

## Call variation in sooglossid frogs

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The frogs of the family Sooglossidae are restricted to the Seychelles islands, although the isolated and anatomically and genetically divergent Indian frog *Nasikabatrachus sahyadrensis* (Nasikabatrachidae) has been suggested to be a member of the family (Frost *et al.* 2006). Here the conventional usage (e.g. Biju and Bossuyt, 2003; Van der Meijden *et al.* 2007) is followed, restricting the Sooglossidae to four species from the Seychelles islands. Naskibatrachidae and Sooglossidae are sister families and the Sooglossidae are believed to have evolved in isolation in the Seychelles islands through vicariance as the continental plates of Seychelles and India separated round 64 million years ago (Mukhopadhyay *et al.* 2012). Today the diminutive Seychelles frogs are restricted to the islands of Mahé, Silhouette and Praslin (Taylor *et al.* 2012).

The Sooglossidae comprise four species: *Sooglossus sechellensis*, *S. thomasseti*, *S. gardineri* and *S. pipilodryas*. These have recently been divided into two genera: *Sooglossus* containing the two former species and *Leptosooglossus* or *Seychellyphryne* containing the latter two. *Leptosooglossus* and *Seychellyphryne* were described simultaneously, and despite the uncertainty of the order of precedence of these names, I use *Seychellyphryne* for the two smaller species: *S. gardineri* and *S. pipilodryas*. It is thought that these species have diverged sympatrically on the larger islands of the Seychelles group, with recent isolation of populations on different islands due to Holocene sea level fluctuations (Van der Meijden *et al.* 2007). Accordingly it may be expected that inter-population variation (particularly between islands) would reflect a recent history of expanding and contracting ranges, with a close similarity between Mahé and Praslin populations, and a moderate degree of structuring within the topographically complex island of Mahé. The results of the study of call variation are described here.

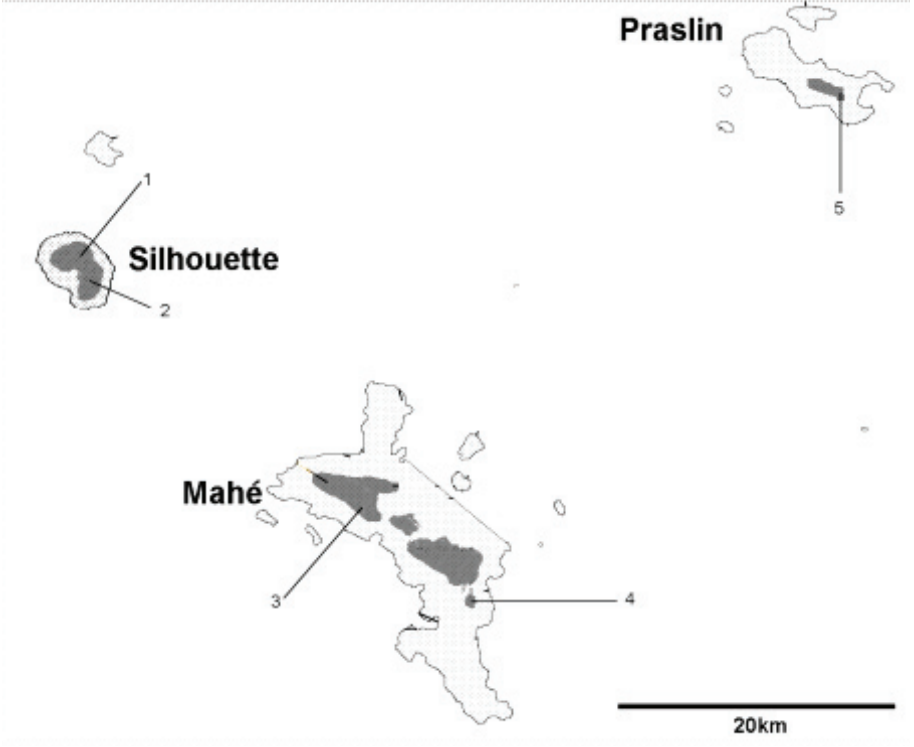
### Methods

Sooglossid calls were recorded in all of the main populations in 2010-12 (Table 1). Locations are marked on Fig. 1. Recordings were made using Song Meter SM2+ (Wildlife Acoustics) and SMXII microphones to record over 24 hours at each site. Files were recorded in uncompressed WAV format. Where possible calls were recorded over a 24 hour period and at different times of year to allow diel changes in calling rates and characteristics to be investigated. The call recorder simultaneously recorded air temperature (to an accuracy of 0.1°C), allowing call characteristics to be compared directly with ambient temperature.

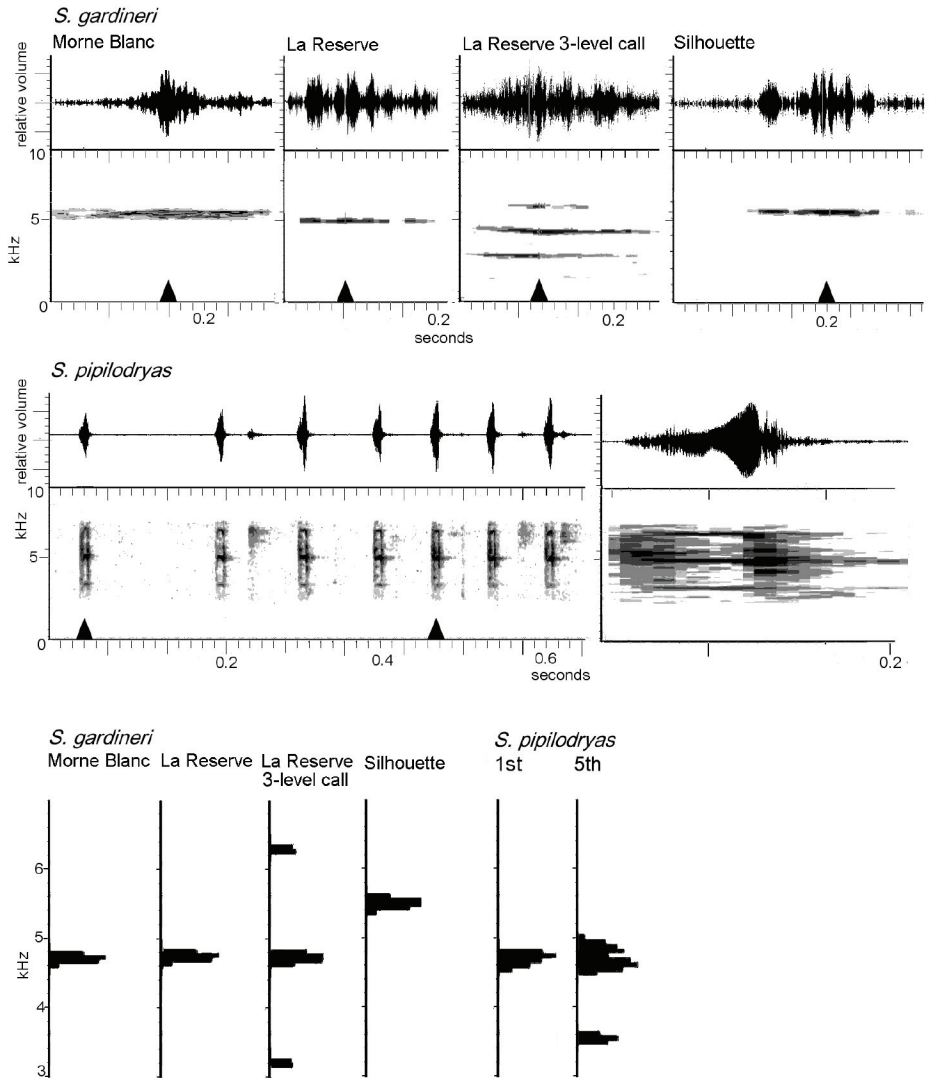
**Table 1.** Sooglossid calls recorded at different field sites

Island	Site	Species	Number of calls	
			recorded	analysed
Mahé	Morne Blanc	<i>S. gardineri</i>	16,440	202
		<i>S. sechellensis</i>	8,940	58
		<i>S. thomasseti</i>	19	19
	La Reserve	<i>S. gardineri</i>	1,824	89
		<i>S. sechellensis</i>	2,278	123
Silhouette	Gratte Fesse	<i>S. gardineri</i>	28	8
		<i>S. pipilodryas</i>	35	12
		<i>S. sechellensis</i>	3	3
		<i>S. thomasseti</i>	2	2
	Mon Plaisir	<i>S. gardineri</i>	600	21
		<i>S. pipilodryas</i>	53	4
		<i>S. sechellensis</i>	180	18
		<i>S. thomasseti</i>	3	3
Praslin	Glacis Noir	<i>S. sechellensis</i>	1	1

**Fig. 1.** Location of call recording points and distribution of Sooglossidae. Sooglossid range shaded. 1- Mon Plaisir, 2 – Gratte Fesse, 3 – Morne Blanc, 4 – La Reserve, 5 – Glacis Noir



For each site several calls of each species (numbers varying per site – Table 1) were analysed. Analysis was carried out using Song Scope Bioacoustics Software V4.0 to determine call and note duration, frequency range, dominant frequency of primary and secondary notes, number of primary and secondary notes, note structure (frequencies pattern and number of pulses). Where calls from different sites overlapped in characteristics the significance of any differences were analysed using a t-test.



**Fig. 2.** Typical calls of *Sooglossus gardineri* and *S. pipilodryas*

## Results

The four species were easily distinguished on recordings by their call frequency and structure (Fig. 2-4; Table 2-3). Due to its geographical restriction and relative scarcity (Gerlach 2011) fewest calls were recorded of *S. thomasseti*, with three calls from Mon Plaisir (Silhouette) and 18 from Morne Blanc. This does not allow geographical

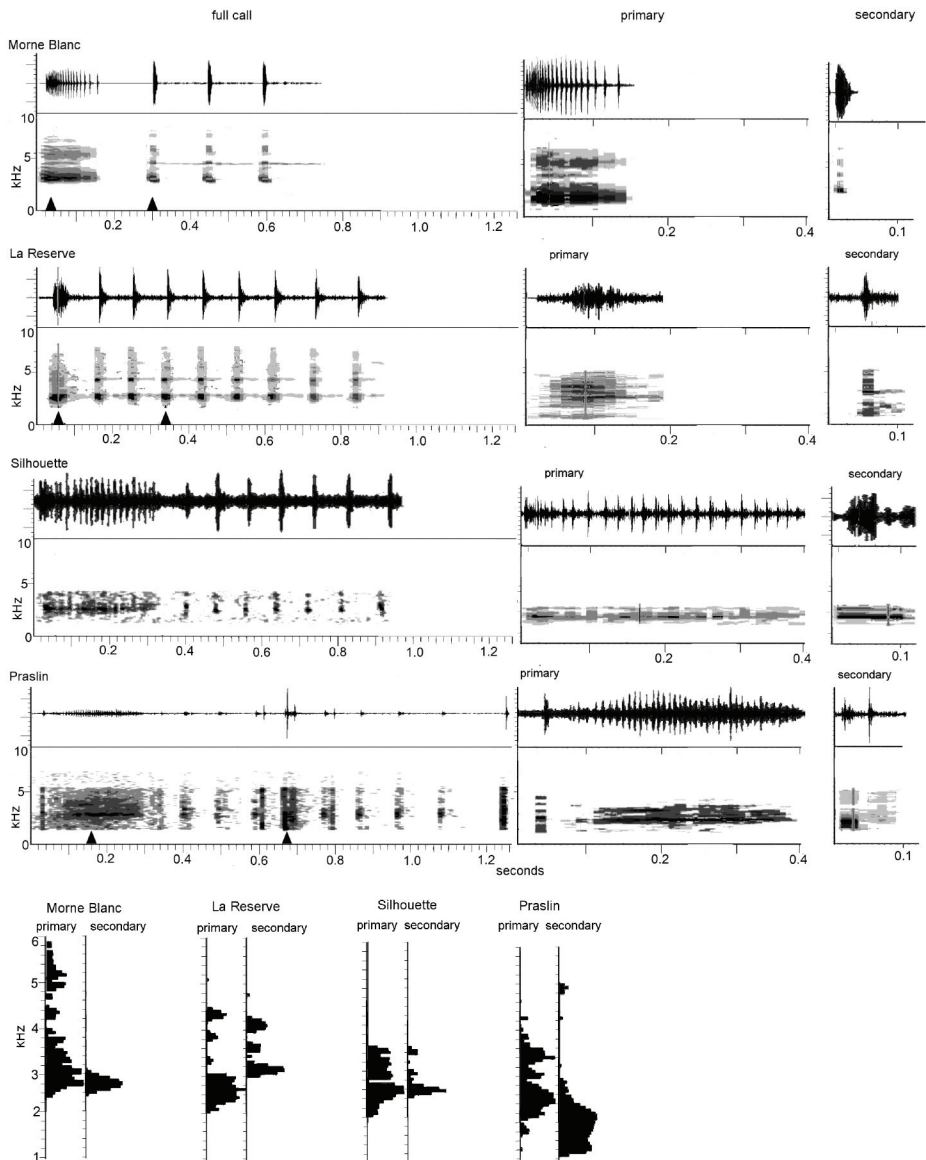
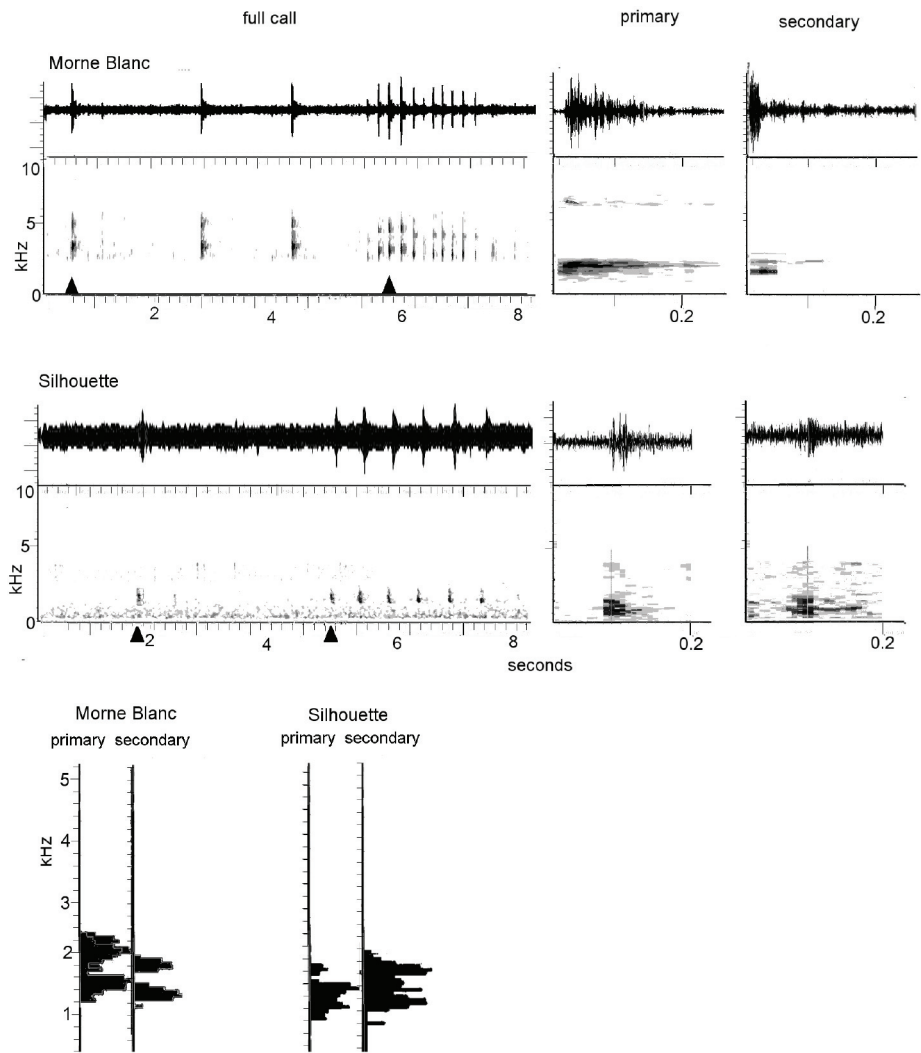


Fig. 3. Typical calls of *Sooglossus sechellensis*

variation in this species to be evaluated. *S. pipilodryas* is restricted to Silhouette island and the distribution of the species suggests that there is a single population, with any structuring being unlikely. Nonetheless comparison can be made between two sites (Gratte Fesse and Mon Plaisir). *S. gardineri* was recorded in abundance at all sites on Mahé and Silhouette and comparative analysis was undertaken. *S. sechellensis* was recorded in all Mahé and Silhouette sites and is also the only species present on Praslin. Only a single call was obtained from that island. The results of call analysis are shown in Table 2.

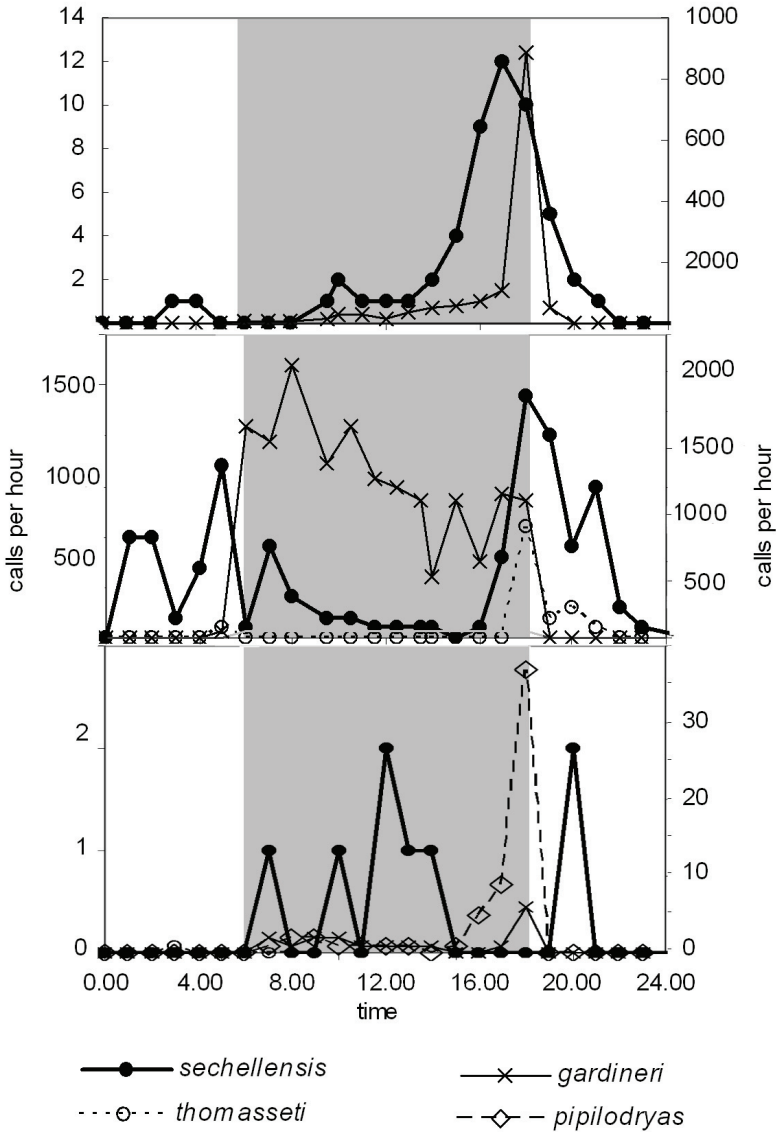


**Fig. 4.** Typical calls of *Sooglossus thomasseti*

**Table 2.** Call parameters and analysis, values are means with ranges in parentheses

species	Call type	Site	N	Full call Duration	Primaries		Secondaries			
					number	duration	frequency	pulses	number	frequency
<i>gardineri</i>		Morne Blanc	42	178 (80-344)	1		5347 (4855-5900)	-	-	
		La Reserve	189	218 (82-387)	1		4840 (4461-5287)	-	-	
		Mon Plaisir	21	170 (56-362)	1		5202 (4725-5727)	-	-	
		Gratte Fesse	8	295 (160-346)	1		5468 (5028-5719)	-	-	
		Mon Plaisir	4	3984 (3471-4622)	6.0 (5-7)	78	4578 (3471-4778)	-	-	
<i>pipilodryas</i>		Gratte Fesse	12	4142 (3144--5232)	6.0 (5-8)	110	4863 (3184-5232)	-	-	
	Full call	Morne Blanc	23	711 (368-1104)	1	152	2969 (344-1104)	144 (142-167)	4.0 (1-6)	2470-4484
		La Reserve	26	542 (56-1014)	1	79	2846 (2470-4095)	481 (320-647)	5.5 (3-10)	2384-4207
		Mon Plaisir	6	887 (187-391)	1	316	2792 (2583-3292)	50-60	4.9 (2-7)	2583-4052
		Gratte Fesse	2	1002 (1000-1003)	1		2528 (2130-4310)	81 (62-100)	4.5 (4-5)	2129-4427
<i>sechellensis</i>		Glacis Noir	1	1656	1	365	2730	142	9	2228
	Primary only	Morne Blanc	35	164 (68-280)	1	164	3141 (2220-4484)	102 (71-167)	-	-
		La Reserve	26	357 (56-763)	1	357	3274 (2962-3538)	500 (480-550)	-	-
		Mon Plaisir	11	311 (256-384)	1	311	2795 (2600-2905)	50-60	-	-
		Gratte Fesse	1	329	1	329	2652 (2203-4250)	59	-	-
<i>thomasseti</i>	Full call	Morne Blanc	14	4921 (1760-7624)	3.1 (2-4)	2749	1028-1918	500-600	9.3 (4-13)	976-2030
		Gratte Fesse	2	2342 (1902-2781)	2.0 (2)		1639 (1006-1954)	?	6.0 (5-7)	958-1855
	Primary only	Morne Blanc	9	1707 (48-1000)	1.8 (1-3)		1312 (968-1832)	200 (125-250)	-	-
		Mon Plaisir	3	1492 (981-2769)	4.7 (4-8)		1676 (1270-2220)	50 (30-71)	-	-

Diel variations in calling rates are shown in Fig. 5. *S. thomasseti* was only recorded at dusk (18:00hrs) and at night, *S. sechellensis* showed a crepuscular peak in calling rate but was active at all times, although only at low levels at night. *S. gardineri* and *S. pipilodryas* were largely diurnal.



**Fig. 5.** Diel variation in calling rates at different sites. Top to bottom: La Reserve, Morne Blanc and Mon Plaisir. *S. sechellensis* and *S. thomasseti* on left axis and *S. gardineri* and *S. pipilodryas* on right. Nighttime hours shaded.

### *S. gardineri*

There is little variation in these simple calls. Duration varies by 323 ms and calls are longest at the lower altitude sites (La Reserve and Gratte Fesse), due to few short calls. Frequency also follows an altitude pattern with lower frequency calls at lower altitudes, although this pattern is not statistically significant. There is no statistical correlation between frequency and duration.

In most sites there was no correlation of call duration or frequency with temperatures. At the high temperature site of Gratte Fesse call duration was correlated with temperature ( $y=98.06x-2138.8$ ,  $R^2=0.10$ ). Taking the data overall there is a correlation between temperature and duration ( $y=10.83x-52.18$ ,  $R^2=0.12$ ) and a much weaker correction between temperature and frequency ( $y=21.35x+4755.5$   $R^2=0.07$ ). Short, high frequency calls are produced in the cooler sites.

### *S. pipilodryas*

No significant differences were found in the two field sites occupied by this species. Although these calls sound superficially similar to those of *S. gardineri* (the latter lacks the characteristic repetition of *S. pipilodryas*) the primary notes are significantly shorter and lower frequency than those of *S. gardineri* (30-196 ms. compared to 64-387 ms and 3184-4863 Hz compared to 4472-5900 Hz), thus they are not simply a repetition of the *S. gardineri* call.

### *S. sechellensis*

Two types of call were recorded: single calls (lacking secondary notes) and full calls (one long primary call followed by one or more short secondary notes). Single calls were slightly longer than the primaries of full calls but did not differ significantly in terms of structure of frequency characteristics.

Full call duration was slightly longer at higher altitudes, with significantly longer primary calls. This is due to local temperature effects as total call duration was positively, but weakly, correlated with temperature ( $y=47.35x-598.7$ ,  $R^2=0.15$ ) and primary call duration strongly affected by temperature ( $y=35.77x-548.56$   $R^2=0.54$ ).

Call frequency (both for primaries and secondaries) was highest at Morne Blanc and lowest at Mon Plaisir, but variability was also greatest at Morne Blanc and a comparison of the two sites does not identify any significant differences. Frequency was also not correlated with temperature; frequencies were highly variable below 21°C

**Table 3.** Significant differences between sites, using two-tailed t-tests with unequal sample size and variance

t-test	Sites compared	Call characteristic	duration		
			T	df	P
<i>gardineri</i>	Mon Plaisir –Gratte Fesse	Duration	-3.7602	13	<0.05
	Mon Plaisir – Gratte Fesse	Frequency of primaries	-2.4228	11	<0.05
<i>sechellensis</i>	Mahe – Silhouette	Frequency of secondaries	9.2672	58	<0.001
<i>thomasseti</i>	Mahe – Silhouette		5.3834	23	<0.001



with very little variation above this temperature. The number of secondaries showed a clear altitude relationship, with the greatest number at the lowest sites, but this was not correlated to temperature. Pulse rate in the primary call did show geographic variation with 50-60 pulses per second at Mon Plaisir, 58-100 (mean 82) at Gratte Fesse, 142-167 (mean 144) at Morne Blanc, 320-647 (mean 481) at La Reserve and 142 on Praslin.

Single calls at Morne Blanc occurred at all hours, being predominant in the early morning (06:00-08:00hrs) and late afternoon (15:00-16:00) (Fig. 6). Between these times calls were scarce and multiple. At Mon Plaisir calling was more restricted, at 6:00 and 19:00, single calls dominated the former and formed 50% of the latter. At La Reserve singles were present throughout the survey, dominating at 15:00.

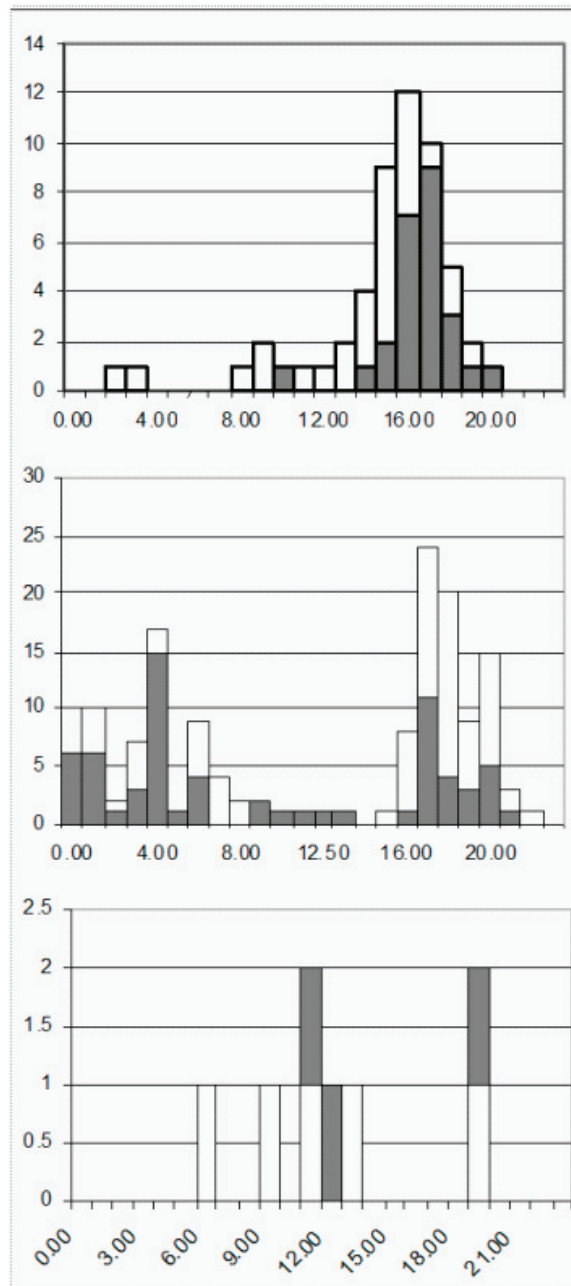
### *S. thomasseti*

The full call of this species recorded at Morne Blanc and Gratte Fesse. Calls lacking secondary notes were longer at Morne Blanc than at Mon Plaisir but not significantly so. Comparing isolated primaries with the primaries of full calls shows that full primaries are longer than the isolated calls. Primary frequencies of full calls are relatively low. The number of primaries is greatest in the full call.

Pulses in the primary notes varied from 30.3-250/second, with Mahé having 91-250 (mean 174.97) and Silhouette 30-71 (mean 49.67), suggesting that there is geographical variation in this feature although the available data are limited.

## **Discussion**

This analysis of sooglossid calls confirms previous descriptions for the four species (Nussbaum *et al* 1982; Gerlach & Willi 2002). Geographical variation in calls is very limited with some evidence of differences in call duration, frequency and the number of secondary calls in species with complex calls. However, characteristics such as pitch, repetition rate and duration are known to be affected by temperature and would therefore be expected to vary with local climate. The correlation with temperature was significant for duration, frequency and number of secondaries, but explained only a small proportion of the variance. This can probably be explained by the temperature data being recorded as ambient temperature for the site, and not temperature at the calling point (as has been the case for most studies: Zweifel 1959). If it had been possible to record temperatures at the exact calling point a more precise relationship may have been identified. Pitch and repetition rate are positively correlated with temperature (Wong *et al.* 2004) whilst duration and inter-call interval have negative correlations with temperature (Schneider 1974; Lingnau & Bastos 2007). Not all characteristics vary; pulses per call does not change (Schneider 1974) and these patterns are most apparent in advertisement calls, being obscured when frogs are duetting or chorusing (Wong *et al.* 2004). Therefore pulses may show more meaningful geographical patterns than pitch or timing. For *S. sechellensis* some geographical variation was found with distinct pulse rates on Silhouette (50-60 pulses/second), north Mahé (144) and south Mahé (448). The single call from Praslin had a value within the range of north Mahé (142). *S. thomasseti* was recorded at 175 pulses/second. Nussbaum *et al.* (1982) recorded similar values from north Mahé: 157-206 and 107-124 respectively.



**Fig. 6.** Proportions of single and multiple calls at different sites. Grey – multiple notes, white – primary note only. Top – La Reserve, middle – Morne Blanc, bottom – Mon Plaisir. Only full calls were recorded at Gratte Fesse.

The number of secondary calls in *S. sechellensis* could not be explained by temperature, although there was a significant negative correlation between altitude and the number of secondaries. Many frogs have different advertisement and territorial calls; in the case of *Rana clamitans* these have been divided into Type I “advertisement call” (Wells, 1978) and a longer call with less distinct harmonics (Ramer *et al.* 1983), the Type II “high intensity advertisement call” (Wells, 1978) or “territorial call” (Littlejohn, 1977). The Type I call is thought to be an advertisement call that enables location of calling individuals. The Type I is an agonistic signal to intruders (Ramer *et al.* 1983). Similarly to *Sooglossus sechellensis* and *S. thomasseti*, *R. clamitans* produces single- and multiple-note versions of its Type I calls. The multiple-note version varies from 2-5 notes, successively decreasing in amplitude (Ramer *et al.* 1983). The normal call is the Type I and this is almost the only call produced by small males (Ramer *et al.* 1983). Large males are more active callers than small males and produce most of the multiple-note calls (Ramer *et al.* 1983). In the single-note call the dominant frequency is negatively correlated with caller size, allowing size evaluation by intruders (Ramer *et al.* 1983) and seems to be an advertisement call revealing the location of a calling male. The multiple-note call is an agonistic version and is suggested to be used in non-directed calling by territorial frogs (Ramer *et al.* 1983). Distinct single- and multiple-note calls (2-10 notes) are also produced by the leptodactylid frog *Eupsophus emiliophuini*. Again, single-note calls predominate. These have a lower intensity than the advertisement calls (Penna *et al.* 2005) and are produced during short-range encounters between males, appearing to be agonistic (Penna *et al.* 2005). It appears that single-note calls are simple advertisement calls whereas multiple-note versions are used in close-range agonistic encounters. This is supported in *Sooglossus* by observations of captive frogs where males kept with females only produced single-note calls, and not the apparently agonistic multiple-note calls (pers. obs.). Courtship is generally simple, with females responding to the advertisement call, which conveys size information in its dominant frequency. Accordingly the number of multiple-note calls is expected to be related to population density, which is supported here by the greatest number of multiple-note *S. sechellensis* calls being recorded in the high density population of Morne Blanc. The number of secondary-notes or repeats is correlated with body size in at least some species (Richardson *et al.* 2010), making this a useful characteristic in size selection in agonistic encounters. This also means that locality differences in call repeats may be due to local differences in size or age of males. At Morne Blanc the number of secondary notes varied from 1-6 with a mean of 4.0, a higher number of notes was recorded at Mon Plaisir (2-7, mean 4.9). A higher number again was recorded at La Reserve (3-0, mean 5.5). This may indicate that males were larger (older) at lower altitudes than the higher altitude ones, which are dominated by younger males. This may be the result of greater breeding success at higher altitudes, giving a younger profile. Such a pattern is to be expected as wetter higher altitude conditions would result in longer breeding seasons and, hence, the potential for higher recruitment.

The only geographical variation in calls that could not be attributed to local differences in temperature or population age structure identified for any sooglossid was the pulse rate of the primary call in *Sooglossus sechellensis*. This formed three distinct

groups: Silhouette, north Mahé and south Mahé. A single call from Praslin grouped with those from north Mahe. It has been suggested (Taylor *et al.* 2010) that some frogs on Praslin had been introduced from Mahé, which may explain this result. These three call groups may reflect geographical isolation of the three populations (see Fig. 1), studies are currently underway to investigate the level of genetic isolation of these populations. Complexity of the call of *S. thomasseti* is comparable to that of *S. sechellensis* but data on that species is insufficient to determine whether or not there are geographical variations in calls of that species.

The lack of geographical pattern in the smaller sooglossid species (*Leptosooglossus/Seychellophryne*) is in marked contrast to some other species of frog where local variation in call is known (e.g. Wycherley *et al.* 2002). This may be due to as yet unexplored local temperature or demographic factors in these frogs, or may indicate a constrained aspect to the calls of small sooglossids. Their vocalisations are relatively simple, and extremely so in the stereotypical call of *S. gardineri*. Although durations and frequencies are variable they only vary by 440% and 11% respectively. One of the notable features of the Sooglossidae is that they lack middle-ears, thus the normal auditory pathway is absent. Sound transmission is thought to occur through the palate rather than through the (absent) ear (Boistel *et al.* submitted). This is most effective with high frequency sounds, with the size of the animal being negatively correlated to the detectable frequency. Accordingly the smallest species (*S. gardineri*) has the highest pitched and narrowest range call. This acoustic limitation may mean that almost all components of their calls are functional and cannot drift to produce geographical variation.

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