Seasonal abundance in the floor-dwelling frog fauna on Iriomote Island of the Ryukyu Archipelago, Japan

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Abstract: Abundance of floor-dwelling frogs was studied in the humid subtropical lowland forest of Iriomote Island, the Ryukyu Archipelago, southern Japan. Field survey was conducted monthly for 1 y, and the seasonal pattern of abundance was examined for each species. We observed 251 frogs belonging to four species of three families in a total sampling of 600 m^2. Of these species, *Microhyla ornata* (66.5% of total frogs) and *Fejervarya limnocharis* (30.3%) were dominant in number. Total abundance of the frogs was strongly seasonal and peaked in the hottest month, August, while the number of frog species was one to three throughout the year. The seasonal pattern of abundance showed considerable variation among species, most likely due to their differences in reproductive season, and in physiological characteristics under the influence of varying temperature and rainfall. These patterns are more similar to those of temperate species than those of tropical species. The estimated density of all frogs ranged from 0.08 to 1.60 individuals m^{-1}, and their average annual density and biomass were 4180 individuals ha^{-1} and 11 460 g ha^{-1}, respectively. These values, among the highest so far reported for floor-dwelling anurans, may be a feature of amphibian fauna in the humid subtropical forests on a small island.

Key Words: amphibian, anurans, biomass, density estimate, frog community, island ecology, quadrat sampling, seasonal change, subtropical forest

INTRODUCTION

In the tropics, it is well documented that many taxa are more diverse (Rohde 1992). Amphibians particularly have much greater diversity in the aseasonal tropics than in higher latitudes or areas having a dry season (Duellman 1999). This is partially due to their physiological requirement for moisture throughout their lives, and to preferring generally warmer environments (Duellman & Trueb 1994).

Amphibians are one of the major constituents of the fauna of the forest floor. They play a major role not only as secondary (or higher) consumers, but also as prey for various predators. Burton & Likens (1975) estimated biomass of floor-dwelling amphibians in a temperate hardwood forest that is about twice that of birds and equal to that of small terrestrial mammals. This means that a large biomass of floor-dwelling amphibians constitutes abundant food sources for various vertebrate and large invertebrate predators, which also have a great impact upon other smaller animals as consumers (Stewart & Woolbright 1996). Therefore, abundance of amphibians can influence various characteristics of food webs in tropical rain forests.

A number of studies on floor-dwelling anurans have demonstrated that in both Old and New World tropics. The species composition and abundance can be influenced by a variety of environmental factors, such as vegetational zones (Allmon 1991, Brown & Alcala 1961, Heatwole & Sexton 1966, Vonesh 2001), elevation gradients (Brown & Alcala 1961, Fauth *et al.* 1989, Giaretta *et al.* 1999, Scott 1976), and environmental seasonality (Giaretta *et al.* 1999, Scott 1976, Toft 1980a, b; Vonesh 2001, Woolbright 1996).

In the tropics (23°S–23°N) where studies of anuran abundances have been conducted, the climate is either aseasonal, consistently hot and humid, or seasonal. Outside the tropics, subtropical dry zones (23°N–30°N, 23°S–30°S) occur mostly under xeric climates characterized by the year-round prevalence of a dry subtropical air
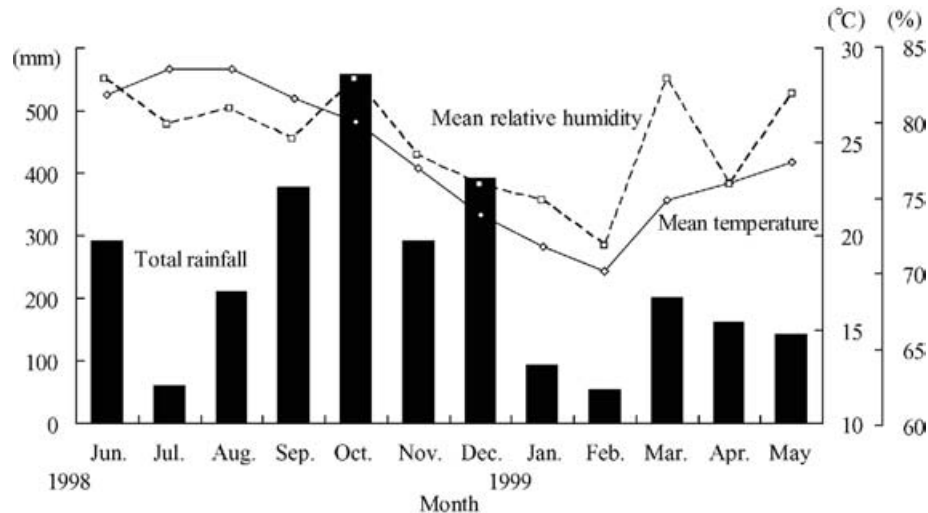
Figure 1. Monthly total rainfall, mean temperature, and relative humidity during the survey (July 1998–May 1999) at Iriomote Meteorological Station.

mass (Kira 1991). However, the south-eastern coast of Eurasia and adjacent continental islands are exceptional in that they, while being located in the subtropics in latitude, receive a large quantity of precipitation and keep a high humidity almost throughout the year under the influence of monsoons, typhoons and warm sea currents (Kira 1991, Numata 1974). The humid subtropical zone includes the long chain of small islands (the Ryukyu Archipelago) which lies to the south of the main islands of Japan between the latitudes 24° and 30°N. In this region, anurans of largely tropical lineages occur under distinctly seasonal variation in temperature without any prominent constraints from xeric climates. Amphibians of the East Asian subtropics thus offer a fascinating opportunity to study biological responses of potentially tropical species to seasonal environments. However, most of the original, natural vegetation has been lost in this region, as a result of widespread cultivation, and also due to heavy damage during World War II. Only Iriomote Island (24°15′–24°26′N), which is now protected as one of Japan's National Parks, contains good examples of the natural subtropical forests (Numata 1974).

In the present study, we investigated the characteristics of floor-dwelling amphibian richness and abundance in lowland forest on Iriomote Island. This is the first attempt to quantify abundance of floor-dwelling frogs in the subtropics of the Old World. We then compare our results with those of the studies on the anuran faunas of both Old and New World tropics.

STUDY SITE

The climate of Iriomote Island, like that of other Ryukyu Islands, is seasonal with a hot season from June to September (the average temperature during the study was 28.2 °C) and a cool season from December to March (20.1 °C) (Iriomote Meteorological Station, Figure 1), which is largely affected by the south or south-west monsoon during the hot season and the north or north-west monsoon during the cool season (Ayoade 1983). The monthly rainfall and relative humidity were 55–560 mm and 72–83%, respectively (Figure 1); the annual rainfall during the study period was 2840 mm. Thus, there is no clear dry season in this area.

Iriomote largely consists of highly folded mountains with the highest peak (Mt. Komi) being 469 m above sea level. Its vegetation is mostly subtropical evergreen broadleaved forest (83% of the island in area), which is largely composed of *Castanopsis sieboldii* (Makino) Hatusima ex Yamazaki & Masiba and *Quercus miyagii* Koidz. in the tree layer of 8–12 m height. The understorey flora is more diverse, consisting of species such as *Daphniphyllum glaucescens* Bl., *Elaeocarpus japonicus* S. & Z., *Rapanea neriifolia* (S. & Z.) Mez and *Ardisia quinquegona* Bl. (Miyawaki 1989, Numata 1974). Field surveys were carried out on the floor of evergreen forest (8–10 m in canopy height, 25 m in elevation, and c. 200 m²) in the eastern part of the island (24°20′N, 123°55′E).

METHODS

From June 1998 to May 1999, field surveys were carried out for a day in each month. The floor-dwelling amphibian fauna was monitored using a method of quadrat (5 m × 10 m) sampling similar to those described by Jaeger & Inger (1994). A quadrat was set as randomly as possible in each monthly survey.

At the beginning of each sampling, we had to trap all frogs in the plot at once. Otherwise, most of the agile frogs would have escaped out of the quadrat. It is generally difficult to enclose a quadrat area with dense vegetation rapidly. If sampling is performed by no less than four persons, effective sampling could be achieved (Jaeger & Inger 1994). However, it was difficult for us to carry out all monthly surveys with the same research team with normal number of observers. Also, sampling was desired to be carried out at night because on Iriomote all frog species are much more active in the night than during the day (Watanabe pers. obs.). Because of the difficulties in availability of personnel and time constraints, we preset the quadrat in the morning (8h00–10h00), materials as mentioned below, and then carried out the sampling at night of the same day (20h00–22h00) after enclosing the quadrat.

Fences (80 cm in height) used to enclose quadrats were made of flexible fine plastic mesh sheets attached to plastic ropes at the top and metal chains at the bottom. In the morning, just prior to sampling, solid iron poles (40 mm in width and 100 cm in height) were fixed at all corners of the quadrat and also on all margins at 2.5-m intervals. Then, ropes suspending rolled mesh sheets with chains were tightly spanned between the tops of these poles. At this stage, mesh sheets were rolled up and tied by strings or simply hooked to the rope. At the beginning of sampling (20h00–23h00), the mesh sheets were dropped down to the ground by rapidly loosing the strings or hooks in a moment with the aid of the weight of the metal chains. In order to close gaps between the sheets and the ground, the chains were immediately pegged to the ground with metal pegs.

These final settings were made by two persons, and were completed in no more than 2 min. Then, the same two observers entered the quadrat to search for frogs. Logs, wood pieces, and rocks on the ground surface were overturned to check for frogs, but living trees and grasses were not removed. Observers moved side-by-side, beating the ground with sticks, and then frogs found were captured. Each sampling bout was continued until all frogs in the quadrat were captured. When a frog successfully breached the mesh sheet and escaped from the quadrat, we visually identified it, roughly estimated its snout-vent length (SVL: <10, 10–20, 20–30, 30–40, 40–50 or $\geq$ 50 mm), and recorded it.

Captured frogs were transported to a laboratory, where they were identified to species, measured for SVL (to the nearest 0.1 mm by micrometer calipers) and weighed (to the nearest 0.1 g) on an electronic balance. Frogs were then divided into two growth stages (juveniles and adults) on the basis of their SVLs. In most frog species on Iriomote, males are smaller than females (Maeda & Matsui 1999). In each frog species, therefore, individuals greater than the smallest known mature male in SVL (Maeda & Matsui 1999) were considered as adults. Frogs were then released at the site of capture within the same night. By applying the mean mass calculated for corresponding size group of each species, we supplemented masses of escaped frogs in obtaining the total frog biomass in each quadrat. Then, seasonal patterns of species richness, density and biomass of the floor-dwelling anurans were examined. We also compared the estimated overall density and biomass of amphibians on Iriomote with corresponding values for other regions provided in earlier publications.

RESULTS

Quadrat sampling

We sampled the frog community 12 times, covering a total of 600 m^2. The total searching time was 675 min, the average search times per quadrat were 56.3 ± 14.6 min ($\bar{x} \pm$ SD, n = 12). We found a total of 251 frogs belonging to four species of three families (Figure 2), of which 228 frogs (90.8%) were captured. The remainder, including 10 ornate narrow-mouthed toads *Microhyla ornata* (Duméril & Bibron), and 13 Indian rice frogs *Fejervarya limnocharis* (Boie), escaped.

Seasonal changes in species abundance and diversity

Of the frog species found, *M. ornata* was the most abundant (42 juveniles and 125 adults, 66.5% of all frogs found), followed by *F. limnocharis* (56 juveniles and 20 adults, 30.3%), Owston's green tree frog *Rhacophorus owstoni* (Stejneger) (6 adults, 2.39%), and Yaeyama harpist frog *Rana psaltes* Kuramoto (2 adults, 0.80%) in order.

Monthly variation in density and biomass of each frog species are given in Figure 2. There were some species-specific seasonal patterns. For instance, the density of *F. limnocharis* was higher during the hot season (June–September) and notably lower during the cool season (December–March), with a prominent increase from April to August and decrease thereafter to November. The density of *M. ornata* also showed some fluctuations with peaks in August, although it exhibited relatively high values throughout the year. *Rhacophorus owstoni* appeared only during the cool season (December–February).

The monthly overall frog density ranged from 0.08 frogs m^{-2} (in November) to 1.60 frogs m^{-2} (in August), the average density throughout the year was 4180 frogs ha^{-1}. The relatively high overall density of frogs in the hot season is attributable to the high density of *M. ornata* and *F. limnocharis*. On the other hand, the abundance of frogs in the cool season was chiefly contributed by *M. ornata* and *Rh. owstoni*. The species
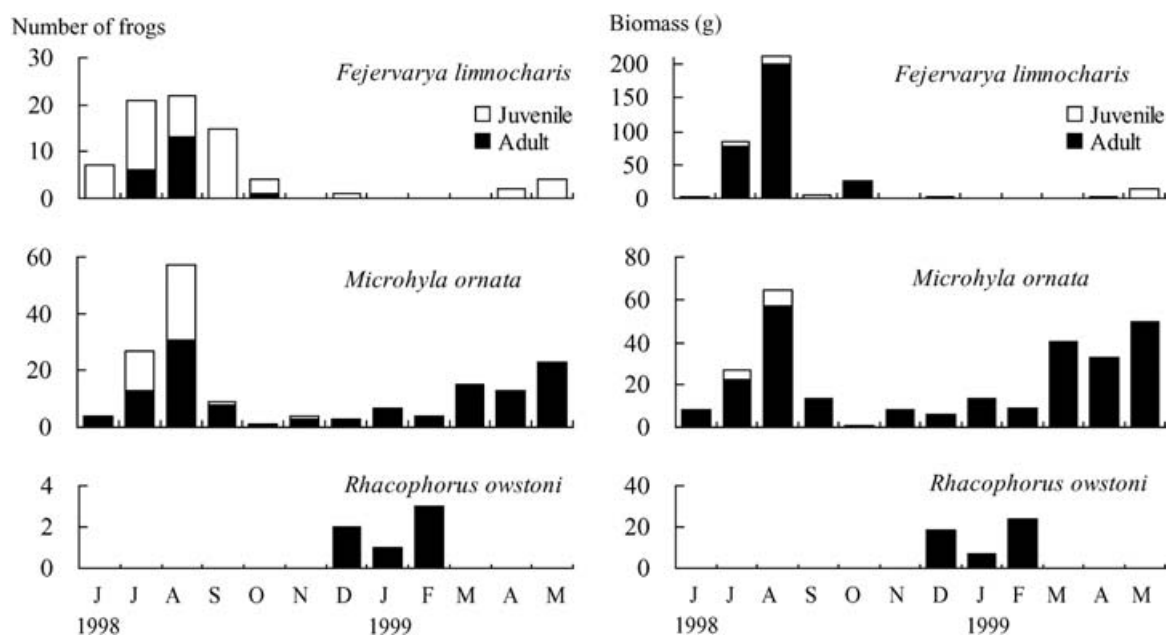
Figure 2. Monthly changes in number of individuals and biomass of each frog species found per quadrat (50 m^2) in humid subtropical forest on Iriomote.

richness was only one to three (2.08 ± 0.51, n $= 12$) throughout the year.

For the estimated biomass, *F. limnocharis* dominated (348 g ha^{-1}, accounting for 50.6% of the whole frog biomass), followed by *M. ornata* (273 g ha^{-1}, 39.8%), *Rh. owstoni* (49.0 g ha^{-1}, 7.13%), and *R. psaltes* (17.3 g ha^{-1}, 2.51%) in order. The estimate of the whole floor-dwelling frog biomass on Iriomote ranged from 0.16 g m^{-2} (in November) to 5.69 g m^{-2} (in August) with the yearly average being 11 460 g ha^{-1} (Figure 2).

Frog size structure

The sizes of *F. limnocharis* and *M. ornata* were highly variable with high proportions of juveniles (< 41 mm in SVL for *F. limnocharis*, and < 22 mm for *M. ornata*: Maeda & Matsui 1999) in the whole species samples (73.7% in *F. limnocharis* and 25.2% in *M. ornata*). During July, August and October, *F. limnocharis* of many sizes were observed, while adult frogs were found only during these months. Juveniles of the species were observed from April to October, and in December, and were particularly abundant from June to September. Adult frogs of *M. ornata* were observed throughout the year, whereas juveniles of the species were observed from July to September (Figure 2).

DISCUSSION

Seasonal patterns

There were some species-specific seasonal patterns in anuran densities in our quadrats. In a given species,

the seasonal variation in observed individual density may reflect three mutually non-exclusive events: (1) fluctuation of actual population density chiefly due to juvenile recruitment and mortality, (2) seasonality in activity due to reproductive and physiological properties and (3) migration to other habitat types within the island. If the first one is the case, numbers of juvenile recruits should be higher when larger samples were obtained. Indeed, juvenile recruits tended to be abundant when individual densities of these species were relatively high, during June, July and September in *F. limnocharis*, and during July and August in *M. ornata*. However, large samples were also obtained before recruitment of juveniles, due chiefly to large number of adult frogs. Adult frogs of *F. limnocharis* and *M. ornata* assemble and breed in April–August and March–July, respectively (Maeda & Matsui 1999). It is likely that active adult frogs, assembling for mating, also increased population density of these species. After juvenile recruitment of these species, the population densities began to lower toward winter. For many amphibians, mortality rates are chiefly influenced by infectious diseases, predation, and some abiotic environmental events, such as droughts, and this is particularly true with juveniles (Duellman & Trueb 1994). From September, the population densities, as well as the number of juvenile frogs, dropped. It is, therefore, likely that the reduction in number of juveniles through high mortality led to the decline of the whole population from October to February.

However, the numbers of adult frogs of these species also fell during the winter, particularly *F. limnocharis*, which is due probably to the second factor. On Okinawa

Island of the central Ryukyus, the species was reported to be inactive at temperatures below 20 °C, and to disappear in winter (Chigira & Shimabukuro 1982). On Iriomote, although rainfall is not so limited, in winter, air temperatures decline to 18 °C. It is, therefore, likely that reduction in number of observed *F. limnocharis* toward winter in the present site is attributable to the decrease of its activity caused by lower temperature, as well as decrease of actual population density due to the high juvenile mortality.

For the third factor, migrations are usually mostly associated with reproductive aggregations in amphibians (Duellman & Trueb 1994). The two most abundant species, *F. limnocharis* and *M. ornata*, breed in various bodies of still water (Maeda & Matsui 1999). These places are abundant around our study site, and we noted calling and egg masses of these frogs there during their breeding periods. It is, therefore, unlikely that these frogs migrated to other habitat types while small numbers were sampled in our quadrats. Although we think there is little effect of seasonal migrations for these two species, the appearance of *Rh. owstoni* was obviously influenced by the seasonal migration involving its reproductive cycle. Although the species is normally arboreal, they come down to forest floor during the breeding season mainly from December to March (Maeda & Matsui 1999). Therefore, it is likely that floor-dwelling *Rh. owstoni* were only observed during the breeding season in our quadrats.

Most tropical anurans are capable of reproducing throughout the year, and rainfall is considered to be the primary extrinsic factor controlling the timing of reproductive activity. In contrast, reproductive activity is cyclic in most temperate species, and is dependent on a combination of temperature and rainfall (Duellman & Trueb 1994). *Fejervarya limnocharis* is distributed widely from tropical to temperate regions (Maeda & Matsui 1999). In aseasonal climates, consistently hot and humid, frogs at various reproductive stages are observed throughout the year (Berry 1964), while reproduction of this frog in typical monsoon forests where water availability is deficient during winter is confined to the rainy season when preferred breeding sites are flooded (Khan 1982). In the temperate zone, the species breed only during summer (Maeda & Matsui 1999), due probably to the physiological condition under the influence of varying temperature and rainfall (Chigira & Shimabukuro 1982). With respect to anurans in the humid subtropics, therefore, we hypothesize that rainfall is not the only primary influential factor upon reproduction, and that the reproductive cycles are controlled by a combination of temperature and rainfall, like those in temperate species.

Abundance of floor-dwelling frogs on Iriomote Island

Floor-dwelling frog densities in lowland forests estimated by similar sampling methods are available for Africa (Scott 1982), South-East Asia (Inger & Colwell 1977, Lloyd *et al.* 1968), Central America (Heatwole & Sexton 1966, Scott 1976, Toft 1980a), and South America (Allmon 1991, Toft 1980b). Although sampling methods varied among the various studies in terms of quadrat sizes and total sampled areas (Table 1), it is generally accepted that

Table 1. Comparison of densities of floor-dwelling frogs on Iriomote Island, with those in lowland forests of the Old and New World tropics estimated by quadrat sampling methods.

Locality	Latitude (degrees)	Annual rainfall (mm)	No. of quadrats	Area sampled (m^2)	No. of species in quadrats	Density (indiv. ha^{-1})	Reference
Ryukyu; Iriomote Island evergreen forest	24N	2800	12	600	4	4180	Present study
Africa Cameroon; Lombe	4N	4000	15	872	8	940	Scott (1982)[1]
Southeast Asia Borneo; Nanga Tekalit	2N	> 5500	402	23340	28	122	Lloyd *et al.* (1968)
Thailand; Sakaerat							
evergreen forest	14N	<1500	479	27670	19	262	Inger & Colwell (1977)
deciduous forest			173	39970	20	55	
Central America Costa Rica							
Osa	9N	4000	20	1160	23	1160	Scott (1976)
La Selva	10N	3600	19	1100	23	1470	
Panama							
Silugandi	9N	>2000	5	235	7	2980	Heatwole & Sexton (1966)
Carti Road	9N	3500	23	756	23	2070	Toft (1980a)
Pipeline Road	9N	2200	15	540	14	1260	
South America							
Peru; Rio Llullapichis	9S	2200	12	432	13	1550	Toft (1980b)
Brazil; INPA–WWF reserves	2N	2000–2500	498	12530	15	476	Allmon (1991)

[1] The data indirectly referred from Allmon (1991).

the Central American lowland forest supports the densest litter anuran populations, followed by Africa and South America, and South-East Asia in order (Allmon 1991, Inger 1980, Scott 1976). Similar results were also shown in those of floor-dwelling lizards (Inger 1980, Scott 1976).

When compared with the results of other studies (Table 1), first of all, it is obvious that on Iriomote, the anuran fauna is less diverse than those in the other regions. In terms of density of individuals, however, the estimated value for the Iriomote anurans is much higher than those for frogs of the Old World tropical forests, being as high as, or even higher than, the amphibian density in Neotropical forests.

For the assessment of the role of anuran community in food webs, biomass which provides important information for an understanding of food-web function on the flow of energy through the system (Burton & Likens 1975, Stewart & Woolbright 1996) might be a better indicator than individual density. Toft (1980b) estimated an anuran biomass of a lowland rain forest of Amazonian Peru in the wet season as 1088 g ha^{-1}. Giaretta *et al.* (1999) estimated that of a montane forest of south-eastern Brazil in the wet season as 781 g ha^{-1}. Roach *et al.* (2001) estimated that of aseasonal tropical rain forest in south-eastern Brazil as 1150 g ha^{-1} (estimated by data only sampled by using larger quadrats). Thus, estimated frog biomass on Iriomote (11 460 g ha^{-1}) is greater than any of the available values for the tropics at least by an order of magnitude.

Scott (1976) considered that divergent abundance in herpetofauna among regions might be a result of either (1) basic differences in the functioning of the total system in forests or (2) differences in the composition of the litter-animal community. Through comparisons of fundamental functions of forests as the first factor, Scott highlighted greater litterfall and faster decomposition rates in tropical forests of the New World. Although no information is available regarding the productivity of the forest on Iriomote, it has been well documented that the humid subtropical forests are fundamentally different from tropical rain forests in terms of phenology, component species and canopy structure (Kira 1991, Miyawaki 1989, Numata 1974). These climatic and structural features of humid subtropical forests may also cause a high abundance of floor-dwelling anurans as demonstrated in this study.

With respect to the second factor of Scott (1976) (see above), significant negative correlation was documented for the density and species richness of leaf-litter herpetofaunas (Scott 1976). While species richness is generally much lower on an island than the adjacent mainland, the opposite is often the case for vertebrate population densities (MacArthur 1972, MacArthur *et al.* 1972, 1973). These patterns appear to hold for amphibians. For instance, densities of salamanders were estimated to be 4000–20 000 ha^{-1} for islands off the California coast and 500–4500 ha^{-1} for the mainland of California (Anderson 1960, conversions by Vial 1968). The composition of anuran community may possibly be strongly influenced either by the community of both predators and non-anuran competitors. Therefore, we assume that the island effect, involving limited numbers of predators and competitors, has also more or less contributed to the remarkably high abundance of the anuran fauna on Iriomote Island. Investigation of amphibian abundances in nearby, more continental places, such as Taiwan, is desired to evaluate those candidates for causal factors responsible for the remarkably high abundances of anurans on Iriomote.

ACKNOWLEDGEMENTS

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