Asian Herpetological Research 2013, 4(4): 248–253
DOI: 10.3724/SP.J.1245.2013.00248

Diet, Food Intake of *Phrynocephalus frontalis* (Agamidae) and Its Potential Role in Desert Habitat

Chunwang LI[1], Xue LIAN[1, 2], Songhua TANG[1], Junhuai BI[2*] and Zhigang JIANG[1*]

[1] *Key Laboratory of Animal Ecology and Conservation Biology*, *Institute of Zoology*, *Chinese Academy of Sciences*, *Beijing* 100101, *China*
[2] *College of Life Science*, *Inner Mongolia Normal University*, *Hohhot* 010022, *China*

Abstract We examined the dietary diversity and food intake of *Phrynocephalus frontalis*, compared the difference of insect diversity in the natural habitats with different lizard densities, and discussed the potential role of this lizard in the desert ecosystem. The results show that: (1) arthropodans of the orders Coleoptera, Hymenoptera and Hemiptera were major dietary components of *P. frontalis*; (2) coleoptera larvae always formed the predominant component of lizard diets; (3) dietary diversities of *P. frontalis* were not significantly different between summer and autumn or between the two sexes; (4) the similarity in trophic niches between seasons was 0.756, whereas the similarity in trophic niches between sexes was 0.994; (5) stomach content weight of lizards varied significantly among different seasons, but there was no significant difference in stomach content weight between sexes; (6) insect diversity differed significantly among the groups of the habitat with different degrees of lizard density, and the habitat with moderate lizards density had the highest insect diversity. We infer that *P. frontalis* prey mainly on insects and change their diet and food intake with season; males and females consumed similar preys in types and weights. As an important predator, *P. frontalis* could affect the insect community in the arid ecosystem of Hunshandak Desert on the Mongolian Plateau.

Keywords Toad-headed lizard, desert lizard, feeding habits, prey diversity, desert grassland

1. Introduction

Many lizards live in arid ecosystems where productivities are low due to low precipitation. Thus how lizards select their diets and maintain food intake are critical issues for these lizards. When the climatic or biological factors restrict food intake, some lizards (e.g. *Sauromalus obesus*) change their diets, adjust the time budgets, and apparently defer reproductive activities to survive the severe environment conditions (Nagy, 1973). As in other animals, lizard diets also relate to intrinsic factors such as hunger impetus and morphological traits (Verwaijen *et al*., 2002).

Lizards consume large numbers of insects each year and assumed to play an important role in insect control (Knowlton, 1938; Pacala and Roughgarden, 1984). The latest studies have focused on the relationship between insect diversity and predation pressure from reptiles and found that lizards influence insect community structure (Murakami and Hirao, 2010; Cozzens, 2011; Garda *et al*., 2012; Borkhataria *et al*., 2012). Similarly, losses of reptiles due to climatic changes in the Mediterranean reduce their potential effects on insect control (Araújo *et al*., 2006; Civantos *et al*., 2012).

Phrynocephalus frontalis (a common name is steppe toad-headed lizard) is a common sand-dwelling lizard in Central Asian deserts (Zhao, 1997; Munkhbaatar *et al*., 2006). Previous reports showed that *P. frontalis* is a dominant predator in some sandy lands or deserts (Wang and Fu, 2004; Zhao, 2001; Liu *et al*., 2008; Li *et al*., 2011). Knowlton (1938) suggested that lizard impacts on insect populations depended upon diet, insect consumption rate and the abundance and distribution

* Corresponding author: Prof. Zhigang JIANG, from Institute of Zoology, Chinese Academy of Sciences, Beijing, China, with his research focusing on animal ecology and conservation biology; and Prof. Junhuai BI, from Inner Mongolian Normal University, Hohhot, China, with his research focusing on zoology.
E-mail: jiangzg@ioz.ac.cn (Zhigang JIANG); bjunhuai@yahoo.com.cn (Junhuai BI)
Received: 24 June 2013 Accepted: 19 October 2013

of lizards. Lian *et al*. (2012) described the abundance, density and distribution pattern of *P. frontalis* in Hunshandak Desert. However, there was no quantitative study of the ecological trophic role of *P. frontalis* in the desert ecosystem. There, these lizards tended to aggregate in suitable habitat patches, and density reached to 0.174 individuals/m^2 (Lian, 2011; Lian *et al.*, 2012). It is necessary to understand the potential effects of *P. frontalis* on insect communities in Hunshandak Desert.

In this study, we investigate the diet and food intake of *P. frontalis* in summer and autumn. Then, we analyze the influences of season and sex that influence dietary diversity of *P. frontalis*. Finally, we compare differences in insect diversity among habitats having different lizard densities and discuss the potential trophic role of *P. frontalis* in desert habitat.

2. Materials and Methods

2.1 Ethics statement In this study, we adhered to the 'Guidelines for the use of animals in research' published in Animal Behaviour 1991 and the Wild Animals Protection Law of the People's Republic of China. All animals in this study were cared for under animal research protocol IOZ-2006 approved by the Animal Care Committee of the Institute of Zoology, Chinese Academy of Sciences.

2.2 Study area This study was conducted in the sand dunes around Sangendalai (115°57' N, 42°40' E) in Xilingole, Inner Mongolia, China. Sangendalai is in the southern region of Hunshandak Desert, with an average elevation of 1813 m above sea level. In this region, mean annual temperature is 1.7 °C, with the maximum temperature of 35 °C in July and the minimum of −33 °C in January. The growing season lasts for 189 d; mean annual precipitation is about 300 mm, with most rain falling in July and August; and mean annual evaporation is 1936.2 mm, which is five times larger than precipitation (Ding *et al*., 2005; Nie and Zheng, 2005). The study area is dominated by sandy soil and also has meadows and saline soil in the lowland region, which is sparsely covered by *Caragana microphylia*, *Artemisia halodendron*, *Ferula bungeana*, *Bassia dasyphylla*, *Agropyron cristatum* and *Cleistogenes squarrosa* (Liu and Guo, 2003; Peng *et al*., 2006).

2.3 Species identification and food intake We carried out observations in June (summer) and September (autumn) of 2011. We totally collected 56 *P. frontalis* adults (27 in summer, 29 in autumn; 31 of males, 25 of females) to form our samples. The existence of hemipenis was used to identify the male *P. frontalis*.

During the morning (9:00–11:00 h) of each sampling day, we captured lizards by hand, intraperitoneally injected 75% ethanol solution in each individual promptly, and then stored lizard samples in 75% ethanol solution for laboratory analysis. We weighed and dissected each lizard, and identified the food items in their stomach contents to degree of Order (Tatner, 1983). We used stomach content weight to represent the food intake of the lizard. We also used Shannon-Wiener index to quantify dietary diversity of the lizards (Shannon and Weaver, 1949; Fialho *et al.*, 2000).

$$H' = -\sum_{i}^{s} p_i \log_e P_i$$

Where: H' = the value of the Shannon-Wiener diversity index, P_i = the proportion of the i^{th} species, s = the number of species in the community.

We used the niche overlap index of Levins (Pianka, 1973; Maia *et al.*, 2011) to assess the degree of similarity of the trophic niche of *P. frontalis* between summer and autumn:

$$O_{jk} = \sum P_{ij} \sum P_{ik} \Big/ \sqrt{(\sum P_{ij}{}^2 \sum P_{ik}{}^2)}$$

Where O_{lk} is Pianka's measure of niche overlap index between two seasons j and k; P_{ij} and P_{ik} are the numerical proportion of prey category i in the diet in seasons j and k, respectively.

2.4 Lizard density, insect diversity and plant coverage We chose 1520 m × 200 m transects in our study area. By using mark-recapture method (Kacoliris *et al.*, 2009), we investigated lizard density of each transect and classified those 15 transects into three categories: (1) Low density, the habitat with low lizard density of less than 0.01 individuals/m^2; (2) Moderate density, the habitat with lizard density of between 0.01 and 0.1 individuals/m^2; and (3) High density, the habitat with lizard density of more than 0.10 individuals/m^2.

To investigate insect diversity in the habitats, we arranged 20 paper cups with baits at 10 m intervals along the length of transect. The baits were combined with sugar, vinegar, 75% ethanol solution, water in the proportion of 1:2:1:20 in weight. We also used insect net to collect insects above each trap. All collected insects were kept in sealed plastic bag and identified in laboratory. We used Shannon-Wiener index to quantify insect diversity (Shannon and Weaver, 1949).

In each transect, we systematically arranged ten 1 m × 1 m wood quadrats at 20 m intervals along the length of transect. Digital cameras have been used for remote sensing over short distances and are considered to be a reliable method for measuring plant coverage (White *et al*., 2000; Chi *et al*., 2007). By this method, we used Photoshop 6.0 (©1990-2002, Adobe Systems Incorporated) to measure plant coverage of those chosen 1 m^2 wood quadrats. The plant coverage was calculated with the formulas below.

$$C = \frac{G}{A} \times 100\%$$

Where: C = plant coverage of a quadrat, G = pixels of green in a quadrat, A= pixels of all colors in a quadrat.

2.5 Statistical analysis All statistical analyses were conducted with SPSS 13.0 (SPSS, Inc., Chicago, IL, U.S.A.). Kolmogorov-Smirnov tests showed that the distribution of variables of dietary diversity, stomach content weight, insect diversity and plant coverage all fit a normal distribution (P >0.05). Thus, we used the Univariate GLM (general linear model) to test the difference of each variable among different experimental groups, as well as the interaction effects of those factors. If necessary, we used multiple comparison of Post Hoc test of Tukey to calculate the significance among pairs of variables. The Bonferroni correction was used for these multiple comparisons. Probabilities lower than 0.05 were considered significant for all tests.

3. Results

3.1 Dietary components in summer and autumn The lizard preyed on Insecta and Arachnida (Table 1). Plant remains were only found in the stomachs of lizards sampled in autumn.

In summer, the first two predominant components of the lizard prey were the Coleoptera (with the percentage of 32.6% of the total weight consumed and the rate of occurrence of 96.3% in stomach, respectively) and the Hymenoptera (with the percentage of 56.39% and the rate of occurrence of 81.48% in stomach, respectively) (Table 1).

In autumn, the predominant prey items were Hymenoptera (50.83% of prey items, present in 93.10% of stomachs), followed by Hemiptera (Table 1). Arachnida animals were also another important prey in autumn (Table 1).

Coleoptera larvae accounted for 5.73% of prey items in summer and 4.79% in autumn; occurring in 37.04% of stomachs in summer and 44.83% in autumn (Table 1).

3.2 Dietary diversity and stomach content weight Dietary diversity indices of *P. frontalis* were not significantly different between summer and autumn (F = 0.082, df = 1, P = 0.776; Table 2) or between the two sexes (F = 0.750, df = 1, P = 0.397; Table 2). The value of trophic niche overlap (O_{ij}) between summer and autumn was 0.756, whereas the value of O_{ij} between two sexes was 0.994.

Stomach content weights showed significant difference between summer and autumn (F = 10.358, df = 1, P = 0.002; Table 2). The lizards preyed more in autumn than in summer (Table 2). There was no significant difference in stomach content weight between two sexes (F = 2.082, df = 1, P = 0.165; Table 2).

3.3 Insect diversity, lizard density and plant coverage Insect diversity indices differed significantly among three habitats with different lizard densities (F = 4.023, df = 2, P = 0.022; Figure 1) Post Hoc tests Tukey showed

Table 1 Percentage and rate of occurrence of prey items in the diet of *Phrynocephalus frontalis* from Hunshandak Desert in Inner Mongolia of China, during the summer and the autumn.

Taxon		Percentage of prey items (%)		Rate of occurrence (%)	
Class	Order	Summer (n = 27)	Autumn (n = 29)	Summer (n = 27)	Autumn (n = 29)
Insecta	Coleoptera	32.16	3.54	96.3	37.93
	Hymenoptera	56.39	50.83	81.48	93.1
	Hemiptera	0.44	34.58	3.7	75.86
	Lepidoptera	0.85	0.42	7.41	6.92
	Diptera	0.88	0.21	7.36	3.52
	Orthoptera	0	0.48	0	6.88
	Coleoptera (larvae)	5.73	4.79	37.04	44.83
	Lepidoptera (larvae)	0	0.42	0	3.44
	Diptera (larvae)	0	0.24	0	3.37
	Hymenoptera (larvae)	0	0.38	0	3.45
Arachnida	Araneae/Acarina	3.52	2.08	25.93	20.69
Plants		0	0.63	0	10.34

that insect diversity of the habitat with moderate lizards density was significantly higher than that of other two habitats (P = 0.014 and P = 0.041, respectively; Figure 1) There was no significant effect of plant coverage on insect diversity index (F = 0.860, df = 4, P = 0.492; Figure 2) The interaction effects of lizard density and plant coverage were also not significant (F = 1.596, df = 8, P = 0.140).

4. Discussion

Phrynocephalus frontalis mainly preyed on Coleoptera, Hymenoptera and Hemiptera. The dietary diversity indices of *P. frontalis* showed no significant difference between summer and autumn, but the main prey items changed from Coleoptera in summer to Hymenoptera in autumn. Insect larvae were also the most important prey items of lizards in growing seasons (Sales *et al*., 2012; Taylor *et al*., 2012). Our data showed that beside of imago, insect larvae were being increasingly preyed on by *P. frontalis* in autumn. Optimal foraging models predict that the shortage of more generalized diets lead predators to consume more "sub-optimal" prey than in periods of greater resource abundance (Maia *et al.*, 2011). Thus, *P. frontalis* could be an opportunistic insectivore lizard which changed their prey according to the seasonally changing environment of Mongolian Plateau. Similar findings were reported in brown anoles (*Anolis sagrei*) that their diet varied from place to place and from season to season (Spiller and Schoener, 1990; Spiller and Schoener, 1997; Huang *et al*., 2008; Norval *et al*., 2010). Moreover, it is suggested that historically shifts of dietary lead to lizard diversity

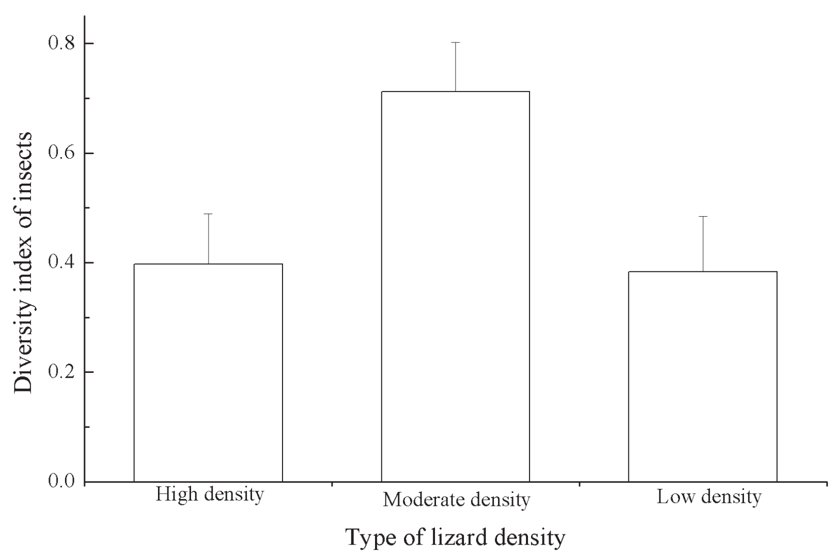

Figure 1 Insect diversity index in habitats having different lizard density. For the X axis, low density: 0.00–0.01 lizards/m^2; moderate density: 0.01–0.1 lizards/m^2; high density: > 0.10 lizards/m^2.

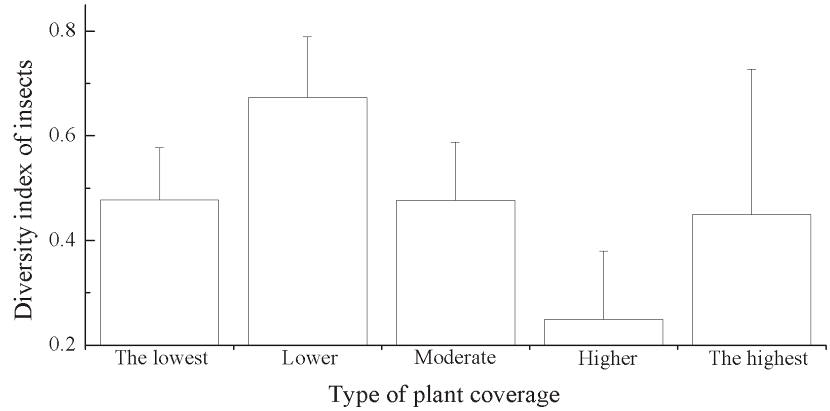

Figure 2 Insect diversity index of the habitat with different plant coverage. For the X axis, plant coverage is: the lowest: 0–10%, lower: 10%–20%, moderate: 20%–30%, higher: 30%–40%, and the highest: >40%, respectively.

Table 2 Dietary diversity and stomach content weight of *Phrynocephalus frontalis* and their influencing factors. * indicates the significant difference between different groups.

Factors		Index of dietary diversity	Niche overlap index (O_{jk})	Stomach content weight (g)
Season	Summer (n = 27)	1.377 ± 0.097	0.756	0.078 ± 0.009
	Autumn (n = 29)	1.373 ± 0.118		0.092 ± 0.009
	Significance	0.776		0.002*
Sex	Male (n = 31)	1.025 ± 0.214	0.994	0.109 ± 0.013
	Female (n = 25)	1.238 ± 0.131		0.144 ± 0.020
	Significance	0.397		0.165

observed today (Vitt and Pianka, 2005). That means the relationships between dietary taxa and phylogeny could result in various dietary of Agamidae lizard in modern time (Vitt and Pianka, 2004; Vitt and Pianka, 2005).

The food intake and energy demands in sand lizards related to the environmental changes and endocrinological action (Telemeco *et al*., 2010). For example, appetite-related hormone secretions of Qinghai toad-headed lizards (*Phrynocephalus vlangalii*) respond to cold stress slightly to mobilize energy and live their vivid life in Qing-Tibetan Plateau (Li *et al.* 2011). Base on our study, stomach content weights of *P. frontalis* varied significantly among different seasons. They preyed more on insects in autumn (non-mating season) than in summer (mating season). Rose (1982) found that there was no overt relationship between stomach content weight and reproductive season in the iguanid lizard *Anolis acutus*. Thus, although they belong to the same superfamily of Iguania, *A. acutus* and *P. frontalis* showed different prey consumptions in different environments they lived.

Generally speaking, animals living under severe conditions would be expected to reduce their sexual differences in foraging patterns and food habits (Hoffman, 1983; Caravello and Cameron, 1987). The indifference of food intake of male and female lizards represented the same food demand of both sexes. In the same way, the types and sizes of prey consumed by male and female whiptail lizards were similar (Sales *et al*., 2012).

Additionally, there was a role of the lizards to their habitat where they could affect animal diversity by predation. We found that the insect diversity indices differed significantly among the groups of habitats with different lizard densities. The insect diversity of the quadrat with moderate density of lizards was significantly higher than that with high or low density of the lizards. Murakami and Hirao (2010) found that the presence of predatory lizards strongly affected species richness of native insects. Biologists suggested that lizards can be used to control invasive species for protecting native diversity and resisting biological invasion (Wanger *et al*., 2011). Lian (2011) also reported the possibility that man use the *P. frontalis* to control pests in desert grassland. We assumed that *P. frontalis* could affect the insect community in the arid ecosystem of Hunshandak Desert on the Mongolian Plateau.

Acknowledgements We acknowledge the financial support of the Knowledge Innovation Project of the Chinese Academy of Sciences (KSCX2-EW-J-2), and the Special Program for Key Basic Research of the Ministry of Science and Technology, China (2013FY110300).

References

Araújo M.B., Thuiller W., Pearson R. G. 2006. Climate warming and the decline of amphibians and reptiles in Europe. J Biogeogr, 33: 1712–1728

Borkhataria R. R., Collazo J. A., Groom M. J. 2012. Species abundance and potential biological control services in shade vs. sun coffee in Puerto Rico. Agr Ecosyst Environ, 151: 1–5

Caravello H. E., Cameron G. N. 1987. Foraging time allocation in relation to sex by the gulf coast fiddler crab (*Uca panacea*). Oecologia, 72: 123–126

Chi H., Zhou G., Xu Z., Yuan W. 2007. Measuring coverage of grassland vegetation using remote sensing over short distances. Acta Pratac Sin, 16(2): 105–110 (In Chinese)

Civantos E., Thuiller W., Maiorano L., Guisan A., Araújo M. B. 2012. Potential impacts of climate change on ecosystem services in Europe: The case of pest control by vertebrates. Bioscience, 62(7): 658–666

Cozzens M. 2011. Food webs, competition graphs, and habitat formation. Math Model Nat Pheno, 6(6): 22–38

Ding G., Li S., Cai J., Zhao T., Wang X., Ling X. 2005. Pasture resources evaluation and stocking density in Hunshandak Sandy Land: Case study of Zhenglan Banner, Inner Mongolia. Chin J Ecol, 24(9): 1038–1042 (In Chinese)

Fialho R. F., Rocha C. F. D., Vrcibradic D. 2000. Feeding ecology of *Tropidurus torquatus*: Ontogenetic shift in plant consumption and seasonal trends in diet. J Herpetol, 34(2): 325-330

Garda A. A., Costa G. C., França F. G. R., Giugliano L. G., Leite G. S., Mesquita D. O., Nogueira C., Tavares-Bastos L., Vasconcellos M. M., Vieira G. H. C., Vitt L. J., Werneck F. P., Wiederhecker H. C., Colli G. R. 2012. Reproduction, body size, and diet of *Polychrus acutirostris* (Squamata: Polychrotidae) in two contrasting environments in Brazil. J

Herpetol, 46(1): 2–8

Hoffman S. G. 1983. Sex-related foraging behavior in sequentially hermaphroditic hogfishes (Bodianus spp.). Ecology, 64: 798–808

Huang S. C., Norval G., Wei C. S., Tso I. M. 2008. Effects of the brown anole invasion and betelnut palm planting on arthropod diversity in southern Taiwan. Zool Sci, 25: 1121–1129

Kacoliris F. P., Berkunsky I., Williams J. D. 2009. Methods for assessing population size in sand dune lizards (*Liolaemus multimaculatus*). Herpetologica, 65(2): 219–226

Knowlton G. F. 1938. Lizards in insect control. Ohio J Sci, 38: 235–238

Li C., Lian X., Bi J., Fang H., Maul T. L., Jiang Z. 2011. Effects of sand grain size and morphological traits on running speed of toad-headed lizard *Phrynocephalus frontalis*. J Arid Environ, 75: 1038–1042

Li C., Gu Y., Tang S., Fang H., Jiang G., Jiang Z. 2011. Effects of acute low temperature stress on the endocrine reactions of the Qinghai toad-headed lizard. Current Zool, 57(6): 775–780

Lian X. 2011. Spatio-temporal Distribution and Habitat Use of Steppe Toad-headed Lizard (*Phrynocephalus frontalis*) and Its Role in Pest Control. Master Thesis. Inner Mongolia Normal University, Huhhot, China (In Chinese)

Lian X., Jiang Z., Ping X., Tang S., Bi J., Li, C. 2012. Spatial distribution pattern of the steppe toad-headed lizard (*Phrynocephalus frontalis*) and its influencing factors. Asian Herpetol Res, 3(1): 46-51.

Liu H., Guo K. 2003. Classification and ordination analysis of plant communities in Inter-dune lowland in Hunshandak Sandy Land. Acta Ecol Sin, 23(10): 2163–2169 (In Chinese)

Liu N., Jin Y., Yang M. 2008. Sand lizards in China. Bull Biol, 43(11): 1–3 (In Chinese)

Maia T, Almeida-Gomes M, Siqueira C. C., Vrcibradic D, Kiefer M. C., Rocha C. F. D. 2011. Diet of the lizard *Ecpleopus gaudichaudii* (Gymnophthalmidae) in Atlantic Rainforest, State of Rio de Janeiro, Brazil. Zoologia 28 (5): 587–592

Munkhbaatar M., Baillie J. E. M., Borkin L., Batsaikhan N., Samiya R., Semenov D. V. 2006. Mongolian Red List of Reptiles and Amphibians. London: Zoological Society of London, Regent's Park, 41–42

Murakami M., Hirao T. 2010. Lizard predation alters the effect of habitat area on the species richness of insect assemblages on Bahamian isles. Divers Distrib, 16: 952–958

Nagy K. A. 1973. Behavior, diet and reproduction in a desert lizard, *Sauromalus obesus*. Copeia, 1973(1): 93–102

Nie C., Zheng Y. 2005. Study on the desertification of Hunshandak Sandy Land: A case in point of the Zhenglan Banner. J Jilin Agric Univ, 27(2): 183–189 (In Chinese)

Norval G., Hsiao W., Huang S., Chen C. 2010. The diet of an introduced lizard species, the brown anole (*Anolis sagrei*), in Chiayi County, Taiwan. Russ J Herpetol, 17(2): 131–138

Pacala S., Roughgarden J. 1984. Control of arthropod abundance by anolis lizards on St. Eustatius (Neth. Antilles). Oecologia, 64(2): 160–162

Peng Y., Jiang G., Niu S., Liu M., Ding S., Liu S. 2006. Communities of typical sand dune-fixed plants in the central part of Hunshandak Sandy Region. Acta Bot Boreal-Occident Sin, 26(7): 1414–1419 (In Chinese)

Rose B. 1982. Food intake and reproduction in *Anolis acutus*. Copeia, 1982(2): 322–330

Sales R. F. D., Ribeiro L. B., Jorge J. S., Freire E. M. X. 2012. Feeding habits and predator-prey size relationships in the whiptail lizard *Cnemidophorus ocellifer* (Teiidae) in the semiarid region of Brazil. S Am J Herpetol, 7(2): 149–156

Shannon C. E., Weaver W. 1949. The Mathematical Theory of Communication. Urbana: University of Illinois Press

Spiller D. A., Schoener T. W. 1990. Lizards reduce food consumption by spiders: Mechanisms and consequences. Oecologia, 83: 150 –161

Spiller D. A., Schoener T. W. 1997. Folivory on islands with and without insectivorous lizards: An eight-year study. Oikos, 78: 15–22

Tatner P. 1983. The diet of urban magpies *Pica pica*. Ibis, 125: 90–107

Taylor D. J., Titus-Mcquillan J., Bauer A. M. 2012. Diet of Chalcides ocellatus (Squamata: Scincidae) from Southern Egypt. Bull Peabody Mus Nat Hist, 53(2): 383–388

Telemeco R. S., Radder R. S., Baird T. A., Shine R. 2010. Thermal effects on reptile reproduction: adaptation and phenotypic plasticity in a montane lizard. Biol J Linn Soc, 100: 642–655

Verwaijen D., Van Damme R., Herrel A. 2002. Relationships between head size, bite force, prey handling efficiency and diet in two sympatric Lacertid lizards. Funct Ecol, 16(6): 842–850

Vitt L. J., Pianka E. R. 2004. Historical patterns in lizard ecology: What teiids can tell us about lacertids. In Pérez-Mellado V., Riera N., Perera A. (Eds.), The Biology of Lacertid lizards. Evolutionary and Ecological Perspectives. Institut Menorquí d'Estudis. Recerca, 8: 139–157

Vitt L. J., Pianka E. R. 2005. Deep history impacts present-day ecology and biodiversity. PNAS, 102(22): 7877–7881

Wang Y., Fu J. 2004. Cladogenesis and vicariance patterns in the toad-headed lizard *Phrynocephalus versicolor* species complex. Copeia, 2004(2): 199–206

Wanger T. C., Wielgoss A. C., Motzke I., Clough Y., Brook B. W., Sodhi N. S., Tscharntke T. 2011. Endemic predators, invasive prey and native diversity. P Roy Soc B-Biol Sci, 278(1706): 690–694

White M. A., Asner G. P., Nemani R. R., Privette J. L., Running S. W. 2000. Measuring fractional cover and leaf area index in arid ecosystems: Digital camera, radiation transmittance, and laser altimetry methods. Remote Sens Environ, 74: 45–57

Zhao K. 1997. Toad-headed agamids in China. Chinese J Zool, 32(1): 15–19 (In Chinese)

Zhao K. 2001. Agamidae. In Rigan X. (Ed.), Fauna Inner Mongolia, Vol. 2. Hohhot: Inner Mongolia University Press, 160–172 (In Chinese)