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Letter to the Editor

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Scatter-hoarding rodent foraging preference on nutrient content is mediated by seed size

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Seed dispersal and predation by scatter-hoarding rodents play an important role in seedling regeneration, community structure and composition, and species coexistence (Vander Wall 2010; Zhang et al. 2016). Rodents generally exhibit seed species preference during their scatter-hoarding behavioral processes (Xiao et al. 2006; Gong et al. 2015; Zhang et al. 2016), and seed traits are a key factor in explaining rodent foraging preference (Wang and Chen 2009; Vander Wall 2010; Zhang et al. 2016). Numerous studies have explored how the diversity of seed traits influences rodent foraging behavior but have shown inconsistent results (Blate et al. 1998; Moles et al. 2003; Xiao et al. 2006; Wang and Chen 2009). These disparate results are likely because of the complicated interactions among traits (Gong et al. 2015; Zhang et al. 2016). In other words, the effect of a given seed trait on rodent foraging behavior may be influenced by other seed traits. However, few studies have directly targeted the interactive effects among seed traits, possibly because of the lack of non-destructive methods for measuring many seed traits, which makes it difficult to compare among individual seeds. Theoretically, multi-species studies provide a potential way to test the interactive effects of different seed traits on rodent foraging preference, by using the mean values of seed traits for each species. However, until now, few studies have included enough species to perform a statistical analysis of the interactive effects among traits (but see Gong et al. 2015; Zhang et al. 2016). Furthermore, large intraspecific variation often exists in many seed traits (Wang and Ives 2017), which may bias the results of interspecific comparisons by using mean values. Artificial seed experimental systems provide an opportunity to ascertain the joint effects of several seed traits by precisely controlling each target trait individually (Wang and Chen 2009, 2012; Wang and Yang 2014). However, all these studies only pointed out the potential interactive effects among traits, and did not analyze how one seed trait would influence the magnitude or intensity of the effect of another trait on rodent foraging preference. In this study, we used artificial seeds to target two important seed traits—seed size and nutrient content—to further explore how one seed trait influences the effect magnitude of another trait on the foraging preference of scatter-hoarding rodents (see Supplementary Material).

Nutrient content showed a positive effect on the probability of seeds being harvested for all seed sizes, with the mean estimate value being 0.183 ± 0.061 (standard deviation), and a range from 0.087 to 0.262 (Figure 1A). Seed size showed a positive effect on the magnitude of nutrient effect on seed harvest, with the nutrient effect on seed harvest being much stronger among large-sized than small-sized seeds (Pearson's correlation, $R^2 = 0.555$, $P = 0.005$; Figure 1A). Of the harvested seeds, nutrient content showed a negative effect on the probability of seeds being removed rather than eaten *in situ*; however, the significant effect only existed among large seeds (>3 cm in diameter), with the mean estimate value being -0.027 ± 0.006, and a range from -0.020 to -0.032 (Figure 1B). Furthermore, a negative correlation was detected between seed size and the magnitude of nutrient effects ($R^2 = 0.590$, $P = 0.006$). No effect was observed between nutrient content and either removal distance or the probability of seeds being cached after removal for all seed sizes, except among the seeds with 3.5 cm diameter, where the nutrient content showed a positive effect on seed removal distance (linear mixed-effects model, $t = 3.023$, $P = 0.004$; Figure 1C).

Our study showed that the magnitude of nutrient effects on seed dispersal and predation by rodents was mediated by seed size, although this pattern did not exist during all the scatter-hoarding processes. Our hypothesis was proved that larger seed size could strengthen the effect of nutrient content on rodent foraging preference. A large seed often represents more absolute nutrients (Gong et al. 2015), which may in turn stimulate the rodent's selection biases during their foraging processes. Decision-making during foraging often costs both time and energy; thus, rodents may show a stronger selection bias among large seeds than among small ones, because of the larger benefit per input cost. In addition, handling large seeds usually requires more foraging investment and involves

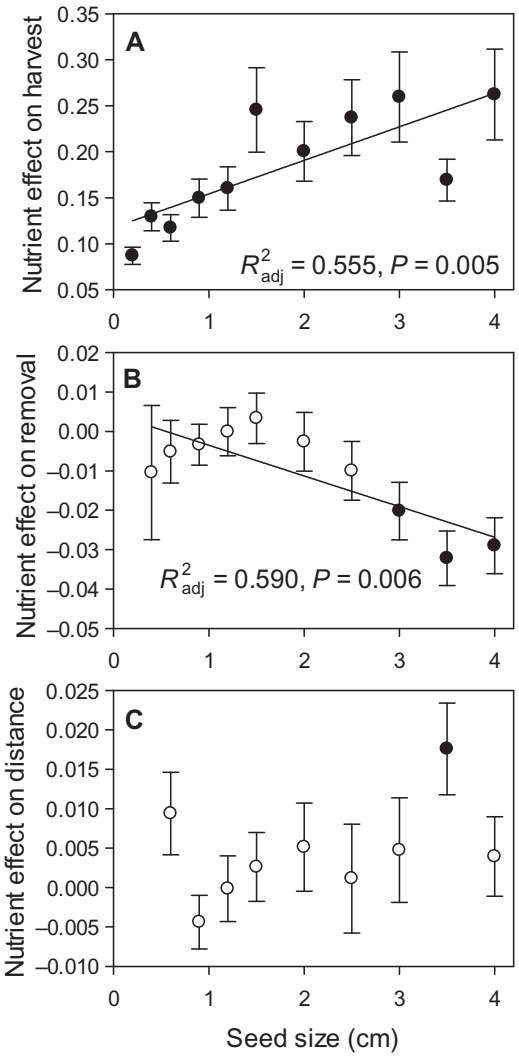

Figure 1. Correlations between seed size and magnitude of nutrient effect on seed harvest by rodent (**A**), seed removal (**B**), and removal distance (**C**). Each symbol stands for the nutrient content effect on seed fate at a given seed size level, that is, the estimate value ± SE from the mixed effect models. Filled circles mean significant effect, whereas open circles mean no significant effect (see Supplementary Table S1). The trend lines are based on Pearson's correlation between seed size and the estimate value of nutrient effects.

more predation risk, and so, with large seeds, rodents may be more selective to obtain a more accurate assessment of nutrient content of the target seed. Conversely, the generally small amount of absolute nutrient content may make the rodent lose interest in selecting among small seeds with different nutrient contents. Moreover, the finite benefit of evaluating and selecting among small seeds may not offset the cost of both energy and time. Our results well explained the inconsistent results of previous studies. For example, nutrient content had a negative effect on the probability of a seed being removed among seeds with diameter larger than 3 cm, but showed no effects among small seeds. This pattern reinforced our previous observations that seed size influenced the effects of nutrient and tannin content on rodent foraging preference (Wang and Chen 2009). Therefore, when discussing the effects of a target factor, we ought to consider the possible influence of other potential factors. Otherwise, a clear effect of the target factor may not be detected or unilateral results may be unintentionally obtained. Two seed traits were considered in our study, whereas more complex interactions among traits often exist *in vivo*. Every single seed is a complex syndrome of multiple seed traits, which together influence seed predation and dispersal by rodents. The effect of each single trait may depend on certain ranges of other traits, which may also explain, at least in part, why current studies including multiple species often find few weak correlations between individual seed traits and seed fate (Gong et al. 2015; Zhang et al. 2016). In conclusion, we strongly suggest that when discussing animal foraging preferences on a target functional trait, the interaction among traits should be considered.

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Authors' Contributions

B.W. conceived the ideas and designed methodology, B.W. and X.Y. collected the data, B.W. analyzed the data and led the writing of the manuscript. Both authors read and approved the final manuscript.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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References

Blate GM, Peart DR, Leighton M, 1998. Post-dispersal predation on isolated seeds: a comparative study of 40 tree species in a Southeast Asian rainforest. *Oikos* **82**:522–538.

Gong H, Tang C, Wang B, 2015. Post-dispersal seed predation and its relations with seed traits: a thirty-species-comparative study. *Plant Spec Biol* **30**:193–201.

Moles AT, Warton DI, Westoby M, 2003. Do small-seeded species have higher survival through seed predation than large-seeded species? *Ecology* **84**: 3148–3161.

Vander Wall SB, 2010. How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals. *Philos Trans R Soc Lond B Biol Sci* **365**: 989–997.

Wang B, Chen J, 2009. Seed size, more than nutrient or tannin content, affects seed caching behavior of a common genus of Old World rodents. *Ecology* **90**:3023–3032.

Wang B, Chen J, 2012. Effects of fat and protein levels on foraging preferences of tannin in scatter-hoarding rodents. *PLoS ONE* **7**:e40640.

Wang B, Ives AR, 2017. Tree-to-tree variation in seed size and its consequences for seed dispersal versus predation by rodents. *Oecologia* **183**:751–762.

Wang B, Yang X, 2014. Teasing apart the effects of seed size and energy content on rodent scatter-hoarding behavior. *PLoS ONE* **9**:e111389.

Xiao Z, Wang Y, Harris M, Zhang Z, 2006. Spatial and temporal variation of seed predation and removal of sympatric large-seeded species in relation to innate seed traits in a subtropical forest, Southwest China. *Forest Ecol Manag* **222**:46–54.

Zhang Z, Wang Z, Chang G, Yi X, Lu J et al., 2016. Trade-off between seed defensive traits and impacts on interaction patterns between seeds and rodents in forest ecosystems. *Plant Ecol* **217**: 253–265.