Behavioural Processes 82 (2009) 7–11

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Hoarding decisions by Edward's long-tailed rats (*Leopoldamys edwardsi*) and South China field mice (*Apodemus draco*): The responses to seed size and germination schedule in acorns

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ARTICLE INFO

Article history:
Received 6 November 2008
Received in revised form 26 February 2009
Accepted 1 March 2009

Keywords:
Edward's long-tailed rats (*Leopoldamys edwardsi*)
South China field mice (*Apodemus draco*)
Germination schedule
Seed size
Hoarding preference

ABSTRACT

Co-varying traits in acorns such as seed size and germination schedule are important to influence the behavioural decisions of hoarding rodents. Using acorn pairs from cork oak (*Quercus variabilis*) (large size and short germination schedules) serrate oak (*Q. serrata*) (small size and short germination schedule) and qinggang (*Cyclobalanopsis glauca*) (small size and long germination schedule) with contrasting seed size and germination schedule, we conducted a series of experiments to investigate hoarding preferences in response to seed size and germination schedule by Edward's long-tailed rats (*Leopoldamys edwardsi*) and South China field mice (*Apodemus draco*) in semi-natural enclosures. We found that the seed size hypothesis was consistently supported: both rodent species ate more small acorns but hoarded more large ones regardless of germination schedules. However, the germination schedule hypothesis was also supported when similar sized acorns were simultaneously provided, e.g. *Q. serrata* versus *C. glauca* or germinating versus non-germinating *Q. variabilis*. Our results, contrary to the studies from North America, indicate that seed size is more important than germination schedules in determining whether the tested animals eat or hoard a given seed.

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1. Introduction

Food hoarding is an adaptive strategy that allows survival during times of food scarcity for many animals (Smith and Reichman, 1984; Vander Wall, 1990). Food preferences by hoarding animals involve a series of behavioural decisions during the foraging process, for example, what to eat or hoard, and where and when to eat or hoard (Smith and Reichman, 1984; Vander Wall, 1990). The characteristics of food items (e.g. seed size, tannin content, and germination schedules) are thought to be key factor that influences such behavioural decisions of food hoarding animals (Vander Wall, 1990, 2001).

Acorns, fruits of oak species (*Quercus sensu*), are important food sources for many wild animals across the Northern Hemisphere. Many hoarding rodents and birds are dependent upon acorns for overwinter survival and reproductive success (Vander Wall, 2001; Shimada and Saitoh, 2006). There are three working hypotheses based on acorn traits to predict hoarding decisions by hoarding animals: first, the high-tannin hypothesis predicts that hoarding animals prefer to hoard high-tannin acorns but eat low-tannin acorns first (Smallwood and Peters, 1986; Steele et al., 1993; Hadj-Chikh et al., 1996; Fleck and Woolfenden, 1997; Xiao et al., 2008). Recently, we provided strong evidence to support this hypothesis in two rat species (Edward's long-tailed rats, *Leopoldamys edwardsi* and chestnut rats, *Niviventer fulvescens*) storing two nut species (Henry's chestnut, *Castanea henryi* and cork oak, *Quercus variabilis*) that show varying tannin levels (0.6% versus 11.7%) but are similar in other traits (Xiao et al., 2008). Second, the seed size hypothesis (or handling time hypothesis, Hadj-Chikh et al., 1996; see also Jacobs, 1992) predicts that hoarding animals prefer to harvest and then hoard more large acorns over small ones. In addition, field studies from our group supported the seed size hypothesis (Xiao, 2003; Xiao et al., 2005, 2006). Third, the germination schedules hypothesis (or food perishability hypothesis) predicts that hoarding animals prefer to hoard acorns with delayed germination schedules and strong evidence for this has been found in North America (Hadj-Chikh et al., 1996; Steele et al., 2001a,b, 2006; Smallwood et al., 2001). Moreover, some studies showed that germination schedules might be the ultimate factor that influences the hoarding decision of squirrels. For example, acorns from the red oak group (subgenus *Erythrobalanus*) with delayed germination are more likely to be hoarded compared to early germinating acorns of the white oak

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doi:10.1016/j.beproc.2009.03.002

Table 1
Predictions of the two alternative hypotheses (i.e. seed size and germination schedule) for each of the five experiments. Shaded boxes indicate predictions which were supported by our results.

Experiment	Acorn species[a]		Prediction of alternative hypotheses[b]			
	A	B	Seed size		Germination schedule	
I	QS_{ng} (S)	QV_{ng} (L)	Less	More	–	–
II	CG_{ng}	QS_{ng}	–	–	More	Less
III	QV_{ng}	QV_{g}	–	–	More	Less
IV	QS_{ng}	QS_{g}	–	–	More	Less
V	CG_{ng} (S)	QV_{ng} (L)	Less	More	More	Less

[a] QV = *Quercus varialilis*; QS = *Q. serrata*; CG = *Cyclobalanopsis glauca*; g = germinating; ng = non-germinating; L = large; S = small

[b] More = hoarded more; less = hoarded less.

group (subgenus *Quercus*) (Hadj-Chikh et al., 1996; Steele et al., 1996, 2001a,b, 2006; Smallwood et al., 2001). There may be some divergence in hoarding preferences to acorns with co-varying traits (e.g. tannins, seed size and germination schedules) for hoarding animals across different continents.

The main objective of the present study was to identify the relative importance of seed size and germination schedules in acorns upon hoarding decisions of two species within the subfamily *Murinae* but different genus to compare with the studies conducted in North America. By presenting acorn pairs with contrasting seed size and/or germination schedules while controlling for differences in other acorn traits (e.g. tannin content), we conducted a series of experiments to test the relative role of seed size (or handling time, see Hadj-Chikh et al., 1996) and germination schedules (i.e. food perishability) in the feeding and hoarding decisions of two rodent species, Edward's long-tailed rats (*Leopoldamys edwardsi*) and South China field mice (*Apodemus draco*) in a subtropical forest, Southwest China. In this study area, these two sympatric species were the major rodent species showing behaviour of scatter hoarding, and they were also the dominant species. There were also other scatter-hoarding species in this area, e.g. Sichuan field mice (*Apodemus latronum*), Chevrier's field mice (*A. chevrieri*), but they were very rare. We hypothesized that the animals would exhibit different hoarding preference to seed size and germination schedules. Predictions were summarized in Table 1 based on the seed size and germination schedules hypotheses.

2. Materials and methods

2.1. Study site and study species

We carried out a series of experiments during the autumn (September to December) in 2006 and 2007 in the Banruosi Experimental Forest (altitude 700–1000 m, 31°4′N, 103°43′E) in Dujiangyan City of Sichuan Province, Southwest China. The vegetation is subtropical evergreen broadleaved forest, where nut-bearing Fagaceae species are most common. In Asia (including China), there are two main oak groups (*Quercus sensu*): white oak group (subgenus *Quercus*) and qinggang oak group (subgenus *Cyclobalanopsis*, treated as an independent genus *Cyclobalanopsis* according to Chun and Huang, 1998). However, no red oak species (subgenus *Erythrobalanus*) are native beyond North America. Acorns from qinggang oaks are similar to red oaks in that they often remain dormant and do not germinate until the following spring. Both white oaks and qinggang oaks co-occur in subtropical evergreen broadleaved forests across south and southwest China, but white oaks are distributed more widely across China. In the study site, there were at least three white oak species (i.e. cork oak *Quercus variabilis*, serrate oak *Q. serrata*, oak *Q. acutissima*) and one qinggang oak species (i.e. qinggang *Cyclobalanopsis glauca*), but cork oak and serrate oak were dominant compared to the other two species. Three oak species, cork oak (QV), serrate oak (QS) and qinggang (CG) were used to test hoarding preferences of rodents because the three oak species showed some variation in seed size and germination schedules, but had similar tannin content (Table 2). QV acorns were the largest (mean, 3.4 g) among the three acorn species, but QS and CG acorns were similar (0.97 g and 0.95 g, respectively). Both QV and QS acorns germinated soon after falling on the ground or even on the tree when mature, but CG acorns did not germinate until the next spring.

Two common rodent species were used in this study: Edward's long-tailed rats (*Leopoldamys edwardsi*) and South China field mice (*Apodemus draco*). Edward's long-tailed rats are large rats (ca. 200–500 g), whereas South China field mice are much smaller (20–30 g). Our previous and ongoing studies have shown that Edward's long-tailed rats and South China field mice scatter hoarded seeds of several large-seeded plants (Xiao et al., 2003, 2005, 2006; Cheng et al., 2005; Chang et al., unpublished data). To trap the animals we used large wired cage traps (30 cm × 25 cm × 20 cm, of our own design approved by the Institute of Zoology, CAS) baited with peanuts and small pieces of cabbage as food and water and provisioned with local dry leaves as nest materials. The traps and nest materials protect animals from cold weather and predators. Traps were deployed at 19:00–19:30 and checked after 12 h (dense vegetation and steep landscape on the study site precluded us from checking traps during the night). When checked that time, all captured animals were healthy. The animals in reproductive conditions were released immediately on site (including three lactating *L. edwardsi* females, which may delay them to feed their litters). Before experiments, all animals were kept individually in a mouse cage (50 cm × 30 cm × 25 cm) with adequate laboratory chow, water and nest structures. The

Table 2
Acorn traits of the three oak species used.

Seed species	Fresh weight[a]	Handling time (S)[b]	Germination schedule	Tannin (%)[b]
Cork oak (*Quercus variabilis*)	3.40 ± 0.06[c]/3.48 ± 0.08[d]	205.0 ± 168.7	Early (Autumn)	11.68
Serrate oak (*Q. serrata*)	0.97 ± 0.26[c]/1.02 ± 0.18[d]	81.6 ± 43.9	Early (Autumn)	10.62
Qinggang (*Cyclobalanopsis glauca*)	0.95 ± 0.19[c]	72.4 ± 41.6	Delayed (Spring)	11.05

[a] Mean ± 1 S.E., *N* = 40.

[b] From Xiao et al. (2003).

[c] Acorn weight was used in Experiments *I*, *II* and *V*.

[d] Acorn weight was used in Experiments *III* and *IV*.

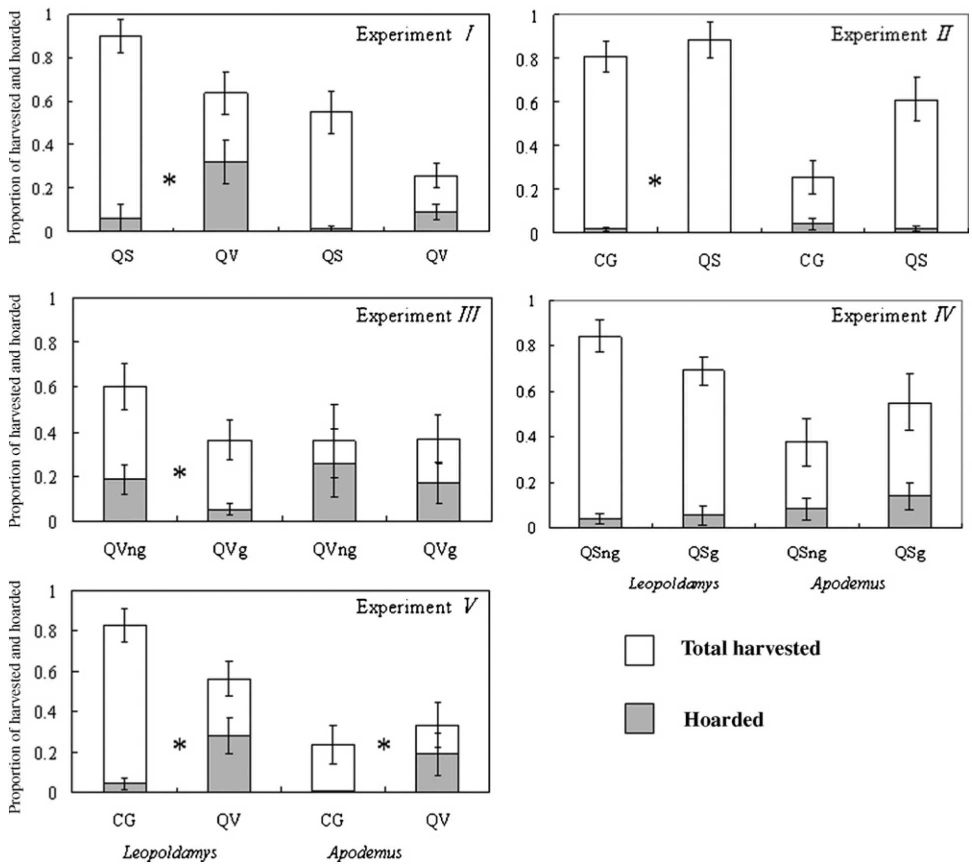

Fig. 1. Hoarding preferences (mean ± S.E.) to acorn pairs from three acorn species by Edward's long-tailed rats (*Leopoldamys edwardsi*) and South China field mice (*Apodemus draco*) in each of the five experiments (QV = *Quercus variabilis*, QS = *Quercus serrata*, CG = *Cyclobalanopsis glauca*, ng = non-germinating, g = germinating. $^*P < 0.05$).

room temperature was 10–15 °C and natural photoperiod was at 12:12 h light:dark cycle. During the experiments, adequate water and nest structures were provided. We trapped 12 adult individuals of Edward's long-tailed rats (six males and six females) and four adult individuals of South China field mice (two males and two females) in 2006, and 11 adult individuals of Edward's long-tailed rats (six males and five females) and six adult individuals of South China field mice (five males and one female) in 2007. Every individual of the two species was used for each experiment. After experiments (up to 2–3 months), all animals were released where they were captured.

2.2. Experimental design

We performed five experiments to test the relative role of seed size and germination schedules in feeding and hoarding preferences. In each experiment, we presented acorn pairs with contrasting seed size and/or germination schedule while controlling for differences in other acorn traits, In Experiment *I*, non-germinating QS and QV acorns were used to test the effects of seed size; similar sized acorns from either different species (i.e. CG and QS) or the same species (i.e. QV or QS) were used to test the effects of germination schedules in Experiments *II*, *III* and *IV*, respectively; and CG and QV acorns with both contrasting seed size and germination schedules were used to see the relative importance of seed size and germination schedules in Experiment *V* (Tables 1 and 2).

We conducted all experiments in four 10 m × 10 m semi-natural enclosures (see Cheng et al., 2005 for details about the enclosure design). Before the experiments, each animal was introduced into the enclosure and allowed to move freely for one night. During each experiment, acorn pairs (i.e. 20 acorns for each individual) from any two of the three acorn species were placed at the center of each enclosure at ca. 1730. We labeled acorns with small coded plastic-tags in order to find the acorns hoarded by animals quickly. Each experiment lasted ca. 14 h from 17:30–07:30. After removing the animal, we searched the target acorns or acorn fragments and recorded their fates (i.e. eaten or hoarded). Harvested acorns are defined as those harvested from food pile (either eaten or hoarded) and hoarded acorns included those buried in soil (scatter-hoarding) and stored in nest boxes (larder-hoarding). Both rodent species showed very little larder-hoarding in the enclosure experiments. Thus, we combined data of scatter-hoarded and larder-hoarded seeds together as 'hoarded seeds'. Acorns placed on the soil surface were not included in analysis, although they were carried some distances away from food pile.

2.3. Statistical analysis

The proportion data (data from both years were combined) of harvested and hoarded seeds were arcsine-square-root transformed prior to statistical analysis. Paired-sample *t*-tests were used to test the difference in food preferences between difference acorn pairs with equal variance, otherwise Wilcoxon Signed-Rank tests were used. All statistical tests are two tailed in this study, and the significance level is set at $P < 0.05$.

3. Results

In Experiment *I*, both Edward's long-tailed rats and South China field mice harvested more small QS acorns than large QV ones ($Z = 2.397$, d.f. = 11, $P = 0.017$ and $t = 2.396$, d.f. = 9, $P = 0.04$, respectively), but they hoarded more large QV acorns ($Z = 2.807$, d.f. = 11, $P = 0.005$ and $Z = 1.703$, d.f. = 9, $P = 0.089$, respectively) (Fig. 1).

In Experiment *II*, both Edward's long-tailed rats and South China field mice hoarded more CG acorns with delayed germination though they harvested and then ate more QS acorns ($Z = 2.000$, d.f. = 11, $P = 0.046$ and $t = 0.433$, d.f. = 9, $P = 0.676$, respectively). The results from Experiment *III* were similar to those from Experiment *II*: both rat species hoarded more non-germinating QV acorns compared to germinating ones (Edward's long-tailed rats, $Z = 2.536$, d.f. = 10, $P = 0.011$; South China field mice, $t = 1.205$, d.f. = 5, $P = 0.282$). In Experiment *IV*, however, there was no difference in hoarding preferences between non-germinating and germinating QS acorns for either Edward's long-tailed rats ($Z = 0$, d.f. = 10, $P = 1.000$) or South China field mice ($t = 1.424$, d.f. = 5, $P = 0.214$) (Fig. 1).

In Experiment *V*, both Edward's long-tailed rats and South China field mice hoarded more large QV acorns over small CG ones even though CG acorns germinated much later than QV ones ($Z = 2.670$, d.f. = 11, $P = 0.008$ and $Z = 2.226$, d.f. = 9, $P = 0.026$, respectively) (Fig. 1).

4. Discussion

We found that the seed size hypothesis was firmly supported: both rodent species ate more small acorns but hoarded more large ones regardless of germination schedules. Germination schedules (food perishability) hypothesis also received some support when similar sized acorns were simultaneously provided, e.g. QS versus CG or germinating versus non-germinating QV. Our results indicate that seed size is more important than germination schedules in determining whether the tested animals eat or hoard a given seed, which is different from results of studies for grey squirrels (*Sciurus carolinensis*) in North America, especially Hadj-Chikh et al. (1996).

In general, seed size is not only related to food value (e.g. Smith and Reichman, 1984), but also proportional to handling time (e.g. Hadj-Chikh et al., 1996). Increasing evidence indicates that hoarding rodents prefer to hoard high-value seeds (e.g. larger seeds) and disperse them farther (e.g. Stapanian and Smith, 1978, 1984; Vander Wall, 1995; Forget et al., 1998; Jansen et al., 2004; Xiao et al., 2005; Moore et al., 2007). Our study using acorn pairs (of either QV versus QS or QV versus CG) showed that large QV acorns are more likely to be hoarded by two rodent species regardless of germination schedule. Field data from the same study site fit the same pattern as this study conducted in semi-nature enclosures (see Xiao, 2003; Xiao et al., 2003, 2005). However, Hadj-Chikh et al. (1996) did not provide positive support for the seed size hypothesis (or handling time hypothesis) when using acorn pairs from either different species (*Q. palustris* versus *Q. alba*) or the same species (*Q. alba*). They indicate that germination schedules are the determining factor to influence hoarding decisions compared to other acorn traits. The inconsistence between this study and Hadj-Chikh et al. (1996) may be contributed to behavioural differences among rodent species studied and nutrient compositions among acorn species used.

On the one hand, both Edward's long-tailed rats and South China field mice did not display embryo excision behaviour during hoarding process compared to grey squirrels (*Sciurus carolinensis*) which can bite off the radical and then excise the embryo from the apical end of the acorn. The result is an intact seed that still stores well for several months, but is unable to germinate (Steele et al., 2001b). Embryo excision may be an adaptive behaviour in squirrels in response to early germination in white oak acorns (Fox, 1982). Recently, Steele et al. (2006) indicate that grey squirrels show a strong innate basis in the hoarding decisions in response to germination schedules in acorns. However, this embryo excision behaviour has never been reported in other continents, especially Asia and Europe, where many white oak species occur, though one tropical rodent species, the red acouchi (*Myoprocta exilis*), is found to remove the protruding radicles and epicotyls of germinating *Carapa procera* seeds for long-term storage (Jansen et al., 2006). This implies that other rodent species (e.g. rats and mice), unlike grey squirrels and other two squirrels (*S. aureogaster* and *S. niger*) reported previously (Steele et al., 2001b), are less sensitive to early germination in acorns from white oak group (see also Steele et al., 2001b). Though germination schedules have some effects on hoarding preferences of tested animals, we found that the animals were responding primarily to acorn size over any other factors. All else being equal, food reserve due to early germination declines less than the net benefit obtained from large QV acorns over small QS or CG ones (over threefolds in size) (Table 2), or food reserve loss is a relatively slow physiological process during seed germination for large acorns (e.g. QV in this study) since at least part of the cotyledons are still edible even after they emerge as young seedlings over several months (Zhishu Xiao, personal observation).

On the other hand, several other traits, besides seed size, also co-vary among different acorn species. For example, acorns from white oaks are different from those from red oaks in several ways: the former germinate soon after falling on the ground and contain less tannin content (<2%; but 5–15% for the latter) and less fat content (ca. 10%; but ca. 20% for the latter) (Smallwood et al., 2001). In this study, QV and QS acorns (white oaks) germinate much earlier than CG acorns (qinggang oak), but the three acorn species have similar tannin content (Table 2) and other nutrient compositions (e.g. caloric value (J/g) 17.63, 17.29 and 16.99 of dry weight for QV, QS and CG, respectively) (see also Xiao et al., 2003, 2006). Thus, seed size and germination schedules are two key co-varying traits among the three acorn species used here (Tables 1 and 2), compared to four co-varying traits (i.e. seed size, germination schedules, tannin and fat levels) among acorn species used in North America (Hadj-Chikh et al., 1996; see also Smallwood and Peters, 1986; Steele et al., 1996, 2001a,b, 2006; Smallwood et al., 2001). In our study site, small oil tea seeds (mean, 0.9 g) with high-fat content (over 50% of dry weight) are found hoarded more than large QV acorns (mean, 2.42 g) (Xiao et al., 2003, Cheng et al., 2005; Chang et al., unpublished data). Thus, high-fat content (ca. 20% of dry weight) may enhance hoarding probability of acorns from red oaks, which may be masked when red oaks are compared with white oaks.

According to this study and Xiao et al. (2008), we found that tannins, seed size and germination schedules all have some impacts on hoarding preferences of acorns by rodents, while germination schedules, rather than seed size, tannin and fat levels, is the key factor influence hoarding behaviour of tree squirrels in North America. Based on experimental and field observations, we found that high tannins do delay the utility of high-tannin acorns (i.e. QV, QS and CG) in contrast to low-tannin nuts (e.g. *Lithocarpus harlandi*, *Castanea henryi* and *Castanopsis fargesii*), but do not affect hoarding of QV acorns compared to *C. henryi* nuts especially in the field condition (Xiao, 2003; Xiao et al., 2003, 2005, 2006, 2008). Moreover, both experimental and field studies provide strong evidence for the seed size hypothesis: large seeds are always hoarded more and dispersed further, and even have a higher probability of survival of cached seeds and then establishment as seedlings (Xiao, 2003; Xiao et al., 2003, 2005, 2006, 2008; this study). In the study site with frequent rainfall and high moisture, acorns from two dominant oak species (i.e. QV and QS) often germinate soon after falling on the ground. Very occasionally, we observed QV acorns germinated when they fall on the tree branches, but this phenomenon was very rare. It seems seed size is more frequently selected than germination schedule. Thus, germination schedules are less likely to influence hoarding decisions of tested animals than tannins and seed size compared to the studies conducted in North America.

In conclusion, our study provides strong support for the seed size hypothesis. However, we also suggest that germination schedules should not be ignored, because of the many past studies supporting this hypothesis (Fox, 1982; Hadj-Chikh et al., 1996; Steele et al., 1996, 2001a,b, 2006; Smallwood et al., 2001; this study). Since there are many differences in acorn species (including their acorn traits) and animal species (including their behaviours) as discussed above, we expect that some divergence and/or convergence may exist in the evolution of hoarding decisions by related animals in response to co-varying traits (e.g. tannins, seed size and germination schedules) in acorns between China and North America. Thus, future studies should focus on the evolution of such behavioural decisions of hoarding animals in response to the evolution of acorn traits across different continents.

Acknowledgements

We are very grateful to Mike A. Steele for valuable comments and suggestions on earlier drafts of this manuscript. We also thank the Subalpine Mountain Plant Garden of West-China, CAS, and the Forest Bureau of Dujiangyan City of Sichuan Province, for support. Funds were provided by National Natural Science Foundation of China (30430130, 30500072 and 30770372), the Knowledge Innovation Program and Innovative Research International Partnership Project (CXTDS2005-4) of Chinese Academy of Sciences. The experiments comply with the current laws of the country in which they were performed.

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