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## Mammal density and patterns of ectoparasite species richness and abundance

Received: 12 June 2001 / Accepted: 16 January 2002 / Published online: 14 March 2002  
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**Abstract** Patterns of species richness, prevalence and abundance of ectoparasites have rarely been investigated at both the levels of populations and species of hosts. Here, we investigated the effects in changes in small mammal density on species richness, abundance and prevalence of ectoparasitic fleas. The comparative analyses were conducted for different small mammal species and among several populations during a long-term survey. We tested the hypothesis that an increase in host density should be linked with an increase in parasite species richness both among host species and among populations within host species, as predicted by epidemiological models. We also used host species density data from literature. We found that host density has a major influence on the species richness of ectoparasite communities of small mammals among host populations. We found no relationship between data of host density from the literature and parasite species richness. In contrast with epidemiological hypotheses, we found no relationships between abundance, or prevalence, and host density, either among host species or among host populations. Moreover, a decrease in abundance of fleas in relation with an increase in host density was observed for two mammal species (*Apodemus agrarius* and *A. flavicollis*). The decrease or the lack of increase in flea abundance in relation with an increase in host density suggests anti-parasitic behavioural activities such as grooming.

**Keywords** Host density · Small mammals · Fleas · Species richness · Comparative analyses

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### Introduction

Host density seems to be an important factor explaining species richness, distribution and abundance of parasites (Arneberg et al. 1998; Morand and Poulin 1998; Poulin and Morand 2000; Morand 2000). Epidemiological models strongly suggest that hosts living at a high density should increase the ability for a given directly transmitted parasite to spread into a host population (Arneberg et al. 1998; Morand and Poulin 1998; Krasnov et al., in press). According to these, it has been emphasised that increases in host density may favour the accumulation of parasitic species and, consequently, that hosts living at a high density should harbour more parasitic species than hosts living at a low density (Morand and Poulin 1998; Morand et al. 2000; Morand 2000). Moreover, the basic models of Anderson and May (1978) also predict that parasite abundance and prevalence would increase with increases in host density.

An increase in density, as it may co-vary with the increase in social group size, is likely to increase the amount of contact between individuals, and to favour the transmission of contagious parasites; this was confirmed using a meta-analysis by Côté and Poulin (1995).

The results of epidemiological models also show that parasite species richness, abundance and prevalence are positively linked with host longevity (Anderson and May 1978; Morand 2000). Several studies also emphasise that host body size is a determinant of ectoparasite species richness (Kuris et al. 1980). These relationships were explained in the light of the island theory (but see Morand 2000).

Other studies, however, emphasise that a host's social behaviour may reduce the risk of being infected (Murray 1987; Hart 1994; Lohle 1995). Many mammals control ectoparasites by grooming (Hart and Hart 1988) and this activity has proven to be effective in removing ectoparasites (Hart 1988). For example, mite infestation increases when mice are prevented from grooming (Wiesbroth et al. 1974). Then changes in host density, as they may interfere with behaviour, may have different influences on

the level of parasite load than expected from epidemiological theory.

The effect of host density on parasite species richness should be observed at inter-specific levels (Poulin and Morand 2000; Morand 2000) as a given host species living at a high density may favour the spread of not only one but all directly transmitted parasites. Then, the effect of host density on species richness and abundance of parasites should be observed at both intra- and inter-specific host levels, which has been rarely tested. Here, we investigated the effect of host density on species richness, abundance and prevalence of ectoparasitic fleas. The analyses were conducted using data from different small mammal species (rodents, insectivores) and among populations within several of the host species using data from a long-term survey in Slovakia. We hypothesise that increases in host density should be linked with an increase in parasite species richness both among host species and among host populations. An increase in abundance and prevalence of ectoparasites should also be observed if there is no control of flea populations, i.e. as predicted by epidemiological models for the case of simple infection without behavioural activity (Arneberg et al. 1998; Krasnov et al., in press). The lack of an increase or a decrease in flea abundance may, in contrast, suggest anti-parasitic behavioural activities.

## Materials and methods

### Small-mammal trapping

Sampling of small mammals and parasitological investigations were carried out using the methods described by Stanko (1987a, 1987b, 1988, 1994).

A total of 10,321 specimens of 24 species of small mammals were trapped from March 1983 until August 1997 in four regions of Slovakia (Javorie mountains and Krupinská Planina plain, Volovské Vrchy mountains, East Slovakian Lowland). The traps (around 60,000 in total) were deposited in each area following the same protocol. Each sample was trapped within a limited period (1 or 2 nights per month) in the same place (77 samples in total). Number of captures per trap and per night gives an estimate of density. We used this estimate as a measure of the relative density for both intraspecific and interspecific comparisons. For the inter-specific analysis, we used the maximum relative density observed among populations of each species, when several populations were investigated. This is because the effect of host density should be more pronounced (i.e. more detectable) at high host densities or when using an average across all populations.

In the case of an interspecific comparison, our estimate of density (relative density) may be biased by the trapping protocol. This is because some species, for example those with large home ranges, are more active than others and therefore have a higher probability of being trapped. We then used the population species density from the literature (data compiled by Damuth 1987, 1993). We conducted our analyses using both types of host density data. Data on host body size and host longevity were obtained from the literature (Table 1).

### Ectoparasites

Twenty-nine species of fleas were removed and identified from the 10,085 small mammals examined for parasites (Tables 1, 2).

**Table 1** Data on mammals and their ectoparasitic fleas. *ESR* Ectoparasite species richness

Host species	Code	Longevity (months)	Body mass (g)	Relative host density	Host density <sup>a</sup>	Hosts examined	Total individual parasites	Prevalence (maximum)	Abundance (maximum)	Observed ESR	Estimated ESR
<i>Apodemus agrarius</i>	AAGR	48	25	0.304	1,240	2,538	2,140	100.0	7.5	18	18
<i>Apodemus flavicollis</i>	AFLA	24	45	0.343	949	3,598	3,893	100.0	10.2	21	21
<i>Apodemus uralensis</i>	AMIC	–	21.5	0.072	–	893	560	86.7	3.9	5	5
<i>Apodemus sylvaticus</i>	ASYL	20	27	0.026	2,550	82	73	100.0	2.0	5	5
<i>Arvicola terrestris</i>	ATER	48	320	0.001	30,900	6	61	100.0	42.0	3	–
<i>Clethrionomys glareolus</i>	CGLA	18	40	0.146	1,890	1,711	3,099	100.0	5.3	23	23
<i>Crocidura leucodon</i>	CLEU	60	15	0.007	–	13	12	50.0	2.0	5	6
<i>Crocidura suaveolens</i>	CSUA	24	6	0.002	167	2	0	0.0	0.0	0	–
<i>Glis glis</i>	GGLI	84	200	0.004	–	4	7	75.0	1.8	4	–
<i>Microtus agrestis</i>	MAGR	24	50	0.003	2,200	3	1	33.3	0.3	1	–
<i>Microtus arvalis</i>	MARV	72	40	0.286	3,770	656	1,014	100.0	4.5	11	11
<i>Muscardinus avellanarius</i>	MAVE	72	30	0.005	–	11	2	50.0	0.5	1	1
<i>Micromys minutus</i>	MMIN	60	11	0.019	–	16	10	50.0	0.7	4	2
<i>Mus musculus</i>	MMUS	30	22	0.004	–	8	1	50.0	0.5	1	–
<i>Microtus nivalis</i>	MNIV	36	60	0.001	–	3	12	100.0	8.0	5	–
<i>Neomys anomalus</i>	NANO	–	16.5	0.023	–	18	38	100.0	4.0	7	8
<i>Neomys fodiens</i>	NFOD	19	23	0.017	–	43	181	100.0	9.5	12	12
<i>Ondatra zibethicus</i>	OZIB	240	2,400	0.004	–	4	0	0.0	0.0	0	–
<i>Pitymys subterraneus</i>	PSUB	–	27	0.013	–	91	253	100.0	20.0	10	10
<i>Rattus norvegicus</i>	RNOR	48	520	0.004	–	5	2	100.0	2.0	2	–
<i>Sorex alpinus</i>	SALP	–	11.5	0.005	–	7	16	100.0	3.5	4	–
<i>Sorex araneus</i>	SARA	23	12	0.036	1,033	262	392	100.0	22.0	4	4
<i>Sorex minutus</i>	SMIN	13	7.5	0.031	621	106	8	17.4	0.3	2	2
<i>Talpa europea</i>	TEUR	84	130	0.002	1,045	5	34	100.0	14.0	7	–

<sup>a</sup> Data were obtained from Damuth (1987) (no. individuals per km<sup>2</sup>)



For each population (with at least 30 individuals) of each species of mammal it was then possible to compute the following variables:

1. Total parasite species richness: the total number of flea species found on a given host species.
2. Abundance: the mean number of ectoparasites found in a population of a given host species.
3. Maximum abundance, the maximum mean number of ectoparasites found in all populations of a given host species.
4. Prevalence: the percentage of hosts found to be parasitised in a population of a given host species.
5. Maximum prevalence: the maximum percentage of hosts found to be parasitised in all populations of a given host species.

In the case of the intraspecific comparison, we used abundance and prevalence data corresponding to each host population.

In the case of the interspecific comparison, we used abundance and prevalence data corresponding to host population with the highest density.

#### Estimates of parasite species richness

Total parasite species richness of a host species is difficult to ascertain because of its dependence on sample size (Gregory 1990; Walther et al. 1995; Walther and Morand 1998). Gregory (1990) and Walther et al. (1995) pointed out that investigations of parasite species richness must account for differential host sampling effort.

With individual host data, it is then possible to correct for the potentially confounding effect of sample size by using estimates of total parasite species richness (Walther and Morand 1998; Poulin 1998; Morand et al. 2000).

We used the program EstiMateS 6.01 (R. K. Colwell) at: <http://viceroy.eeb.uconn.edu/Estimates6/> to estimate total parasite species richness for each host species (see Colwell and Coddington 1994). EstiMateS computes species richness estimators from species-by-sample incidence or abundance matrices.

Three estimators were used: (1) Chao 2 [a non-parametric incidence-based estimator of species richness; Chao (1987)]; (2) Jackknife 1 [first-order jackknife estimator of species richness, incidence-based, Heltsh and Forrester (1983)]; and (3) Bootstrap estimator of species richness incidence-based (Smith and van Belle 1984).

All estimators gave similar values ( $R^2=1$  for all pairwise correlations between sets of estimates).

#### Statistical analysis

##### *Interspecific analysis*

We performed the analyses using the method of phylogenetically independent contrasts (Felsenstein 1985). We used a working phylogenetic tree of the hosts obtained from various sources [see Morand and Harvey (2000); and including the recent phylogeny of Soricidae; Fumagalli et al. (1999)] (the phylogeny will be provided on request). We used CAIC 2.0 (Purvis and Rambaut 1995). Branch lengths were assigned to one. Fourteen species of mammals were considered for this analysis (at least ten individual hosts examined; see Table 1). Thirteen independent contrasts were obtained. The densities of eight species were obtained from Damuth's data base (1987). In this case, seven independent contrasts were obtained. Estimated host density was arcsin transformed and all other variables were log-transformed in order to linearize correlations. Regressions on independent contrasts were forced through the origin (Garland et al. 1992).

We analysed the effect of host density (either from our estimates or from Damuth's data base), host body size and host longevity on estimates of species richness, abundance and prevalence of fleas.

##### *Intraspecific analysis*

We analysed the effect of host density for seven species of small mammals, for which we obtained a sufficient number of populations (at least 30 populations), by using simple linear regression.

## Results

A total of 11,809 individual fleas were collected. The distribution and intensity of fleas among the mammal species are given in Table 2. Most flea species were poorly host specific and were found on several host species (Table 2).

#### Interspecific relationships between mammal density and ectoparasite species richness

We found a positive and strong relationship between host sample size and host relative density ( $n=18$ ,  $r=0.896$ ,  $P<0.0001$ ; Fig. 1A)

A positive relationship was found between flea species richness (bootstrap estimates) and estimates of host density using independent contrasts ( $n=13$  sets of contrasts,  $P<0.05$ ; Fig. 1B). No relationship was found between host relative density and host body size ( $P>0.05$ ). However, the increase in host density was not linked with an increase in both abundance ( $P>0.05$ ; Fig. 1C) and prevalence of parasites ( $P>0.05$ ; Fig. 1D).

No significant relationships were found between values of host density obtained from Damuth's data base and species richness ( $n=7$  contrasts,  $P>0.05$ ), abundance ( $P>0.05$ ) and prevalence of parasites ( $P>0.05$ ).

We found a positive relationship between host body size and prevalence ( $n=13$ ,  $r=0.55$ ,  $P<0.05$ ) but the statistical significance was due to one contrast ( $P=0.08$ , when removing the outlier). There were no relationships between body size and either parasite species richness ( $n=13$ ,  $P>0.05$ ) or abundance ( $P>0.05$ ).

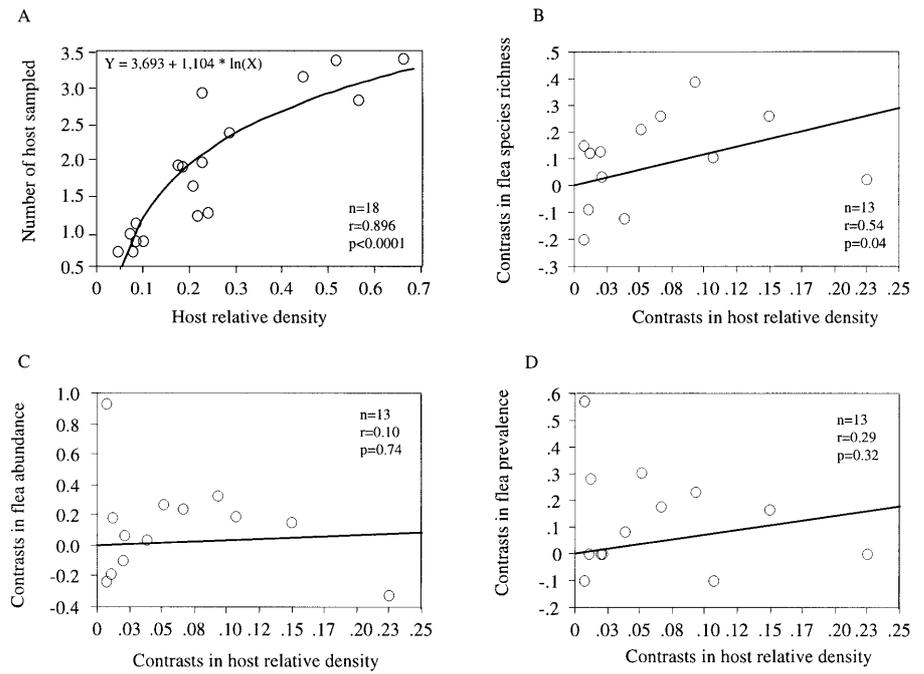
We found no relationships between host longevity and either parasite species richness ( $n=10$  sets of contrasts,  $P>0.05$ ), abundance ( $P>0.05$ ) or prevalence ( $P>0.05$ ).

#### Intraspecific relationships between mammals density and ectoparasite species richness

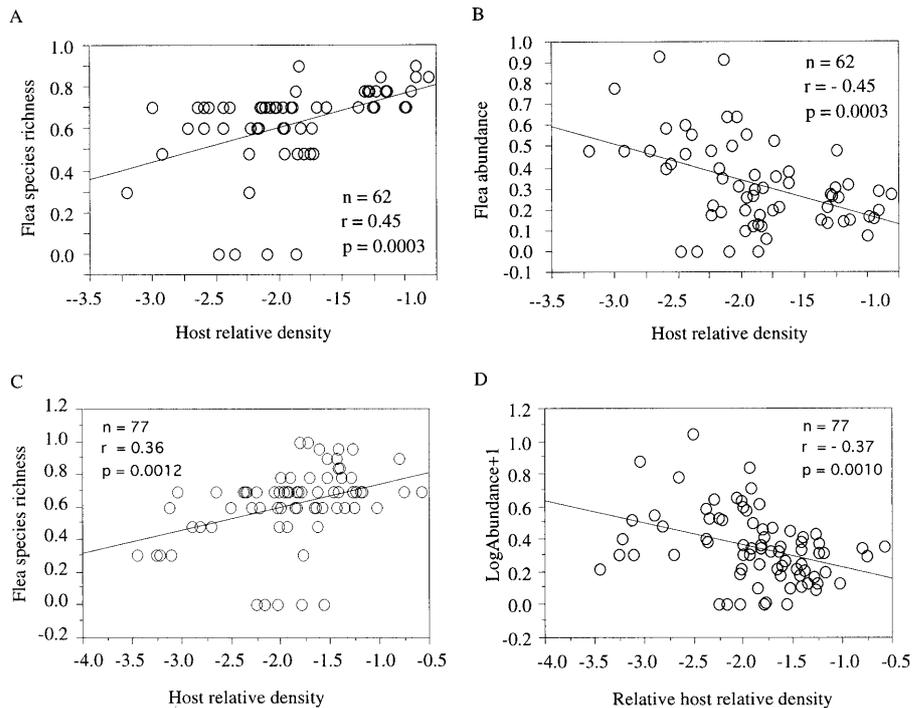
Linear regression analyses showed a positive effect of host density on flea species richness for five species of the small mammal species examined (see Fig. 2A, C for the case of *Apodemus agrarius* and *A. flavicollis*) and no effect for *A. uralensis* and *M. subterraneus* (Table 3).

We found a negative effect of host density on the abundance of fleas for *A. agrarius* (Fig. 2B) and *A. flavicollis* (Fig. 2D), whereas there was no influence of host density on abundance for the other mammal species. We also found a negative effect of host density on the prevalence of fleas for the case of *A. agrarius* and *A. flavicollis* (Table 3).

**Fig. 1** **A** Relationship between host sampling size and host relative density (arcsin of the number of captures per trap and per night). **B** Relationship between contrasts in ectoparasite species richness (bootstrap estimates) and host density (arcsin of the number of captures per trap and per night). **C** Relationship between contrasts in ectoparasite abundance and host relative density (arcsin of the number of captures per trap and per night). **D** Relationship between contrasts in ectoparasite prevalence and host relative density (arcsin of the number of captures per trap and per night)



**Fig. 2** Relationship between host relative density (arcsin of the number of captures per trap and per night) and ectoparasite species richness (log+1) (**A**) or abundance (log+1) (**B**) for the case of *Apodemus agrarius*. Relationship between host relative density (arcsin of the number of captures per trap and per night) and ectoparasite species richness (log+1) (**C**) or abundance (log+1) (**D**) for the case of *Apodemus flavicollis*



**Table 3** Results of linear regressions showing the effect of host densities on flea species richness (ESR, log), abundance (log+1) and prevalence (arcsin square root) of ectoparasitic fleas

Host species	Number of populations	ESR versus host density	Abundance versus host density	Prevalence versus host density
<i>A. agrarius</i>	62	$r=0.448^{***}$	$r=-0.449^{***}$	$r=-0.373^{**}$
<i>A. flavicollis</i>	77	$r=0.364^{**}$	$r=-0.366^{***}$	$r=-0.437^{***}$
<i>A. uralensis</i>	51	$r=0.260$ n.s.	$r=-0.123$ n.s.	$r=-0.153$ n.s.
<i>C. glareolus</i>	70	$r=0.435^{***}$	$r=-0.039$ n.s.	$r=-0.225$ n.s.
<i>M. arvalis</i>	49	$r=0.427^{**}$	$r=0.046$ n.s.	$r=-0.217$ n.s.
<i>M. subterraneus</i>	30	$r=0.027$ n.s.	$r=-0.167$ n.s.	$r=-0.220$ n.s.
<i>S. araneus</i>	55	$r=0.437^{***}$	$r=0.115$ n.s.	$r=0.117$ n.s.

\* $P<0.02$ , \*\* $P<0.01$ , \*\*\* $P<0.001$ , n.s. non significant

## Discussion

Several studies have focused on the effect of abiotic factors on the structure of ectoparasite communities (Krasnov et al. 1997; Heeb et al. 2000). Nest properties, such as humidity, influence the abundance of fleas in birds (Heeb et al. 2000), whereas Krasnov et al. (1997) showed the importance of host habitat on the abundance of fleas in rodents. A positive effect of increasing host density on prevalence and abundance of two flea species was observed in the desert rodent *Gerbillus dasyurus* (Krasnov et al., in press). However, the effects of host density on the success of parasite infection are rarely tested at both the levels of host populations and host species.

### Sampling effort and confounding effects

Guégan and Kennedy (1996) emphasised the confounding relationship between host sampling, area and parasite species richness. They pointed out that a host living in a large area has a higher probability of being sampled and analysed for parasites than a host living in a smaller area. In turn, a host living in a large area has more opportunities to be in contact with various sources of infection and, hence, to accumulate individuals and species of parasites. The same confounding relationship may occur between host sampling, host density and parasite species richness (Morand et al. 2000). Hence, a host living at a high density may sustain a high number of parasites (and may harbour a high number of parasite species), but is also more likely to be more trapped and sampled for parasites than a rarer host. Here, we found positive relationships between host sample size and density. Our results show that the confounding effect of host sample size on host density may operate in the interspecific analyses, as has previously been shown by Morand et al. (2000) for the case of fish parasites. However, such a confounding result is less likely in the intraspecific analyses, because there is no reason to believe that density and area covered by a population are correlated among populations within species. Additionally, in these analyses, we only used data from well sampled populations ( $n > 29$  individual hosts), meaning that flea species richness estimates are fairly accurate and unrelated to sample size.

### Species richness of fleas

Host body size has been recognised as a determinant of parasite species richness (Kuris et al. 1980), where hosts are considered islands providing habitat for parasites. However, our results show a lack of correlation between host body size and parasite species richness. According to epidemiological models (Anderson and May 1978; Morand 2000; Krasnov et al., in press) both host density and host longevity would increase the spread and maintenance of a given parasite. We found no influence of

host longevity on the richness of flea communities, but we found that host density has a major influence on the richness of ectoparasite communities of small mammals among host populations. The pattern is less clear concerning the interspecific comparison, as we found: (1) no relationship between parasite species richness and host density using the data from the literature, and (2) a positive relationship between them when using our estimates of host density. Indeed both measures of host density suffer from potential biases. The estimates of density reported by Damuth (1987) concerned a small number of species and were not obtained in the same geographical region as our data set. And our estimates also suffer from potential biases (i.e. the differential ability to capture different species of small mammals using the same trapping methodology).

### Abundance of fleas and host density

In accordance with epidemiological hypotheses, we found an increase in ectoparasite species richness linked with an increase in host density. There are, in contrast, no relationships between abundance and prevalence and host density (among host species or among host population). Moreover, a decrease in abundance in ectoparasitic species was observed in two mammal species (*Apodemus agrarius* and *A. flavicollis*). We should note that we referred to simple epidemiological models that, for the great majority, do not take into account host behaviour (see Krasnov et al., in press).

### Costs of flea infection

The impact of ectoparasites on host fitness is important (Hart 1988). For example, ectoparasitism may represent a cost of coloniality (Brown and Brown 1986).

The costs associated with flea infection are linked with: (1) a direct effect of blood removal, (2) grooming activities, and (3) immunological function.

Our results suggest that an increase in host density increases the flea species diversity a given individual host should encounter. But because of the decrease (or the stability) in the abundance, this should not increase the total blood removal. Hence, an individual host living at a high density does not seem to suffer high loads of ectoparasites compared with hosts living at a low density.

Nevertheless, the lack of increase (or the decrease in flea abundance) suggests the control of flea parasitism. This control may be obtained by an increase in host grooming activities. These activities are obviously costly because of evaporative water loss, or distraction from other activities such as vigilance (Bolles 1960; Hart 1988). On the basis of our results, we hypothesise that grooming activities should increase with an increase in density or because of an increase in ectoparasite diversity. This hypothesis remains to be tested.

The increase in flea diversity may increase the immunological responses through antibodies produced against antigens injected by flea sucking. By their sucking activities on different hosts, fleas are also able to transmit pathogens. The risks of being infected by various microorganisms (viruses, bacteria, protozoans) that are actively injected by fleas during blood sucking are then enhanced with the increase in both host density and flea species richness. This would also stimulate the immune system, which is energetically costly to the host (Lochmiller and Deerenberg 2000).

**Acknowledgements** This paper has been partially supported by grant no. 2/6010/99 from the Slovakian Grant Agency VEGA. We thank Dr L. Mořanský and Dr J. Fričová for their help with the fieldwork. Joëlle Goüy de Bellocq is supported by a scholarship from the French Ministère de la Recherche.

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