second, we examined whether Bullfrogs consumed similar proportions of four Chinese natives: Black-Spotted Pond Frog (Rana nigromaculata), Green Pond Frog (Rana plancyi plancyi), Rice Frog (R. limnocharis), and Zhoushan Toad (Bufo bufo gargarizans). We found that larger Rana catesbeiana consumed more R. limnocharis per day than did smaller R. catesbeiana, and that daily consumption of R. limnocharis was positively related to R. catesbeiana body size. When provided with adults of four anurans that differed significantly in body size, R. catesbeiana consumed more individuals of the smallest species (R. limnocharis). However, when provided with similarly sized juveniles of the same four species, R. catesbeiana did not consume any species more than expected by chance. Our results suggest that body size plays an important role in the predatory interactions between R. catesbeiana and Chinese native anurans and that, other things being equal, smaller species and individuals are at greater risk of predation by R. catesbeiana.

The American Bullfrog, Rana catesbeiana, is considered one of the 100 worst invasive alien species in the world (IUCN, 2003). Native to eastern North America, the Bullfrog has been widely introduced to various regions of the world (Bury and Whelan, 1984; Lever, 2003). Adult Bullfrogs are efficient, generalist predators that may affect other amphibians through direct predation (Bury and Whelan, 1984; Werner et al., 1995). Establishment of Bullfrogs and coincident declines in native anurans has led to the hypothesis that Bullfrog predation may be affecting native populations (Moyle, 1973; Hayes and Jennings, 1986). Predation impacts of Bullfrogs are hard to quantify in the field for several reasons, including the likelihood that interactions are condensed in time and the difficulty of extrapolating diet composition into conclusions relevant at a population scale (Kupferberg, 1997).

Since 1959, Bullfrogs have been introduced to most provinces of mainland China and have established breeding populations in Yunnan, Sichuan, Shanxi, and Zhejiang Provinces including the Zhoushan archipelago (He, 1998; Li and Xie, 2004; Wu et al., 2004; Li et al., 2006). The Bullfrog is much larger than any native anuran in China (Fei, 1999) and is known to consume at least four of 10 native species in the Zhoushan archipelago: four Zhoushan Toads (Bufo bufo gargarizans), 14 Rice Frogs (Rana limnocharis), five Black-Spotted Pond Frogs (Rana nigromaculata), and one Zhenhai Brown Frog (Rana japonica) were consumed by 356 American Bullfrogs (Wu et al., 2005; Wang et al., 2006). However, their impacts as predators on native anurans in China, as in most invaded regions, are difficult to extrapolate into population effects in the field.

Estimating food consumption is central to defining the ecological role of predators (Body, 2002) and, thus, provides an important way to quantify the predatory impacts of Bullfrogs on native anurans. Factors influencing daily consumption by Bullfrogs on native anurans may be helpful in understanding and predicting Bullfrog effects as they join anuran communities in their expanding global range. The first objective of this study was to quantify the

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potential predatory impacts of Bullfrogs, by examining daily consumption of Bullfrogs on Chinese native anuran *R. limnocharis*.

Because of variation in antipredator behaviors, chemical cues (e.g., skin palatability), and differential temporal and spatial use of resources (Laurila, 1998; Kiesecker et al., 2001; Pearl et al., 2004) among species, native anurans may not be impacted by Bullfrogs equally. Identifying which species in an invaded community may be most at risk is crucial to predicting and quantifying the impacts of exotic species (Parker et al., 1999), and it also has important implications for developing conservation priorities for these species. Therefore, the second objective of our study was to examine whether Bullfrogs consumed four Chinese native anurans (B. b. gargarizans, R. limnocharis, R. nigromaculata, and R. plancyi plancyi) equally.

## MATERIALS AND METHODS

All experiments were conducted in a greenhouse at Taimen town on Liuheng Island, the Zhoushan archipelago, Zhejiang Province, China. Liuheng Island is approximately 100 km² and hosts seven native anurans and breeding Bullfrogs in many of its approximately 100 ponds and reservoirs (Gu and Jin, 1985; Li et al., 1998, 2006). Approximately 30% of Liuheng Island is plains and 70% is hills. Vegetation is predominately subtropical evergreen broadleaf forest. The climate is typical of the subtropical monsoon zone with hot summers and cold winters. Annual precipitation at the site is about 1200 mm (Zhoushan City Government, 1992).

We collected Bullfrogs from Daao Reservoir (2 km from Taimen town). We collected four native anurans (*B. b. gargarizans, R. limnocharis, R. nigromaculata,* and *R. p. plancyi*) from the ponds, rivers, and farmlands in Shuangtang town about 10 km northwest of Taimen town. All frogs were captured by dip-net or by hand at night (1900–2230 h) with the help of a 12-volt DC lamp. Bullfrogs were not detected at any site where native species were collected. Bullfrogs were raised in a plastic tank and were fed crickets ad libitum until 48 h before trials. Native anurans were raised with only conspecifics in four plastic tanks and were fed crickets ad libitum until 24 h before trials.

Experiments were conducted in 12 circular plastic tanks (70 cm diameter, 20 cm depth) that were arrayed in two equal rows separated from each other by 1.0 m. Each tank was on a slope and had sufficient water to produce equal aquatic and terrestrial area. Water at the aquatic end was 6.5–9.6 cm maximum depth. A 1-cm diameter PVC pipe supplied each tank with water from Daao Reservoir at a steady drip, and

a drain-pipe outflow, extending 0.5 cm above the water surface, was used to maintain water levels. All tanks were covered with nets (mesh size  $1.90 \times 1.24$  mm) to prevent escapes. We thoroughly rinsed all tanks three times with reservoir water and allowed them to air-dry before and between experiments. The experimental temperature was  $29.0–29.5^{\circ}$ C, and day/night length was 14:10 h light: dark.

We assessed sex and body size for all frogs just before adding them to experimental tanks. We measured body mass to the nearest 0.1 g: we used body mass (rather than length) because mass is the most common surrogate for body size in the literature (Peters, 1983; Calder, 1984), and it also provided a direct measure of daily consumption of R. limnocharis. Sex of mature frogs was determined using secondary sexual characteristics: male Bullfrogs had nuptial pads and yellow throat pigments; and male native anurans had nuptial pads and linea masculina (Huang, 1990; Fei, 1999). We considered individuals smaller than the adult male minimum size (34.2 g, 54.5 g, 1.2 g, 21.2 g, and 3.4 g for *B*. b. gargarizans, R. catesbeiana, R. limnocharis, R. nigromaculata, and R. p. plancyi, respectively) to be juveniles (see Hirai, 2004; Wu et al., 2005). All test animals were used only once in the experiments. All analyses were performed with the SPSS statistical package (SPSS Inc., Chicago, 1998). We present means  $\pm$  1 SE.

Experiment 1: Daily Consumption of Rana limnocharis by Rana catesbeiana.—We used a 2 × 2 factorial design with three replicates to assess the effects of body size and sex of R. catesbeiana on the consumption of the native anuran R. limnocharis (Table 1). Rana limnocharis was chosen to represent Chinese anurans because it is widely distributed, occupies many habitat types, and is commonly found in the diet of R. catesbeiana in the Zhoushan archipelago (Wu et al., 2005; Wang et al., 2006). All R. limnocharis used in the experiment were males.

We randomly drew three R. limnocharis from holding cages and placed them at the center of each tank used for the predation trial. One toe was removed from each R. limnocharis for individual identification, and we observed no obvious behavioral differences or health effects of toe clipping on R. limnocharis preceding or during the experiment. After 1 h acclimation, we introduced one *R. catesbeiana* into each tank. Rana catesbeiana were matched in size to form two size groups in each sex, with the large group significantly larger than small group  $({\rm mass_{large}} = 205.23 \pm 9.94 \ {\rm g, \ mass_{small}} = 89.28 \pm 13.04 \ {\rm g; \ } t_{10} = 7.07, \ P < 0.001). \ {\rm Male \ and}$ female R. catesbeiana did not differ significantly in body size (mass<sub>male</sub> =  $132.95 \pm 27.24 \text{ g}$ ,  $\text{mass}_{\text{female}} = 161.57 \pm 28.10 \text{ g}; t_{10} = -0.73, P =$ 

1D

combinations of <i>Kana catesvetana</i> on male <i>Kana limnocharis</i> .									
Experiment design	Species	Sex	Number tanks	Frog per tank	Body mass (Mean ± SE) (g)				
1A	Rana catesbeiana	O'	3	1	$73.10 \pm 10.12$				
	Rana limnocharis	O*	3	3	$3.39 \pm 0.33$				
1B	Rana catesbeiana	O'	3	1	$192.80 \pm 5.02$				
	Rana limnocharis	O"	3	3	$5.96 \pm 0.39$				
1C	Rana catesbeiana	Q	3	1	$105.47 \pm 22.04$				
	Rana limnocharis	O'	3	3	$3.12 \pm 0.17$				

Q

O

3

3

TABLE 1. Experimental design and characteristics of frogs used in experiment 1. All frogs were measured at the start of the experiment. 1A, 1B, 1C, and 1D were experiment groups, representing different sex and body size combinations of *Rana catesbeiana* on male *Rana limnocharis*.

0.481). These sizes are comparable to field-caught *R. catesbeiana* in the region (50.80–607.40 g; Wang et al., 2006).

Rana catesbeiana

Rana limnocharis

We inspected each tank every 6 h and replaced consumed *R. limnocharis* with individuals of similar size. Each trial lasted for seven days (27 August to 3 September 2005). Air temperature during the experiment was 29.0–29.5°C, and water temperature in test tanks was 28.0–28.5°C.

We calculated mean daily consumption by *R. catesbeiana* by dividing the total mass of *R. limnocharis* consumed in each tank by seven days. We used ANOVA to test for the effects of body size and sex of *R. catesbeiana* on daily *R. limnocharis* consumption, and we considered both factors to be fixed. We regressed the daily consumption of *R. limnocharis* against *R. catesbeiana* size (both were ln-transformed) and regressed the maximum size of *R. limnocharis* that *R. catesbeiana* consumed in each tank against *R. catesbeiana* size (both were ln-transformed).

Experiment 2: Comparative Predation by Rana catesbeiana on Four Native Anurans.—We experimentally examined whether male or female Bullfrogs consumed the same proportion of four native anurans (B. b. gargarizans, R. limnocharis, R. nigromaculata, and R. p. plancyi). Because the

females of tested native species are larger than males and juveniles (Huang, 1990; Fei, 1999), size differences may affect their susceptibility to R. catesbeiana (Pearl et al., 2004); therefore, we separated native anurans into three groups (males, females, and juveniles). One individual of each native anuran was randomly drawn from holding tanks to form female or male groups or selected and matched for size to constitute similar size groups (Table 2). Then, they were carefully introduced to the center of each tank and given 1 h to acclimate, after which one R. catesbeiana was added. Rana catesbeiana were matched for size across each treatment (Table 2), and males and females did not differ in body size (mass<sub>male</sub> =  $163.08 \pm 13.32$  g, mass<sub>female</sub> =  $187.50 \pm 16.51 \text{ g}$ ;  $t_{10} = -1.15$ , P = 0.277). We examined each tank carefully every 6 h to determine whether native anurans were preyed upon by R. catesbeiana. We replaced consumed individuals with frogs of the same species that were similar in mass. The experiment lasted for seven days (5-12 September 2005). Air temperature during the trial was 29.0–29.5°C, and water temperature ranged from 27.0 to 27.5°C. Water depth at the deep end of the tanks was 7.0-

3

 $217.67 \pm 17.73$ 

 $6.83 \pm 0.37$ 

We used one-way ANOVA to compare body size among the four native anurans at the start

TABLE 2. Experimental design and characteristics of frogs used in experiment 2. All frogs were measured at the start of the experiment. 2A, 2B, and 2C were experiment groups, representing different sex of *Rana catesbeiana* on male, female, and similar size groups of four native anurans, respectively. \* Values followed by different letters indicated significant differences in body mass among four native anurans.

	Sex			Number Frog per .	Body mass (Mean ± SE)* (g)			
Species	2A	2B	2C	tanks	tank	2A	2B	2C
Rana catesbeiana	O'	O'	O'	2	1	$137.70 \pm 12.00$	$152.90 \pm 2.60$	198.65 ± 22.35
Rana catesbeiana	Q	Q	Q	2	1	$147.25 \pm 11.05$	$180.00 \pm 2.00$	$235.25 \pm 2.75$
Rana nigromaculata	O'	Ŷ	_	4	1	$34.75 \pm 8.97a$	$58.40 \pm 6.97a$	$5.24 \pm 0.99a$
Rana plancyi plancyi	O"	Q	_	4	1	$7.63 \pm 0.30b$	$20.10 \pm 0.83b$	$5.56 \pm 1.01a$
Rana limnocharis	O"	Q	_	4	1	$3.70 \pm 0.00c$	$6.54 \pm 0.40c$	$6.20 \pm 0.56a$
Bufo bufo gargarizans	O'	Ŷ	_	4	1	$36.45 \pm 1.94a$	$59.60 \pm 7.37a$	$6.21 \pm 0.42a$

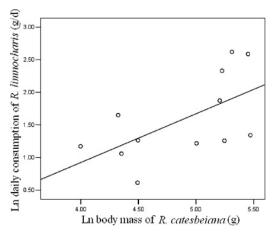


Fig. 1. Daily consumption of male *Rana limnocharis* by *Rana catesbeiana* as a function of *Rana catesbeiana* body mass (r = 0.599; df = 10, P = 0.039).

$$W_i = O_i/P_i$$
.

where  $O_i$  is the proportion of anuran species i in the diet,  $P_i$  is the proportion of anuran species i available in the environment. A  $W_i$ -value > 1.0 indicates greater consumption of prey than would be expected by its availability, and a  $W_i$ -value < 1.0 indicates consumption below availability of the prey. We used  $S_{wi}$  as the standard error of  $W_i$  (Krebs, 1999):

$$S_{wi} = \sqrt{\frac{O_i(1 - O_i)}{UP_i^2}}$$

where  $O_i$  and  $P_i$  are the same as above, and U is the total number of anurans consumed by Bullfrogs. We also used a chi-square test (Krebs, 1999) to evaluate the null hypothesis that R. catesbeiana in the experiment consumed native anurans at random.

### Results

Experiment 1: Daily Consumption of Rana limnocharis by Rana catesbeiana.—A total of 108 R. limnocharis were consumed by the 12 R. catesbeiana during the experiment. Six male R. catesbeiana consumed 63 R. limnocharis, and six female R. catesbeiana consumed 45 R. limnocharis. We found no significant difference in daily R.

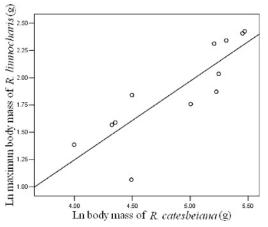


Fig. 2. Maximum body mass of male *Rana limno-charis* consumed by *Rana catesbeiana* in each tank as a function of *Rana catesbeiana* body mass (r = 0.848; df = 10, P < 0.001).

limnocharis consumption between male (6.31  $\pm$  1.91 g/d) and female *R. catesbeiana* (5.57  $\pm$  1.63 g/d) ( $F_{1,8}=0.026$ , P=0.877). Larger *R. catesbeiana* consumed significantly more *R. limnocharis* per day (8.53  $\pm$  1.86 g/d) than did smaller *R. catesbeiana* (3.35  $\pm$  0.45 g/d) ( $F_{1,8}=7.129$ , P=0.028). Daily consumption of *R. limnocharis* was positively related to *R. catesbeiana* body size (Fig. 1). The maximum body size of *R. limnocharis* that *R. catesbeiana* consumed in each tank increased significantly with *R. catesbeiana* size (Fig. 2). The interaction between *R. catesbeiana* sex and size was not significant ( $F_{1,8}=0.074$ , P=0.793).

Experiment 2: Comparative Predation by Rana catesbeiana on Four Native Anurans.-When provided with four male or female native anurans that differed significantly in body size  $(F_{3,12} =$ 14.82, P < 0.001 for males;  $F_{3.12} = 28.21$ , P < 0.001for females; Table 2), R. catesbeiana preyed only on the two smaller species, *R. limnocharis* and *R*. p. plancyi. Among 20 male R. limnocharis and 11 male R. p. plancyi consumed, R. catesbeiana of both sexes took more R. limnocharis (Table 3:2A), which was significantly smaller than R. p. plancyi (Table 4:2A). Among 18 female R. limnocharis and one female R. p. plancyi consumed, R. catesbeiana of both sexes took more R. limnocharis (Table 3:2B), which also was significantly smaller than R. p. plancyi (Table 4:2B). When provided with juveniles of the four native anurans that were similar in body size ( $F_{3,12} = 0.377$ , P =0.771, Table 2), R. catesbeiana of both sexes consumed statistically similar proportions of each species: 11 B. b. gargarizans; five R. limnocharis; five R. nigromaculata; and five R. p. plancyi (Tables 3:2C and 4:2C).

Table 3. Selection indexes ( $W_i$ ) of four native anurans consumed by *Rana catesbeiana* in 12 tanks, with chi-square test examining the null hypothesis that *Rana catesbeiana* were selecting native anurans at random (df = 3). A  $W_i$ -value > 1.0 indicates greater consumption of prey than its availability, and a  $W_i$ -value < 1.0 indicates consumption below availability of the prey. For detailed descriptions of 2A, 2B, and 2C, see Table 2.

		Selection	on index (W <sub>i</sub> ) (Mea	an ± SE)				
Experiment group	Rana catesbeiana	Rana nigromaculata	Rana plancyi plancyi	Rana limnocharis	Bufo bufo gargarizans	$\chi^2$	P	
2A	O'	0	$1.00 \pm 0.61$	$3.00 \pm 0.61$	0	13.18	< 0.005	
	O"	0	$0.89 \pm 0.55$	$3.11 \pm 0.55$	0	15.42	< 0.005	
	Q	0	$1.09 \pm 0.54$	$2.91 \pm 0.54$	0	17.61	< 0.001	
	Q	0	0	4.00	0	8.32	< 0.05	
2B	O'	0	0	4.00	0	13.86	< 0.005	
	O"	0	$0.67 \pm 0.61$	$3.33 \pm 0.61$	0	11.23	< 0.025	
	Q	0	0	4.00	0	11.09	< 0.025	
	Q	0	0	4.00	0	11.09	< 0.025	
2C	o"	$0.80 \pm 0.72$	$0.80 \pm 0.72$	$0.80 \pm 0.72$	$1.60 \pm 0.88$	0.54	> 0.05	
	O'	$0.80 \pm 0.72$	$0.80 \pm 0.72$	0	$2.40 \pm 0.88$	4.36	> 0.05	
	Q	$0.50 \pm 0.47$	$1.00 \pm 0.61$	$1.00 \pm 0.61$	$1.50 \pm 0.68$	1.05	> 0.05	
	Ŷ	$1.00 \pm 0.61$	$0.50 \pm 0.47$	$1.00 \pm 0.61$	$1.50 \pm 0.68$	1.05	> 0.05	

### DISCUSSION

Understanding the mechanisms underlying interactions between invasive and native species is extremely important to minimize the effects of exotic species and develop conservation and management priorities (Parker et al., 1999; Kiesecker et al., 2001). However, such mechanisms are often hard to understand because of complicated interspecific, intraspecific, and synergistic effects in natural conditions. Our experiments, controlling the body size and sex of *R. catesbeiana* and Chinese native anurans, simplify the complicated field conditions that confound the predatory interactions between *R. catesbeiana* and native anurans in China.

Our experiments demonstrated clearly that body size played an important role in the predatory interactions between *R. catesbeiana* and native anurans in China. We found that body size of *R. catesbeiana* was a good predictor of their daily consumption rates as well as maximum prey size. This finding coincides with field diet studies that show larger *R. catesbeiana* ingest more prey than smaller ones (Werner et al., 1995; Wu et al., 2005). Part of the explanation for this pattern may be the greater standard metabolic rates of larger predators (Peters, 1983;

Schmidt-Nielsen, 1990). Our finding of a positive correlation between *R. catesbeiana* size and maximum prey size is a general trend of predator-prey relationships (Aljetlawi et al., 2004) and was also found in field diet studies of *R. catesbeiana* (Werner et al., 1995; Wu et al., 2005). Others have suggested that this relationship may be explained in terms of energetic advantage for individual predators (Werner and Hall, 1974; Sherwood et al., 2002).

Our feeding trials suggested that, other things being equal, *R. catesbeiana* could exert different predation effects on four Chinese natives. Our results indicate that smaller native anurans are likely to be consumed more readily by *R. catesbeiana*. At least two factors are likely to explain this higher predation by *R. catesbeiana* on smaller species, such as *R. limnocharis*. First, most predators are gape-limited, and gape limitation is less likely to mediate interactions with smaller prey (Osenberg and Mittlebach, 1989, Persson et al., 1996). Second, smaller frogs are likely to have lower escape ability than larger conspecifics (Pearl et al., 2004).

Although intersexual differences in prey consumption and prey selection have been commonly found in other ranid frogs (Jenssen

TABLE 4. Body size comparisons between native anurans consumed by *Rana catesbeiana* in experiment 2. t = t-test, F =one-way ANOVA. For detailed descriptions of 2A, 2B, and 2C, see Table 2.

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Experiment group	Rana nigromaculata	Rana plancyi plancyi	Rana limnocharis	Bufo bufo gargarizans	Test statistics	P
2A	_	$6.56 \pm 0.56$ (11)	$4.53 \pm 0.27$ (20)	_	$t_{29} = -3.71$	0.001
2B	_	19.4 (1)	$6.96 \pm 0.21 (18)$	_	$t_{17} = -59.98$	< 0.001
2C	$5.07 \pm 0.78 (5)$	$6.72 \pm 0.29 (5)$	$5.69 \pm 0.79 (5)$	$7.39 \pm 0.68 (11)$	$F_{3,22} = 2.14$	0.124

and Klimstra, 1966; Lamb, 1984; Bull, 2003), R. catesbeiana showed no sexual differences. The lack of differences between male and female Bullfrogs may be explained in three ways. First, male and female R. catesbeiana are similar in growth rate and metabolic rate (Durham and Bennett, 1963; Schroeder and Baskett, 1968); thus, they need similar amounts of food for maintenance. Second, the dietary divergence noted in studies of other ranid frogs may be a reflection of sexual differences in body size. Male and female R. catesbeiana in our trials did not differ significantly in size, and we did not detect divergence in prey consumption. Finally, differences in diet between sexes can be focused on seasons when energetic needs differ between sexes, such as pre- and postbreeding (Jenssen and Klimstra, 1966; Lamb, 1984; Bull, 2003). Our tests were conducted during a short window in late summer; thus, feeding differences between sexes in R. catesbeiana associated with other seasons would be difficult for us to detect.

Our experiments indicated that adult R. catesbeiana could consume all four Chinese native anurans. These findings concur with field collected diets of R. catesbeiana in China (Wu et al., 2005; Wang et al., 2006). Many studies from North America or Europe have shown that some toads of the genus Bufo are unpalatable to predators because of their dermal toxins (Laurila, 1998; Pearl and Hayes, 2002; Ahola et al., 2006), and Huang (1990) suggested *Bufo* are more unpalatable than other Chinese amphibians. Interestingly, we found that B. b. gargarizans were frequently consumed by R. catesbeiana in our experiment, as well as in field diet studies (Wu et al., 2005; Wang et al., 2006). Therefore, R. catesbeiana may have the potential to affect a wider range of amphibians in China than previously thought.

It is important to note several caveats associated with our conclusions. First, our estimation of daily consumption by R. catesbeiana may be higher than that in the field, because placing *R*. catesbeiana with native anurans and without alternative prey promotes the targeting of amphibians by *R. catesbeiana*. Second, although we found that R. catesbeiana more frequently consumed the smaller species (R. limnocharis), other factors such as refuge use are likely to influence anuran prey selection in the field. Therefore, research that compares the role of size with the roles of behavior and habitat selection by prey is needed to better understand interactions with R. catesbeiana in the field. Finally, our data were derived from a limited time, with each trial lasted for seven days. Longer time trials and experiments in different seasons will help elucidate temporal aspects of native interactions with R. catesbeiana.

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