Body size and gastrointestinal morphology of nutria (*Myocastor coypus*) reared on an extensive or intensive feeding regime

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ABSTRACT: Although plasticity of growth rates is mainly associated with ectotherm species, it does occur in endotherms as well, but has not been documented systematically for many species. We compared the effect of 2 common types of feeding systems, differing in energetic value, on body size and gastrointestinal tract morphology in nutrias (*Myocastor coypus*). A total of 30 extensively (E) fed and 20 intensively (I) fed animals were used in the study. We noted significant effects of age, sex, and feeding regime on body weight and length, with 1-yr-old females attaining 3.7 ± 0.4 kg and 33.4 ± 1.5 cm on E and 4.9 ± 0.3 kg and 36.1 ± 2.3 cm on I. A significant treatment-sex interaction indicated that treatment had a greater effect on the length growth

in males (1-yr-old males attaining 4.0 ± 0.2 kg and 34.7 ± 1.2 cm on E and 5.4 ± 0.4 kg and 41.0 ± 1.4 cm on I). The differences matched individual literature reports of free-ranging or intensively fed nutrias. The majority of gastrointestinal tract measurement results were only related to body weight, without additional effect of the diet regime, except for a higher small intestinal tissue weight on I (79 ± 14 g vs. 61 ± 7 g on E). In contrast, the wet content weight of the stomach, caecum, and the total gastrointestinal tract was higher on E (196 ± 34 g vs. 164 ± 51 g on I). Overall, we observed strong influence of dietary regime on body development but not on digestive anatomy, indicating a distinct phenotypic flexibility in growth rates in nutrias.

Key words: anatomy, digestive tract, growth, nutria, phenotypic flexibility

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INTRODUCTION

Phenotypic flexibility is an important characteristic of living organism that allows them to adapt to a variety of environmental factors without incurring risks posed by demands of rigid internal developmental programs (Piersma and Van Gils, 2011). Both the growth of the whole body (Francisco et al., 1995; Cameron and Eshelman, 1996) and in particular the development of the gastrointestinal tract (Naya et al.,

2007; Naya, 2008) react flexibly to resource availability and type of diet consumed.

In intensively reared nutria (*Myocastor coypus*), growth rate can vary with diet nutrient composition (Niedźwiadek et al., 1987a; Niedźwiadek et al., 1987b; Niedźwiadek and Piórkowska, 1993; Cabrera et al., 2007; Głogowski and Czauderna, 2012; Januškevičius et al., 2015). Nutria growth rates have also been estimated for free-ranging animals, differing between males and females (Dixon et al., 1979; Willner et al., 1980; Sherfy et al., 2006). In reptiles, differences in growth rates between extensively fed/free-ranging and intensively fed individuals of the same species delineate the range of growth possible for a species (Ritz et al., 2010; Ritz et al., 2012). To the best of our

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knowledge, the amount of similar comparisons in mammalian species is limited to accounts of some domestic species; for example, higher growth rates have been reported for rabbits on diets of higher energetic value (Clauss et al., 2012; Daszkiewicz et al., 2012; Prebble et al., 2015).

We investigated 2 groups of nutrias reared on 2 feeding regimes. The first was typical for a traditional husbandry method still present in some European countries that continue to maintain small population of animals, for example, included in genetic diversity conservation programs, or zoological collections. This type of feeding usually employs low energetic value diets such as fresh green forage and plant production by-products offered in relatively large amounts. The second was more typical for conditions of meat production in countries with a continuous interest in the production and consumption of nutria meat products, consisting of animals housed on farms supplying the continuous market demands (Cabrera et al., 2007). We compared both the age-related growth of the animals (measuring body weight [BW] and body length at death of animals of varying age) and differences in the macroscopic anatomy of the digestive tract. Corresponding to the literature on nutrias and rabbits mentioned above, we expected intensively reared animals to have a higher growth rate both in terms of body mass and body length. Additionally, we expected extensively reared animals to have a generally higher gut fill and longer and heavier sections of the gastrointestinal tract as an adaptation to a more fibrous diet, as reported in rodents and rabbits (Gross et al., 1985; Liu et al., 2017).

MATERIALS AND METHODS

All animals were kept and slaughtered during routine procedures in the respective facilities. The study was conducted under the authority of the Third Local Commission of Animal Experiment Ethics at the University of Life Sciences, Ciszewskiego 8, 02786 Warsaw.

Animals, Housing, Feeding, and Sampling

For the extensive feeding regime (EFR), 12 males and 18 females were kept in indoor open pens without water pools; these animals had been part of a study on the influence of the feeding regime on fatty acid composition of nutria meat (Głogowski et al., 2010). Their diet was based exclusively on fodder produced on the farm: potatoes and fresh

forage. Forage was harvested on a daily basis, alternating daily between a grass meadow and a clover field. Nutrias were fed twice daily; in the morning the animals received steamed potatoes ad libitum, and in the evening fresh grass or clover ad libitum. Daily intake and feed leftovers were not recorded. Based on literature data from the National Research Institute of Animal Production (2010) and an assumed as-fed intake of 50% steamed potatoes and 50% forage mix, the estimated concentration of this regime was 125.2-g crude protein and 151.7-g crude fiber in kg dry matter.

For the intensive feeding regime (IFR), 10 males and 10 females were housed in wire mesh cages in a sides-open building in groups separated by sex. The composition of the diet in the year of slaughter was a mixture (in % as fed) of corn (57.4%), sunflower meal (17.2%), soybean meal (6.9%), rice bran (17.2%), calcium carbonate (1.1%), and a vitamin supplement (0.1%). The calculated average daily feed allowance was 150 and 200 g of feed for females and males, respectively. Based on literature data (National Research Institute of Animal Production, 2010; Moongngarm et al., 2012), the estimated concentrations of this regime were 179.9-g crude protein and 95.7-g crude fiber per kg dry matter. These animals had also been used in previous descriptive anatomical studies of nutria (Pérez and Lima, 2007; Pérez et al., 2008).

All animals had been raised on their respective diet since weaning. All animals had constant access to drinking water.

Slaughter and Dissection Procedures

On the day of the slaughter, animals were weighed for total BW to the nearest gram after their morning feed and immediately stunned using a strong electrical impulse (230 V), bled, pelted, and deliberately eviscerated in the abattoir on the farm. All slaughter procedures were performed by the farmer, in strict accordance with the EU legislation (EC, 2009). The total length of the body was taken from atlas to the root of the tail with a measuring tape.

Dissection was performed via a ventral incision and the entire gastrointestinal tract was removed. All major intestinal organs were carefully ligated. The stomach was separated cranially at the esophageal junction and caudally at the pyloric sphincter. The small intestine was separated from the caecum caudally at the ileocecal junction. The caecum was separated from the proximal colon, and the proximal colon was separated from the rest of the colon

and rectum, which were assessed together. All compartments were weighed individually in full and empty states. For all parts of the intestines, emptying was achieved by carefully stripping contents out of the intestinal structures. All structures were rinsed several times and allowed to drip-dry for approximately 10 min before weighing after rinsing.

Statistical Analysis and Interpretation

Because our sample groups consisted of animals of both sexes, measurements were compared by general linear models (GLM) in which age, body length or BW were covariates, sex, and feeding intensity were factors (including their interaction), and the measurements were dependent variables. Additionally, simple correlations were assessed by Spearman's *R*. Analyses were performed in SPSS 24.0 (SPSS, Inc., Chicago, IL, USA). The significance level was set to 0.05.

For comparative purposes, data on age and BW were plotted against literature data on nutria from the wild (Peloquin, 1969; Dixon et al., 1979; Willner et al., 1980; Sherfy et al., 2006) and intensive rearing systems (Niedźwiadek et al., 1987a; Niedźwiadek and Piórkowska, 1993; Sirotkin et al., 2003; Cabrera et al., 2007; Beutling et al., 2008; Tůmová et al., 2015; Tůmová et al., 2017).

RESULTS

There was no difference in age between the groups or sexes (Table 1). Age and sex had a significant influence on body length and BW (Table 1). Males had higher body length and BW than the females, and animals from IFR were longer (Figure 1) and heavier (Figure 2) for their age than EFR animals (Table 1). When compared against literature data, the age-BW pattern of EFR animals corresponded to that reported previously for free-ranging animals, whereas that of IFR animals corresponded to that previously reported for intensively farmed nutria (Figure 2). Although there was a significant correlation between body length and BW ($R = 0.67$, $P < 0.001$; Figure 3), body length was not a significant covariable in the GLM that also included sex and feeding regime as cofactors influencing BW, due to the overruling effect of feeding regime (Table 1). In other words, although IFR animals were heavier and longer for their age than EFR animals, they were not heavier than EFR animals for their length.

Most length measurements of the GIT were significantly related to BW (Table 2), but only the greater stomach curvature and the length of the distal colon and rectum differed significantly

Table 1. Age, body size, and weight in nutria (*Myocastor coypus*) raised on an extensive or intensive feeding regime

	Extensive			Intensive		Covariable	Sex	Feeding regime	Feeding*sex
	Male (n = 12)	Female (n = 18)		Male (n = 10)	Female (n = 10)				
Age (mo)	13.8 ± 2.2	15.8 ± 3.4		15.6 ± 10.8	13.5 ± 8.0	–	$F = 0.000$ $P = 0.984$	$F = 0.015$ $P = 0.903$	$F = 1.229$ $P = 0.273$
Body length (cm)	35.1 ± 0.9	34.4 ± 1.5		41.9 ± 1.8	37.1 ± 3.1	Age $F = 22.743$ $P < 0.001$	$F = 38.494$ $P < 0.001$	$F = 114.799$ $P < 0.001$	$F = 13.837$ $P = 0.001^*$
Body weight (kg)	4.1 ± 0.4	3.9 ± 0.3		5.4 ± 0.7	4.9 ± 0.4	Age $F = 23.860$ $P < 0.001$ Body length $F = 2.598$ $P = 0.114$	$F = 12.306$ $P = 0.001$	$F = 118.310$ $P < 0.001$	$F = 0.683$ $P = 0.413$
Gut contents-free body weight (kg)	3.9 ± 0.4	3.7 ± 0.3		5.2 ± 0.7	4.7 ± 0.4	Age $F = 19.932$ $P < 0.001$	$F = 11.808$ $P = 0.001$	$F = 17.291$ $P < 0.001$	$F = 0.169$ $P = 0.683$
								$F = 120.120$ $P < 0.001$	$F = 1.018$ $P = 0.318$

*Significant results in bold. Significant interaction indicates that the difference between the feeding regimes is more pronounced in males than females.

between feeding regimes (both being longer on EFR, Table 2). Females had a longer minor curvature of the stomach (Table 2).

Figure 1. Relationship between age and body length in nutria (*Myocastor coypus*) males and females maintained either on an extensive (ERF) or intensive (IFR) feeding regime.

GIT tissue weight was significantly related to BW (Figure 4a) and differed only in small intestine weight between the feeding regimes (being higher on IFR, Table 3). GIT content weight was significantly higher for stomach, caecum, and consequently also the total GIT in EFR compared with IFR, and was generally not related to BW in our sample (Table 4). The ratio of GIT contents to GIT tissue weight was significantly higher in EFR than in IFR animals (Table 4 and Figure 4b).

DISCUSSION

The results of the present study indicate small differences between the feeding groups in terms of digestive anatomy, but enormous differences in terms of body size development. These findings are not necessarily only interesting for animal

Figure 2. Relationship between age and body weight in nutria (*Myocastor coypus*) males and females maintained either on an extensive (ERF) or intensive (IFR) feeding regime (lower figure represents longer time window). Grey data points without border represent literature data on intensively reared animals (Niedźwiadek et al., 1987a; Niedźwiadek and Piórkowska, 1993; Sirotkin et al., 2003; Cabrera et al., 2007; Beutling et al., 2008; Tůmová et al., 2015; Tůmová et al., 2017), the black and dotted lines represent growth curves for free-ranging males and females, respectively (Dixon et al., 1979), the small black symbols represent free-ranging animals from Sherfy et al. (2006), and the crosses represent free-ranging animals of unknown sex from Peloquin (1969) in which an increase in body weight in the spring (1 yr after birth) from the extensive feeding regime (ERF) level to the intensive feeding regime (IFR) level is visible.

Figure 3. Relationship between body length and body weight in nutria (*Myocastor coypus*) males and females maintained either on an extensive (ERF) or intensive (IFR) feeding regime.

production, but for general concepts on the determine growth of endotherms.

When animals are raised on diets of differing energetic values, the question arises to which extent differences in BW are due to the accretion of adipose tissue or somatic growth. In the nutrias of the present study, the clear difference in age-dependent body length between the feeding regimes (Figure 1), in combination with the simple correlation of body length and BW that was not influenced by the feeding regime (Figure 3), gives a clear indication that differences in BW were not due to increased body fat stores. In other words, the nutrias on IFR had a faster somatic growth.

A potential for compensatory growth has been described both in ectotherm (Radder et al., 2007; Türkmen et al., 2012) and endotherm (Wilson and Osbourn, 1960) species. This is particularly relevant for production animals, where compensatory growth can be used to achieve desired weight gains without a permanent provision of high-quality feeds. For example, compensatory growth is a well-known physiological phenomenon of accelerated final growth rate induced by a restricted feed supply during the growing period followed by ad libitum feeding during finishing in pigs (Heyer and Lebret, 2007). Although not directly tested in our study, the potential for compensatory growth is evident in the literature reviewed for Figure 2: The data on free-ranging nutria from Peloquin (1969), which show a distinct increase in age-related BW corresponding to the second spring these animals lived through, indicate that compensatory growth can likely occur in nutria. This might have potential relevance for feeding regimes for nutria production if animals can be slaughtered as late as slightly more than 1 yr of age.

In nutria meat production, the age at which the optimal slaughter weight is achieved depends

Table 2. Length measurements of the digestive tract in nutria (*Myocastor coypus*) raised on an extensive or intensive feeding regime

	Extensive				Intensive		Sex	Feeding regime		Feeding*sex
	Male (n = 12)	Female (n = 18)	Male (n = 10)	Female (n = 10)	Male (n = 10)	Female (n = 10)		Extensive	Intensive	
Stomach greater curvature (mm)	285 ± 20	273 ± 29	271 ± 21	277 ± 30	271 ± 21	277 ± 30	F = 0.508 P = 0.480	F = 7.674 P = 0.008	F = 2.961 P = 0.092	
Stomach lesser curvature (mm)	39 ± 8	46 ± 7	36 ± 7	44 ± 9	36 ± 7	44 ± 9	F = 7.983 P = 0.007	F = 0.375 P = 0.543	F = 0.039 P = 0.844	
Small intestine (mm)	4570 ± 374	4396 ± 393	4862 ± 737	4532 ± 634	4862 ± 737	4532 ± 634	F = 0.411 P = 0.525	F = 1.073 P = 0.306	F = 0.003 P = 0.955	
Caecum (mm)	416 ± 37	425 ± 40	427 ± 68	437 ± 76	427 ± 68	437 ± 76	F = 2.899 P = 0.096	F = 3.183 P = 0.081	F = 0.355 P = 0.554	
Proximal colon (mm)	733 ± 46	688 ± 97	774 ± 78	773 ± 80	774 ± 78	773 ± 80	F = 0.092 P = 0.764	F = 0.145 P = 0.705	F = 1.535 P = 0.222	
Distal colon and rectum (mm)	442 ± 33	433 ± 98	336 ± 78	361 ± 80	336 ± 78	361 ± 80	F = 1.973 P = 0.167	F = 21.707 P < 0.001	F = 1.690 P = 0.200	
Total intestine (mm)	6161 ± 380	5942 ± 435	6399 ± 843	6103 ± 757	6399 ± 843	6103 ± 757	F = 0.079 P = 0.781	F = 2.830 P = 0.099	F = 0.128 P = 0.722	

Significant results in bold.

Figure 4. Relationship between body weight and (a) total fresh tissue weight of the gastrointestinal tract (GIT) and (b) the ratio of fresh GIT contents to total fresh GIT tissue weight in nutria (*Myocastor coypus*) males and females maintained either on an extensive (ERF) or intensive (IFR) feeding regime.

on feeding and rearing conditions (Tůmová et al., 2017). Two main feeding regimes are known and used in various countries that have or had an interest in the rabbit and nutria meat consumption. One is based on the continuous offering large amounts of low energy ingredients as in our EFR group (Głogowski et al., 2010), and the other uses more energetically dense feeding materials as in our IFR group (Cabrera et al., 2007). IFR nutrias have higher live weights at the commonly accepted slaughter age of 8 mo. With the typical decrease in nutria growth intensity, starting at the age of 6 mo, intensive feeding is considered an optimal strategy for maximizing economic gain.

In contrast to findings in other species (Gross et al., 1985; Hammond and Wunder, 1991), differences in the length or tissue weight of gut compartments were not pronounced in the nutria of the present study—differences in overall gut tissue weight were explained by the differences in BW and independent of the feeding regime (Figure 4a). The only exception was the tissue weight of the small intestine, which was higher in the IFR group. An increase in small intestine tissue on diets of higher energetic value is, for example, also observed in ruminants (Tahas et al., 2017). It is tempting to speculate that this is a response to a higher proportion of auto-enzymatically digestible substrate in IFR. For a functional understanding of the diet effect, experiments with a more differentiated nutrient manipulation, together with histological analyses, are required. A possible reason for a lack of major differences in digestive tract macromorphology between the feeding regimes (Tables 2 and 3) could also be that nutrias are among the species that practice coprophagy (Gosling, 1979; Takahashi and Sakaguchi, 1998, 2000). Typically, the extent by which coprophagy contributes to the overall intake depends on the quality of the diet, with lower-protein, higher-fiber diets typically triggering more

coprophagy (García et al., 1995; Nogueira-Filho et al., 2013). Therefore, differences between dietary regimes, in particular in dietary protein levels, might be partially compensated. To which extent the presence or absence of coprophagy affects digestive tract anatomy has, to the best of our knowledge, not been investigated.

By contrast, the amount of gut contents was higher in the EFR group. When compared across different diet regimes, animals typically have a higher gut fill on the less digestible (and hence less energy-dense) diets. This has been shown in a large number of domestic species reared for production purposes, such as pigs (Ngoc et al., 2013), sheep (Jaborek et al., 2017), goats (Goetsch et al., 2011), cattle (Schlecht et al., 2003), rabbits (*Oryctolagus cuniculus*) (Clauss et al., 2012), but also in nondomestic species such as voles (*Microtus ochrogaster*) (Gross et al., 1985; Hammond and Wunder, 1991) and also in free-ranging animals such as wallabies (Munn et al., 2009). On artificial diets, such as pelleted compound feeds, this is often the consequence of a higher food intake, whereas evidence on natural forages suggests that the option of increasing food intake is mainly used by small mammalian herbivores (Meyer et al., 2010). In an experimental design like ours, where animals are habituated to a certain diet for long time periods, intake apparently is adjusted to optimize growth under the given conditions.

The most impressive result of the present study is the difference in growth rate indicated by our data. Although matching previous literature reports on nutrias, it appears that nutria can vary in BW by a factor of 2 (3 to 4 kg vs. 7 to 8 kg), depending on diet (Figure 2), and this is accompanied by an increase in body size as measured by length (Figure 3). The adaptive value of such a distinct phenotypic flexibility lies in the optimal use of resources without being limited to either a

Table 3. Wet tissue weight (in g) of different sections of the digestive tract in nutria (*Myocastor coypus*) raised on an extensive or intensive feeding regime

	Extensive		Intensive		Sex	Body weight	Feeding regime	Feeding*sex
	Male (n = 12)	Female (n = 18)	Male (n = 10)	Female (n = 10)				
Stomach	23.2 ± 2.4	22.1 ± 3.7	27.4 ± 4.6	24.6 ± 4.5	F = 0.588 P = 0.447	F = 8.511 P = 0.005	F = 0.032 P = 0.860	F = 0.079 P = 0.780
Small intestine	65.9 ± 4.8	58.2 ± 5.7	87.2 ± 13.6	76.4 ± 15.8	F = 4.194 P = 0.046	F = 6.933 P = 0.012	F = 5.072 P = 0.029	F = 0.001 P = 0.978
Caecum	42.6 ± 5.4	40.4 ± 4.3	41.4 ± 6.9	41.2 ± 8.7	F = 0.034 P = 0.854	F = 4.228 P = 0.046	F = 2.898 P = 0.096	F = 0.889 P = 0.351
Proximal colon	30.2 ± 5.9	30.1 ± 5.1	44.4 ± 9.2	39.8 ± 10.3	F = 0.006 P = 0.941	F = 8.584 P = 0.005	F = 1.740 P = 0.194	F = 0.299 P = 0.587
Distal colon and rectum	9.8 ± 3.1	9.0 ± 3.5	8.4 ± 2.5	9.8 ± 3.0	F = 0.188 P = 0.667	F = 0.067 P = 0.797	F = 0.163 P = 0.689	F = 1.398 P = 0.243
Total GIT	171.7 ± 13.2	159.8 ± 12.6	208.8 ± 23.8	191.8 ± 37.0	F = 0.940 P = 0.001	F = 11.923 P = 0.001	F = 0.893 P = 0.350	F = 0.050 P = 0.823

Significant results in bold.

Table 4. Wet content weight (in g) of different sections of the digestive tract in nutria (*Myocastor coypus*) raised on an extensive or intensive feeding regime

	Extensive		Intensive		Sex	Body weight	Feeding regime	Feeding*sex
	Male (n = 12)	Female (n = 18)	Male (n = 10)	Female (n = 10)				
Stomach	55.8 ± 13.0	45.8 ± 16.4	35.6 ± 12.8	49.6 ± 18.0	F = 0.791 P = 0.379	F = 1.488 P = 0.229	F = 4.373 P = 0.042	F = 8.343 P = 0.006*
Small intestine	40.1 ± 12.8	43.6 ± 13.1	39.8 ± 16.2	33.0 ± 16.2	F = 0.125 P = 0.725	F = 0.000 P = 0.999	F = 0.627 P = 0.432	F = 1.456 P = 0.234
Caecum	93.0 ± 25.7	92.9 ± 28.1	70.2 ± 19.8	81.2 ± 37.6	F = 1.017 P = 0.319	F = 1.056 P = 0.310	F = 4.377 P = 0.042	F = 0.742 P = 0.393
Proximal colon	42.0 ± 10.0	33.9 ± 12.6	47.9 ± 12.4	39.6 ± 17.2	F = 2.741 P = 0.105	F = 0.666 P = 0.419	F = 0.076 P = 0.784	F = 0.017 P = 0.898
Distal colon and rectum	13.1 ± 6.3	10.4 ± 4.1	8.2 ± 3.3	11.3 ± 7.9	F = 0.293 P = 0.591	F = 1.170 P = 0.285	F = 2.684 P = 0.108	F = 3.972 P = 0.052
Total GIT	244.1 ± 41.1	226.7 ± 52.6	201.7 ± 46.2	214.7 ± 72.2	F = 0.118 P = 0.733	F = 1.460 P = 0.233	F = 4.107 P = 0.049	F = 1.426 P = 0.239
Ratio content:tissue total GIT	1.43 ± 0.28	1.43 ± 0.36	0.97 ± 0.24	1.11 ± 0.21	F = 0.249 P = 0.620	F = 0.302 P = 0.585	F = 5.368 P = 0.025	F = 0.484 P = 0.490

*Significant results in bold. Significant interaction indicates that the male-female ranking is different for the 2 feeding systems.

fast growth (which means death at low resource availability) or a slow growth (which would be a competitive disadvantage at high resource availability). Similar variation in diet-dependent growth rates is known in domestic mammals such as cattle (Scaglia et al., 2012), sheep (Borton et al., 2005), or rabbits (Pla, 2008), and in a variety of nondomestic mammals from rodents (Lochmiller et al., 2000) to carnivores (Hofer and East, 1993) and primates (Altmann and Alberts, 2005). They speak against a set growth rate in mammals, as is often assumed in comparative biological studies (Case, 1978).

CONCLUSION

Diet-dependent, flexible growth rates are a general characteristic of mammals. Nutrias appear to represent an extreme case of such flexibility, with sex-specific adult BWs nearly varying by a factor of 2. Differences in growth are not paralleled by differences in macroanatomical measurements of the digestive tract, suggesting that nutrias do not try to compensate for lower diet quality by increasing gut tissue, only by increased gut fill. By contrast, a higher tissue mass of the small intestine on the higher quality diet suggests a positive reinforcement where the organism invests in more tissue that can process more of the high-quality diet. Intensive rearing can make use of these mechanisms to achieve higher weight gains in a shorter period of time.

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