The Journal of Experimental Biology 209, 3164-3169
Published by The Company of Biologists 2006
doi:10.1242/jeb.02366

The energetic consequences of dietary specialization in populations of the garter snake, *Thamnophis elegans*

E. J. Britt*, J. W. Hicks and A. F. Bennett

Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697, USA

*Author for correspondence (e-mail: ebritt@uci.edu)

Accepted 5 June 2006

Summary

We investigated the intraspecific variation in digestive energetics between dietary specialist and generalist populations of the Western Terrestrial garter snake (*Thamnophis elegans*) in northern California. Coastal populations have a specialized diet of slugs and inland populations have a generalized diet of fish, anurans, mice and leeches. The difference in prey preference between the two populations is congenital, heritable and ontogenetically stable. To examine energetic specializations and trade-offs in these populations, we measured the net assimilation efficiency of each snake population on both slug (*Ariolimax columbianus*) and fish (*Rhinichthys osculus*) diets. The net assimilation efficiency was measured during digestion of a meal and continued until metabolic rate re-attained prefeeding levels. Coastal snakes were able to utilize 62% more of the ingested energy towards production from slug diets through both increased assimilation of nutrients and reduced digestive costs. For fish, assimilation and digestive costs were the same in both coastal and inland populations. These results support the hypothesis that snakes with specialized diets can evolve physiological traits to extract nutrients more efficiently. However, there was no apparent trade-off on the more generalized diet that was associated with this specialization.

Key words: *Thamnophis*, dietary specialization, digestive energetics, assimilation efficiency, SDA, banana slug.

Introduction

Although local dietary specialization is a widespread biological phenomenon (Fox and Morrow, 1981), the underlying ecological and evolutionary mechanisms responsible are not well understood. The evolution of specialization has been based on the concept of behavioral and physiological trade-offs, and specialist–generalist trade-offs in fitness under different environmental conditions are fundamental to most models of specialization (e.g. Fry, 1996; Angilletta et al., 2003). In contrast to numerous studies on phytophagous insects, from which most of the empirical support for these models comes, there have been few investigations in vertebrates on the evolution of dietary specialization (Futuyma and Moreno, 1988). In this study, we describe two geographically separated populations of garter snakes in which a dietary specialization based on behavior (prey preference) has evolved in one of the populations. Specifically, we investigated the energetics of digestion in order to determine the relationship between resource specialization and the adaptation of physiological traits.

The North American garter snakes, *Thamnophis* spp., have very diverse diets and habits, both within and among species. The Western Terrestrial garter snake, *Thamnophis elegans*, has one of the largest ranges in the genus and is characterized by a generalized diet over most of its species range; however, some local *T. elegans* populations have more narrowed, specialized diets. We studied *T. elegans* from two geographically isolated populations in northern California: *T. e. terrestris*, a coastal population with a specialized diet of slugs, and an inland population, *T. e. elegans*, with a generalized diet primarily of fish, but also including anurans, mice and leeches. It has long been assumed that this feeding polymorphism in coastal *T. e. terrestris* is a result of niche contraction by westward invading populations of *T. e. elegans* (Arnold, 1981a; Drummond and Burghardt, 1983). However, the phylogenetic relationships within *Thamnophis* spp. and within *T. elegans* remain unresolved. Molecular phylogenetic data suggest a non-monophyletic grouping of *T. elegans* with other garter snakes (de Queiroz et al., 2002) and the coastal geographic race may be paraphyletic and basal to other *T. elegans* subspecies (Bronikowski and Arnold, 2001).

Neonates of both populations demonstrate a high chemoreceptive response to fish, whereas only the slug specialists have a high chemoreceptive response to slugs (Arnold, 1981a). In addition, the inland snake populations have a high frequency of slug-refusing morphs, in which animals will refuse to ingest slugs until starvation and death (Arnold, 1981a). The difference in chemoreception and feeding behavior between the two populations is thus congenital, heritable and ontogenetically stable. The intraspecific geographic variation in prey detection and consumption found among populations of *T. elegans* thus presents an excellent opportunity to study digestion of different prey types in two diverse populations of conspecifics with different niches and selective pressures. If specialization did not involve costs, we would predict that the coastal population would have (1) a higher assimilation and net assimilation efficiency on a slug diet than would the inland population, and that the two populations would have an equal efficiency on fish prey, and (2) a lower percentage of ingested energy devoted to the metabolic cost of digestion on a slug diet than would the inland population, and that the two populations would have equal metabolic costs of digestion on fish prey. Alternatively, if slug specialization by the coastal population resulted in trade-offs in their digestive performance, then we would expect both populations to be optimized on their native diets and have decreased efficiencies on non-native diets.

To test these hypotheses, we measured net assimilation efficiency of snakes from each population on both prey types. The coastal slug specialists received an experimental diet of fish after a control diet of slugs, and the reciprocal treatment was given to the inland generalist snakes. Net assimilation efficiency was measured upon digestion of the meal for each of the snakes. By standardizing the meal and determining its energetic content, the amount of energy remaining in the feces gave an estimate of total assimilation energy. The assimilation energy minus the cost of respiration resulted in an estimate of the net assimilated energy available for growth, storage and activity. In addition to feeding intact prey, since inland snakes will not accept slugs voluntarily, we also fed both populations capsules containing freeze-dried prey, in order to determine digestive energetics independent of prey preferences.

Materials and methods

Collection of snakes and prey

Slug specialist (coastal) snakes (subspecies *Thamnophis elegans terrestris* Fox 1951 were collected near the mouth of the Mad River in Humboldt County, CA, USA and adult slugs (*Ariolimax columbianus* Gould 1851) were collected near Prairie Creek, Humboldt County. Generalist (inland) snakes (subspecies *Thamnophis elegans elegans* Cope 1892) and speckled dace (*Rhinichthys osculus* Girard 1856) were collected from two mountain meadow sites near Eagle Lake, Lassen County, CA, USA. All specimens were taken under the permission of the California Department of Fish and Game (SC# 006587) during the years 2003, 2004 and 2005. The snakes and prey items were transferred to the University of California Irvine, where all procedures were performed under IACUC Protocol Number 1999-2123. Fifteen adult generalist snakes from Eagle Lake (mean mass=32.4 g) and 16 specialist snakes from the coast (mean mass=25.2 g) of undetermined sex were used in these experiments. All fish and slugs were immediately frozen after capture.

Animal maintenance and feeding experiments

Garter snakes are relatively easy to keep in a laboratory environment due to their small size, diet and ease of handling (Rossman et al., 1996). Snakes were maintained on a 12 h:12 h L:D photoperiod at a constant temperature of 30°C, the field body temperature of this species (Stevenson et al., 1985; Peterson, 1987). It is also the temperature at which the metabolic increase during digestion was largest for the closely related and sympatric garter snake *T. sirtalis* (Bear, 1994). Snakes were kept on a maintenance diet of newborn mice and fish until feeding experiments began 2–4 months after arrival in the laboratory. The fasting period for each animal prior to feeding and metabolic measurements during each trial was 6–10 days. Animals from each population were first presented with their native diet (i.e. slugs for coastal and fish for inland populations), and after another week-long fasting period, were presented with the alternative meals, which were isoenergetic for both prey.

Energy content and assimilation efficiency

Assimilation efficiency [(ingested energy–egested energy)/ingested energy] was measured for each snake on meals of both fish and slugs. Nutrient composition of samples of slug and fish were determined commercially (Food Products Laboratory, Portland, OR, USA) and are reported in Table 1. Energetic content (kJ g^{-1}) of dry, ash-free samples of slug and fish were determined using a Phillipson Microbomb Calorimeter (Gentry Instruments, Aiken, OH, USA) following the methods described elsewhere (Paine, 1971) and are also reported in Table 1. The primary objective in standardizing the meals was to feed each snake the equivalent energetic content of a single meal in nature. Each animal was fed a meal containing 0.46 kJ g^{-1} of either slug or fish, which would have corresponded to a meal size of 16% of the snake's body mass on a slug diet or 11% on a fish diet. Whole slugs were thawed prior to feeding, and presented to each snake from both populations. Goldfish were sometimes used to supplement *Rhinichthys* because of their similar nutritive content. Snakes that attacked and ingested slugs or

Table 1. *Energetic content and tissue composition of the two prey types*

	Fish	Slugs
Energetic content (kJ g^{-1})		
Dry, ash-free	24.98±1.52	18.82±2.28
Dry	22.27±3.29	17.14±2.01
Live	4.38±0.65	2.49±0.29
Tissue composition (%)		
Carbohydrate	0.4	5.1
Fat	4	0.5
Protein	12.2	7.1
Moisture	80.3	85.5

fish were used for the intact meal metabolic feeding trials, but snakes from the inland population would not consume slugs voluntarily. In order to feed both populations standardized meals, slugs and fish were lyophilized, homogenized using a Thomas Scientific (Swedesboro, NJ, USA) mini mill grinder, and condensed into pill form in Torpac™ capsules (5.31 mm outer diameter, 0.21 ml total volume). The meals in pill form were then inserted through a soft plastic tube into the stomach.

When all excreta had been passed (4–5 days after ingestion), snake feces and urates were collected by washing and scraping each metabolic chamber clean. The content of the snake chambers were then dried at 50°C, and dry mass from each chamber was recorded. The energy content (kJ g^{-1}) of fecal and urate samples was again measured by bomb calorimetry to determine the assimilation efficiency.

Measurement of respiration and net assimilation efficiency

Net assimilation efficiency [(ingested energy–egested energy–specific dynamic action)/ingested energy] of each individual snake was measured for both fish and slug diets. Net assimilation efficiency (Brody, 1974) is the fraction of energy remaining for maintenance, activity, growth, reproduction and storage, after digestive costs are subtracted from the energy assimilated. Specific dynamic action (SDA) is the total postprandial oxygen consumption $\dot{V}_{O_2}$ exceeding the rate of oxygen consumption at rest (standard metabolic rate, SMR). SDA was calculated as the area beneath the curve resulting from increased $\dot{V}_{O_2}$ minus the area representing SMR for each snake. Ingested energy is the total initial energetic content of the ingested meal. All measurements of SMR were taken in a post-absorptive state during the 24 h time period prior to feeding. SMR was taken to be the average $\dot{V}_{O_2}$ during this time period. Oxygen consumption was determined using open-flow respirometry for each snake (Withers, 1977). Snakes were placed into sealed 850 ml metabolic chambers with a small water dish containing 70 ml of water. Using Drierite™ as a desiccant, ambient air was pumped (100 ml min^{-1}) into the metabolic chamber and downstream oxygen content was analyzed using an Ametek S-3A oxygen analyzer (Pittsburgh, PA, USA) and recorded on a flatbed (Servogor Recorders; Sun Valley, CA, USA) chart recorder. Measurements proceeded for approximately 4–5 days after ingestion of meals until $\dot{V}_{O_2}$ returned to SMR levels (Fig. 1). All gas volumes are corrected to dry gas at standard temperature and pressure conditions. A respiratory quotient of 0.8 is assumed throughout all experiments (Gessaman and Nagy, 1988), with an energy conversion factor of 20.09 kJ l^{-1} O_2 (Brody, 1974). SMR and postprandial $\dot{V}_{O_2}$ measurements were converted to kJ estimates to calculate the production efficiency of each snake. We also measured the fraction of assimilated energy used to meet SDA costs (SDA/assimilated energy). Assimilation efficiency, SDA, SDA/assimilated, and net assimilation efficiency were compared within and between populations using two-tailed *t*-tests (paired by prey type within populations). Statistical significance was assessed at $P<0.05$. We report mean values with 95% confidence limits.

Results

Nutritive quality of the prey

The energetic value of the two prey items differs considerably (Table 1). Nutritionally, fish are superior to slugs in almost every way. Slugs have a considerably lower dry mass energy content per unit wet mass (less than 75% that of fish). Even on a dry mass basis, slugs contain only 75% the energy of fish, a difference of over 6 kJ g^{-1} ash-free dry mass. The combination of higher water and lower energy nutrient content gives slugs only 57% of the nutrient content of fish on a wet mass basis. Slugs have almost no fat content and only half the protein content of fish and contain significant amounts of carbohydrates (Table 1), largely in the form of mucus on the surface of the body (Denny, 1980).

Energy extraction from specialized prey: slugs

Intact slugs were presented to each snake from both populations. While the coastal specialist snakes readily ingested intact pre-weighed pieces of slug, every snake from the inland generalist population refused to ingest pieces of slug tissue after striking the carcass several times. Therefore, while energy extraction efficiencies can be measured for the coastal specialists eating intact slug prey, comparisons of energy

Table 2. *Energetics of digesting slugs, a specialized prey, by two populations of the garter snake Thamnophis elegans*

	N	Assimilation efficiency	SDA/assimilated energy	Net assimilation efficiency
Intact slug				
Specialist snakes	13	0.653±0.047	0.235±0.038	0.498±0.047
Generalist snakes	–	NA	NA	NA
Lyophilized slug				
Specialist snakes	15	0.780±0.045	0.312±0.070	0.547±0.070
Generalist snakes	15	0.671±0.050	0.521±0.120	0.337±0.090
Significance (*P*)		0.003	0.002	<0.001

Slugs were presented in both intact and lyophilized form; snakes from the generalist population would not consume intact slugs.

Efficiencies and ratios are defined in the text. Mean values (± 95% CL) are reported from single trial measurements on each individual snake. NA, not applicable.

processing efficiencies for slugs between the populations can be made only for lyophilized prey (Table 2).

After ingestion of an intact slug meal equaling 16% body mass, or 0.46 kJ g^{-1} wet snake mass, the specialist population's metabolic rate increased to a maximal value of 0.14 ml O_2 h^{-1} g^{-1}, 2.9× the SMR (Fig. 1). 65.3% of the total ingested energy was assimilated, and about 1/4 of that was used as SDA, resulting in a net assimilation efficiency of approximately 50% of the total energy ingested in the slug meal. When digesting lyophilized slug meals, metabolic rate of the specialist population increased to 3.2× SMR. Lyophilized slugs were digested with a higher assimilation efficiency than whole slugs (78% *vs* 65%, $P<0.01$), but the fraction of assimilated energy devoted to SDA was also higher for lyophilized slugs (31% *vs* 24%, $P=0.05$), resulting in a net assimilation efficiency similar to that of intact meals (54.7% *vs* 49.8%, $P=0.16$).

In the inland generalist population of *T. elegans*, which refused to eat intact slug prey, metabolic rate increased to a maximal value of 3.6 times SMR. Only 67% of energy ingested was assimilated and over half that assimilated energy (52%) was used in SDA. Thus only about 1/3 of the ingested energy appeared as net assimilation. In comparison to the specialist population, when both digested lyophilized slugs, assimilation efficiency was lower ($P=0.003$), SDA costs were higher ($P=0.002$), and net assimilation ($P<0.001$) was lower in the generalist snakes.

Energy extraction from generalized prey: fish

In contrast to slugs, snakes from both populations readily accepted and ingested intact fish; for comparison with slug data, they were fed meals of lyophilized fish as well (Table 3). Snakes from both populations had very similar digestive energetics when eating intact fish. Eating meals equivalent to 11% body mass (0.46 kJ g^{-1} wet snake mass), metabolic rate increased to about 3.2× SMR. Assimilation efficiency was approximately 80%, and about 15% of that was used in SDA, resulting in net assimilation of approximately 70%. There were no significant differences between the two populations in any of these values. Assimilation efficiency was higher for

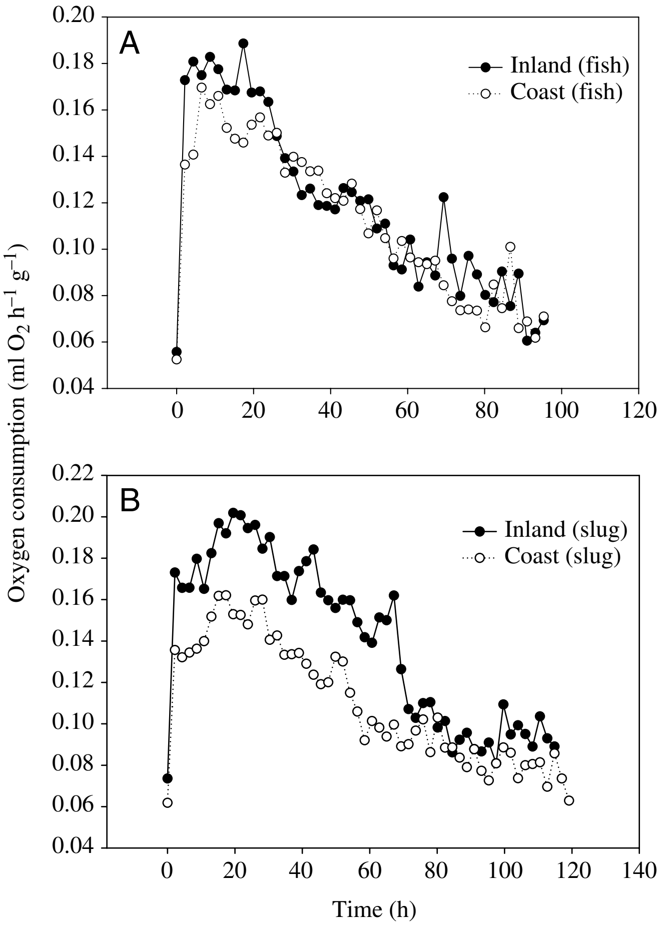

Fig. 1. The time course in oxygen consumption (ml O_2 h^{-1} g^{-1}) between coastal (open circles) and inland (closed circles) *T. elegans* on a lyophilized fish diet (A) and slug diet (B). The standard metabolic rates of coastal specialist snakes and inland generalist snakes were 0.058 ml O_2 h^{-1} g^{-1} and 0.70 ml O_2 h^{-1} g^{-1} at 30±1°C, respectively ($P=0.07$). Each data point represents the mean metabolic value of a group of snakes. The total energy devoted to SDA was calculated for each snake by subtracting SMR from total metabolic rates during digestion. Post-prandial metabolic rates reached maximal levels of 3.0- to 4.0-fold resting rates and lasted nearly 80–110 h.

Table 3. *Energetics of digesting fish, a generalized prey, by two populations of the garter snake Thamnophis elegans*

	N	Assimilation efficiency	SDA/assimilated energy	Net assimilation efficiency
Intact fish				
Specialist snakes	12	0.824±0.027	0.154±0.018	0.695±0.027
Generalist snakes	11	0.800±0.020	0.145±0.021	0.685±0.026
Significance (*P*)		NS	NS	NS
Lyophilized fish				
Specialist snakes	5	0.849±0.040	0.139±0.012	0.734±0.035
Generalist snakes	7	0.850±0.030	0.272±0.040	0.619±0.042
Significance (*P*)		NS	<0.001	0.002

Fish were presented in both intact and lyophilized form.

Efficiencies and ratios are defined in the text. Mean values (± 95% CL) are reported from single trial measurements on each individual snake. NS, not significant.

lyophilized than for intact fish, but there was no indication of greater digestive costs for the slug specialist in comparison to the generalist in any category. In fact, digestive costs were lower and net efficiencies were higher for the slug specialist than for the generalist when eating lyophilized fish.

In addition to having an inherently lower nutritive value (Table 1), slugs were more difficult and more expensive to digest than fish for both specialist and generalist snakes. Assimilation efficiency of slugs was lower and the fraction of assimilated energy devoted to SDA was higher, resulting in substantially lower net assimilation efficiency (Tables 2 and 3).

Discussion

Dietary specialization in natricine snake species is a widespread phenomenon, and the garter snakes of North and Middle America represent a group of ecologically diverse habitat and dietary generalists in which to study the evolution of specialization. As we come to understand the evolutionary history by which these animals have exploited new environments (e.g. Arnold, 1981b; Alfaro and Arnold, 2001), it has become of increasing interest to determine the physiological processes (e.g. energy expenditure) and ecology that led to differences in foraging behavior and prey specialization. Although there are many examples of specialist species within the garter snake group, *T. elegans* and *T. sirtalis* are the most varied in diet. Ecological, morphological and behavioral investigations have been extensively undertaken on natural populations located at study sites near Eagle Lake California for approximately 30 years (Arnold, 1981a; Kephart and Arnold, 1982; Jayne and Bennett, 1990; Bear, 1994; Bronikowski, 1997; Bronikowski, 2000; Bronikowski and Arnold, 1999; Arnold and Phillips, 1999). *T. elegans* feed mainly on anurans in mountain meadow areas and fish near the lakeshore areas of Eagle Lake. In addition it has been found that lakeshore snake life history is characterized by faster growth, earlier maturation, larger adult body size, and lower adult survival than the meadow populations. These life-history differences can also be attributed to genetic differences among populations (Bronikowski, 2000).

The polymorphic feeding behavior between the inland (*T. e. elegans*) and coastal (*T. e. terrestris*) populations represents a much larger scale of geographic variation and genetic diversity. With such a difference in feeding behavior, an important and relatively poorly studied aspect is the effect these diets have on acquisition of energy and the partitioning into maintenance, activity, digestion, growth, reproduction and storage. *T. elegans* is an example of a generalized carnivore that exhibits local specialization on both microgeographic and geographic scales. The propensity to feed on slugs is a heritable trait and is found only where snakes are sympatric with slugs (Arnold, 1977). Their abundance in the Pacific Northwest and ease of capture make slugs a potentially profitable item to include in the diet of garter snakes. However, the sticky secretions from slugs can impede ingestion by a garter snake [see fig. 3.13 (Arnold, 1993)], making slugs a difficult prey to consume physically. Since free-ranging garter snakes may have high metabolic rates associated with high feeding rates (Peterson et al., 1998; Peterson et al., 1999), the costs of digestion and its associated energetics may have a substantial influence on the daily activity levels and growth rates. Energy allocation and digestive physiology may therefore be important templates of selection in these animals.

By all measures, gram for gram, slugs are a less profitable prey than fish for garter snakes. Their water content is higher and their protein content is lower, and they contain almost no fat. On a per gram wet mass basis, fish contain 81% more energy than slugs. Their greater energy concentration may be very significant to small animals with high rates of prey processing and growth, and short active seasons. In addition to their lower energy content, for both intact and dried homogenized prey treatments, assimilation efficiency was lower and digestive costs were higher for slugs than for fish in both populations. Mean assimilation efficiency for lyophilized slugs was significantly higher ($P<0.001$) than that for intact slugs, suggesting that the polysaccharide mucus on the surface of a live slug may impede assimilation; intact and dried fish had similar efficiencies in the coastal population. By contrast, inland snakes were able to digest intact fish more efficiently than dried fish due to large SDA values during their feeding trials. Finally, even the slug specialists would have to eat 2.5 g wet mass of slugs to obtain the same amount of energy they can extract from 1 g wet mass of fish; the generalist snakes, if they could be persuaded to eat slugs, would certainly require an even greater ratio.

The results of this study show that the coastal population of snakes is physiologically, as well as behaviorally (Arnold, 1977; Arnold, 1981a; Arnold, 1981b), adapted to eating slugs. Assimilation efficiency is higher in coastal snakes ($P=0.003$) when both populations were fed dried homogenized slug meals, snakes from the coastal population are able to extract over 60% more usable energy from a slug meal than can inland generalist snakes. We conclude that the dietary specialization of coastal *T. e. terrestris* on slugs is accompanied by an increase in net assimilation efficiency when digesting slugs compared to that of the inland *T. e. elegans* populations.

However, contrary to generalist–specialist trade-off theory, this specialization on slugs was not accompanied by a concomitant loss of digestive efficiency on fish, a more widespread and generalized prey among other populations of *T. elegans*. When digesting fish, slug specialist snakes can assimilate and extract useful energy as well as (intact fish) or better than (lyophilized fish) the inland populations can. Snakes from both populations have a greater assimilation efficiency for fish than that previously measured for their congener *Thamnophis sirtalis* (70%) (Bear, 1994), which usually eats anurans. Likewise, they have higher net assimilation efficiency than those previously measured on another colubrid snake, *Natrix maura*, eating fish (Hailey and Davies, 1987). Most specialist-generalist trade-offs are associated with broad ecological utilization or environmental conditions that result in differential performance between specialists and generalists

(Futuyma and Moreno, 1988; McPeek, 1996). The results of this study suggest that the evolution of dietary specialization and the ability to digest certain prey items may not be associated with trade-offs on more generalized prey. Due to the relatively large SDA values from digesting dried fish, it is still uncertain whether inland snakes are indeed poorer digesters on fish as well as slug prey. Additional work among different species of garter snakes is needed to support our results and identify potential energetic trade-offs between species that specialize and those that do not.

We thank Steve Arnold, Anne Bronikowski and their team of field assistants for their help in locating and capturing our study animals. Further laboratory assistance was provided by David Richards. This work was supported by NSF grant IBN 0091308 to A.F.B. and J.W.H.

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