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Social vocalisations in the Seychelles sheath-tailed bat *Coleura seychellensis*

Justin Gerlach
133 Cherry Hinton Road, Cambridge CB1 7BX, U.K. E-mail : jstgerlach@aol.com

Abstract. Social vocalisations of the Seychelles sheath-tailed bat *Coleura seychellensis* are described from observation made during the breeding season. Four main call types used in social situations were recorded. These vary from simple screech calls used in aggressive or distressed contexts to appeasement and male 'song'. Juveniles used a combination of high pitched screeches and appeasement calls to attract lactating females. Males 'song' was basic in form, consisting of a single repeated syllable. Individual variation in this syllable was detected in frequency and duration, this allows individual recognition.

Key words : *Coleura seychellensis*, Emballonuridae, Seychelles, Silhouette, social behaviour

Vocal communications is an important feature of many vertebrate social interactions. In Microchiropteran bats vocalisations are used in mating displays (SLUITER & VAN HEERDT, 1966 ; WICKLER & SEIBT, 1976 ; BRADBURY, 1977), territorial defence (BRADBURY & EMMONS, 1974 ; BARLOW & JONES, 1997 ; DAVIDSON & WILKINSON, 2004) and extensive repertoires of social calls may exist, allowing individual discrimination (BOUGHMAN & WILKINSON, 1998). However, this has been investigated in only a small number of species, mostly in a laboratory context (NELSON, 1964 ; BROWN, 1976 ; BARCLAY *et al*., 1979 ; PORTER, 1979 ; BROWN *et al*., 1983 ; DAVIDSON & WILKINSON, 2004). The most extensively studied species, *Saccopteryx bilineata*, has complex calls, including male song. Although social calls have been identified in this species and in some other Emballonuridae species very few species have been studied in their roosts. The present paper reports on the social interactions within the largest known roost of the Critically Endangered Seychelles sheath-tailed bat *Coleura seychellensis*. Vocalisations used by *C. seychellensis* in foraging and navigation have been reported elsewhere (GERLACH, 2008) but social behaviour and communication in this species has not been studied previously.

Coleura seychellensis has been reported to form harem groups of approximately 6 females, guarded by a single male (NICOLL & SUTTIE, 1982). This is similar to the description of roost behaviour in the congeneric African *C. afra*. *C. afra* forms large colonies in cave systems (over 50,000 individuals in some cases), within these roosts bats sometimes form small clusters of up to 20 individuals, solitary individuals occur rarely and are usually males. Most clusters appear to be female groups with a single male, sometimes with satellite males on the periphery. There is a short period of competition between males for control of these clusters during short synchronous breeding events. Otherwise there is little social interaction within the roost (MCWILLIAM, 1987).

During research into the ecology and conservation requirements of *Coleura seychellensis* data were gathered on the behaviour of bats within the roost, in particular their social interactions and communication.

METHODS

In 2006 a monitoring video camera was installed in the largest known roost of *Coleura seychellensis*, at La Passe, Silhouette island (this roost is described in GERLACH, 2004). Data from the camera were recorded at least once a month from September 2006. In December 2006 this was combined with recording of ultrasound calls within the roost recorded using the Anabat II bat detector and ZCAIM storage system. 52 hours of video and sound data were recorded. Recorded calls and observations of interactions were grouped into recognisable categories. Calls were initially divided into two main categories (after GERLACH, 2008) :

1. Social calls - vocalisations made by a bat and directed at another bat (observed during recording), with no clear regular pulse repetition ; complex calls covering a wide frequency range (typically 12-40 kHz), with a significant audible component (at around 5 kHz).
2. Orientation within the roost - broadband frequency modulated (FM) calls (16.6-41.0 kHz) with a characteristic upsweep followed by a downsweep, produced by bats flying within the roost.

Further subdivisons were made of the social calls based on the frequency range, characteristic frequency and duration through analysis using Analook (CORBEN, 2000). The characteristic frequency is the frequency at the point of the lowest slope of the call, usually produced towards the terminal part of the call (excluding any initial and terminal downsweeps). This frequency is consistent between calls and has low variability.

Film of the bats was synchronised with the sound recordings in order to interpret the communication and behaviour.

RESULTS

Interactions within the roost could be divided into five main categories:

1. Calling - bats performing calling behaviour held onto the roost ceiling with all four limbs, the mouth could be seen to be open and the head usually moved in a scanning motion. Some, but not all, calls appeared to be directed at a single individual.
2. Aggression - bats vigorously pushing each other with their wings, calling frequent
3. Grouping - bats moving towards other individuals, and pulling them, often leading to clustering, usually silent
4. Suckling - juvenile bat suckling from an adult female, silent
5. Begging - juvenile bat following an adult female, calling repeatedly

Four of these interactions were associated with distinct calls (behaviours 1, 2, 3 and 5). The identified calls, their characteristics and the associated behaviours are summarised in Table 1 and Fig. 1. Foraging pulses were not normally recorded in the roost (one single observation) and navigation calls did not involve any social context.

These call types were recorded throughout the day when bats were resident within the roost. In December bats were present in the roost throughout the night (5 non-flying juveniles, 2 flying juveniles and 2-4 adults), these bats produced only sweeps, with occasional screeches and navigational calls made either by these bats or additional returning adults. No identifiable social calls were recorded at night.

DISCUSSION

The majority of calls recorded in the present study are basic in structure and apparently also in function (primarily navigation or social spacing). Nocturnal communications in the roost were all of this type; the more complex calls were only recorded during daylight when the full colony was present in the roost. The foraging pulses were only recorded away from the roost, with the exception of a single call made by a flying bat returning to the roost at night. The characteristics of this type of call and the navigational calls are described elsewhere (GERLACH, 2008).

These social call types correspond to categories identified in similar social contexts in other studies. PFALZER & KUSCH (2003) identify type B 'trills' (call type 2, Table 1) as representing 'increased irritation' between individuals, including between mothers and young. Type C 'cheeps' (call type 3, Table 1) have been identified as identification calls between females and their young with variability allowing individual identification. This call

Table 1: Call types, frequency (kHz) given as minimum-mean-maximum.

Call type	Characteristics	Frequency	Characteristic frequency	duration (ms)	context
1. Pulses	Shallow quasi CF	36.4-40.1-44.0	38.1-43.0	1.0-1.3	foraging
2. Sweeps	Steep pulses, 'trill' or short FM tone	23.4-24.3-26.2	23.4-24.9	1.7-2.1	aggression
3. Screech	CF	24.7-26.6-29.4	25.1-27.6	1.1-2.3	begging approach
	CF	40.8-41.4-42.2	41.2-41.4	1.2-1.3	begging, rejected
4. Broad sweeps and screech-inverted-V calls	Quasi CF pulses and FM tones	37.8-44.3-49.1	44.2-44.4	3.2-7.3	interaction, begging
5. Navigation call	FM tone rising then falling steeply	33.2-4.31-49.1	40.6-44.4	1.7-7.3	Flying or walking in roost
6. Song	Complex call of short FM-tones	35.9-38.3-45.0	38.1-43.7	1.0-6.1	male calling

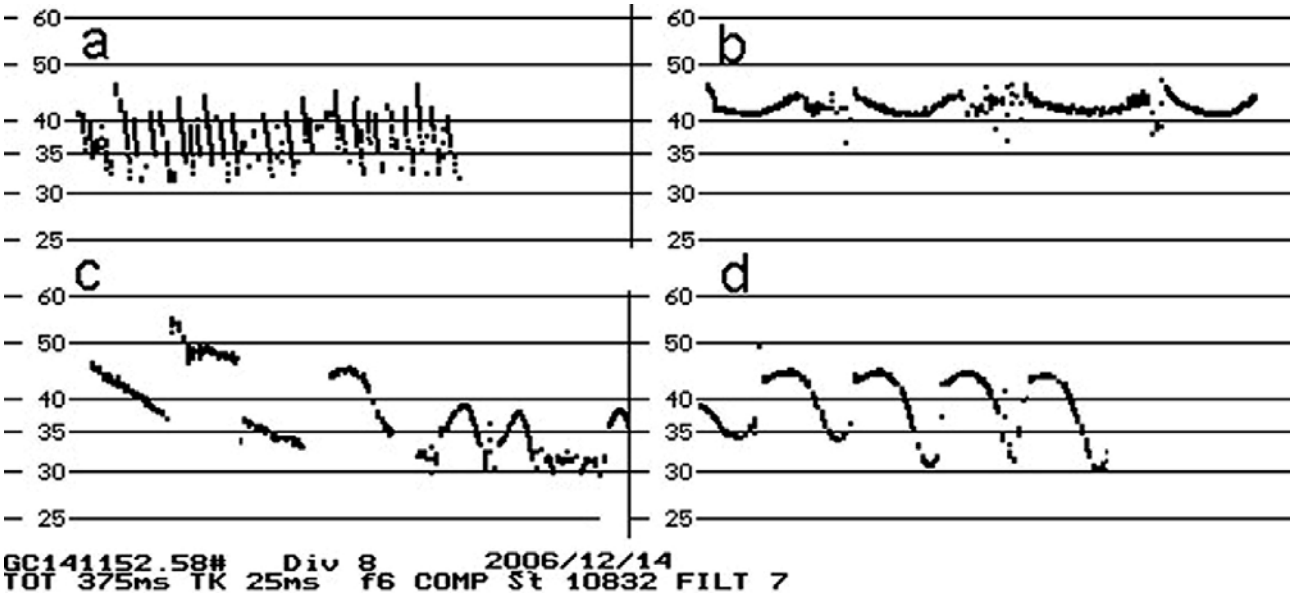

Fig. 1: Social calls of *C. seychellensis*
a) agonistic sweeps; b) begging screech; c) begging sweep; d) male song

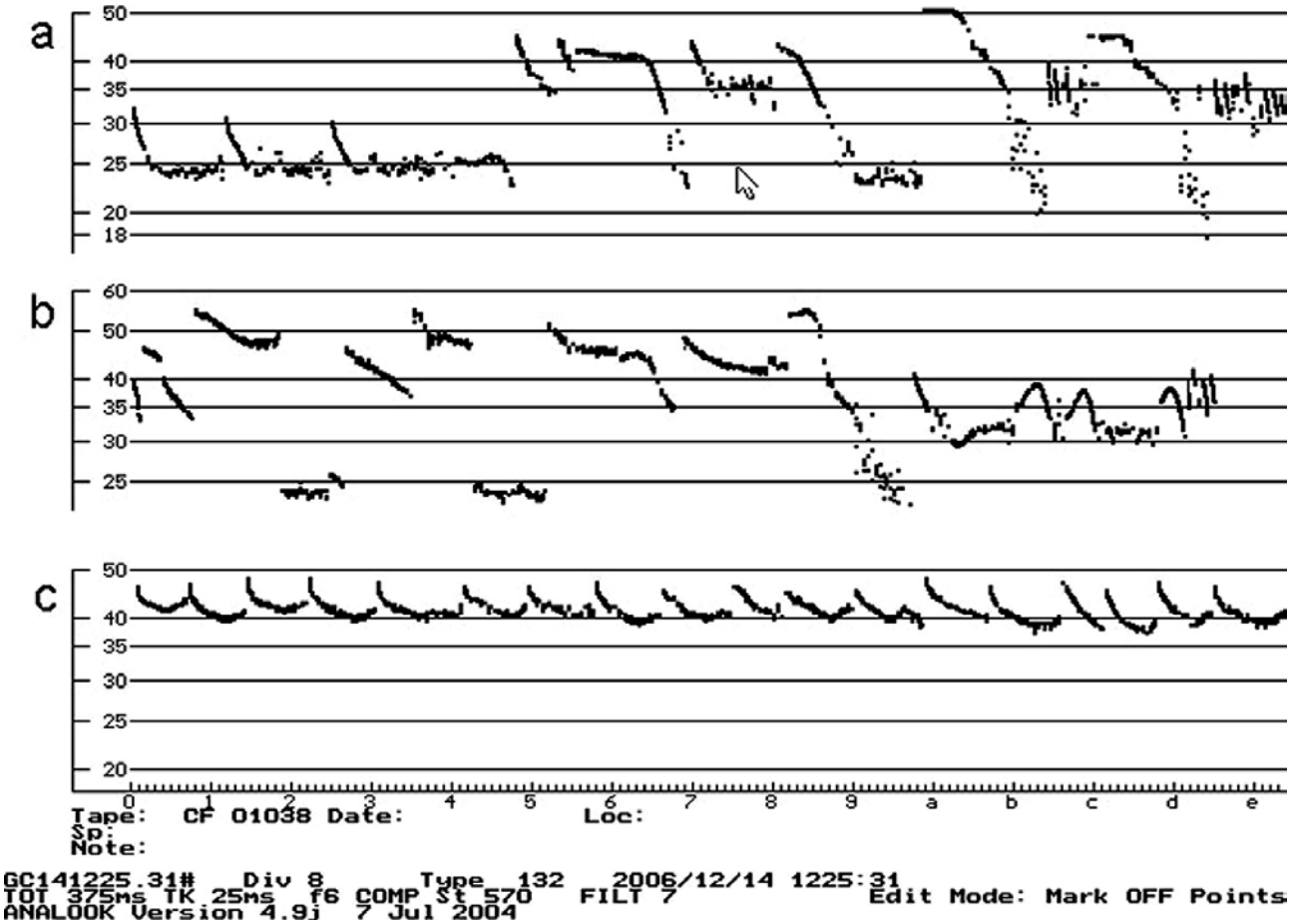

Fig. 2: Effects of acceptance and rejection on begging juveniles
a) approach; b) accept; c) rejection

may also be used by males to attract females and between mothers and young when foraging. Type D song (call type 5, Table 1) was considered by PFALZER & KUSCH (2003) to be used by males to attract females.

Calls associated with agonistic behaviour comprise sweeps and screeches. Sweeps are low frequency narrowband FM calls of short duration ; these will provide little information in a spatial context and serve to convey information when bats are disputing position within a cluster. Frequent sweeps were recorded when a bat tried to join a cluster, disturbing the bats within it. Screeches were recorded in a similar context but where more aggression was involved, such as when a bat tried to join a cluster but was repulsed. The screech call appears to be an exaggeration of the sweep, having a similar frequency and shape, but being broader, more varied and less well defined. This call was most frequently recorded when juveniles were approaching adult females. Juveniles approaching females called at 37.3-39.2kHz (1.8ms duration) combined with short FM tones. Rejection of this approach (show by the female moving away from the begging juvenile) was followed by the juvenile raising its call frequency (Fc 41.2 compared to 25.1-27.6) and reducing the duration of calls (1.2 ms compared to 1.1-2.3 ms) through omission of the FM tones. Females rejecting juveniles remained silent, those accepting the juvenile responded with screech calls at the normal frequency (Fig. 2). This call was also used by females making unsolicited approaches to juveniles.

The screech call shows some resemblance to the broad sweeps characteristic of more complex social interactions. Broad sweeps are broadband calls of comparatively long duration. These were expressed by bats attempting to join clusters and by bats actively rejecting such attempts. These interactions involved aggressive behaviour (using wings to push and pull the other bat) and were only observed between males. Prolonged agonistic interaction results in the calls becoming more complex and with long harmonic tones (Fig. 5). A more ritualised interaction between males was observed when song was recorded. The full song of *C. seychellensis* were produced by males in a stereotypical posture (Fig. 3). A simplified form was produced when hanging by the hind feet. These bats

Fig. 3 : Song posture of male *C. seychellensis*

were either roosting solitarily or on the edge of a cluster. Males approached existing groups by landing 15-30 cm away, calling and then approaching closer to the group. They may move directly into the group which remains silent, or may call from a position 5-10 cm from the group. This repeated calling is associated with significant colony disturbance with screeches from within the group and other clusters. In this context the song appears to be directed at the flying bats, rather than at the group, and may serve to discourage the approach of other males. When the disturbance reduces screeching and song are replaced by the interactive sweep calls and the male joins the group. Individual variation in full song was detected in the degree of development of the initial upsweep, characteristic frequency and duration (Fig. 4, Table 2).

The findings of the present study are in accordance with findings of other studies of emballonurid bats. The calls of *C. seychellensis* are less complex than those reported for *Saccopteryx bilineata* (DAVIDSON & WILKINSON, 2002) but correspond to the same call types and social significance. From the few studies available it appears

Table 2 : Male song variation

Fig.	Frequency range (kHz)	Frequency mean	Characteristic frequency	duration (ms)
4a	37.8-43.9	40.0	39.2	6.1
4b	35.9-41.0	38.6	38.3	3.2
4c	37.0-41.8	38.6	38.7	5.1
4d	35.9-41.0	38.6	38.3	3.2
4e	35.9-41.8	40.3	40.0	4.0
4f	33.6-40.5	38.6	38.8	5.1

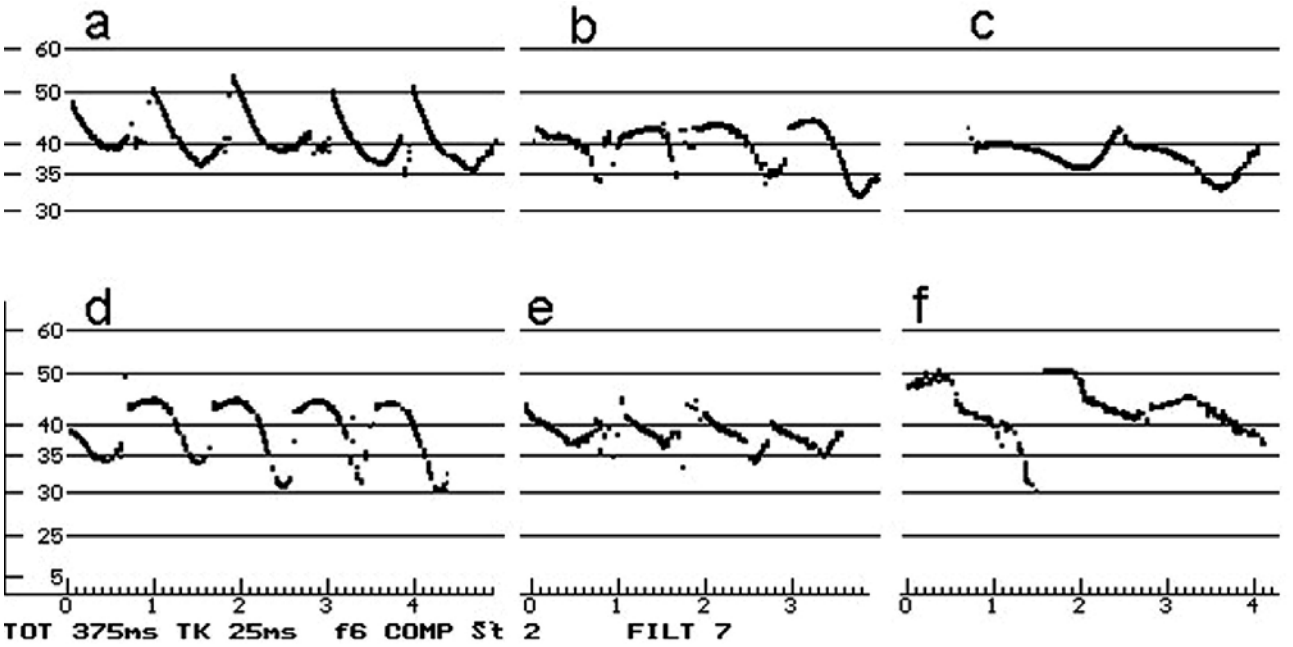

Fig. 4 : Variation in male song elements ; a-f) individual variations in typical song

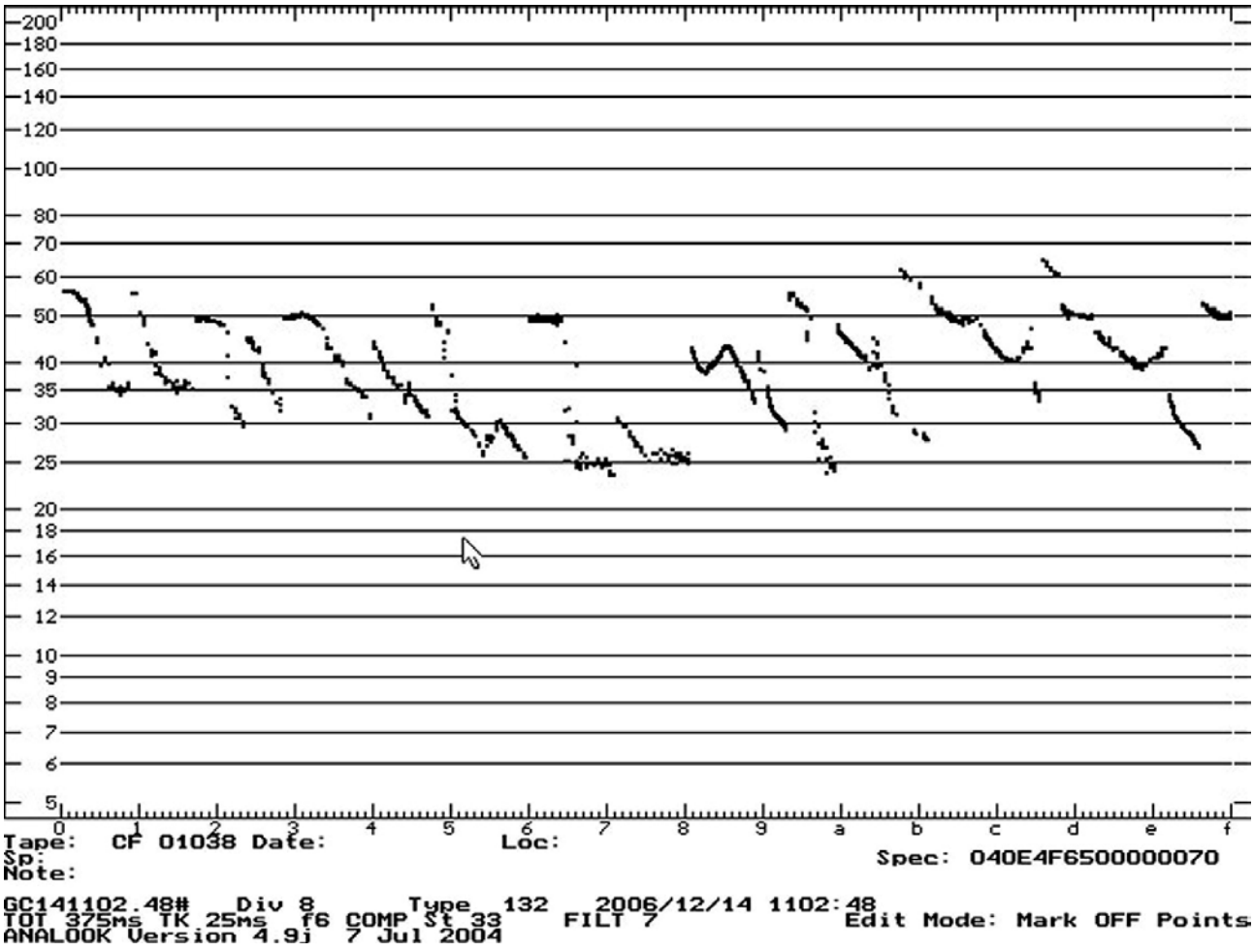

Fig. 5 : Conflict between two males showing partial overlay of distinct song elements

that *S. bilineata* has an unusually complex repertoire of calls, the significance of this is currently unknown. As hypothesized by OWINGS & MORTON (1998) the FM tones of the juvenile appeasement ('begging') call is structurally similar to the elements of the male song. The song shows individual variation, with six individual calls being identified within the roost. At this time the colony numbered 20 individuals, including 6-7 males. These males moved between groups within the roost although only one male at a time was recorded within a group. It appears that during the breeding season *C. seychellensis* groups are composed of females and juveniles, associated with a single adult male as suggested by NICOLL & SUTTEE (1982). However, the males do not defend fixed territories but associated temporarily with females. This may be a practical mate guarding strategy in this species where groups are small and highly mobile ; males cannot monopolise females for long periods but by excluding other males from the group they increase their chance of mating with any females that become reproductively receptive during the time that the male is in association. In the absence of fixed territories there is no possibility of true territorial song developing (as in the display songs of *S. bilineata*) and only the most stereotypic song elements are required.

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