Distribution and status of the Seychelles frogs (Amphibia: Anura: Sooglossidae)

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The distribution and population densities of the Sooglossidae are evaluated. This family of frogs is endemic to the Seychelles islands where four species are restricted to high forests on the islands of Mahé and Silhouette. New distribution data are presented and habitat preferences quantified. Previously *Sooglossus thomasseti* was considered to be restricted to moss forest; here it is shown that the species is found in boulder fields, with the highest population densities in the moss forest zone, but occurs down to 80 m above sea level. *Sooglossus sechellensis* is also largely associated with higher altitudes, but suitable microclimates may occur at 300 m a.s.l. *Sooglossus pipilodryas* is restricted to palm-rich habitat on Silhouette island. *Sooglossus gardineri* is the most widespread and tolerant species and the only one to occur in degraded habitats. Monitoring methods are evaluated, with direct estimation from quadrats being the preferred method. All four species are considered Vulnerable due to their restricted ranges; S. thomasseti and S. sechellensis may also be threatened by habitat loss.

Key words: Mahé, monitoring, population, Sooglossus, status

INTRODUCTION

mphibian populations have been noted to be in decline over the past few decades because of habitat loss. More recently there has been an increase in the attention amphibian populations receive due to other causes of decline and their role as potential indicators of climate and ultraviolet radiation change. Dramatic declines have been identified in several species and recognized as a global phenomenon. The Global Amphibian Assessment classified 32.5% of amphibian species as threatened, with 43.2% experiencing some form of population decline (Stuart et al., 2004). The main causes of these declines have been identified as habitat loss or degradation, pollution and disease (Baillie et al., 2004). Enigmatic declines considered to be largely due to infection by chytrid fungi (Stuart et al., 2004) affect 17% of threatened species (Baillie et al., 2004). Many amphibians (22.5%) remain too poorly known for reliable assessment to be possible; these are considered Data Deficient (Stuart et al., 2004). The distribution of Data Deficient taxa reflects research effort, with the highest proportions being found in African countries. Research into amphibian populations is largely concentrated in a few areas of North America, Europe, South Africa and Australia. Given the widespread nature of the threat of sudden amphibian declines monitoring is needed across the geographical and ecotypic range of amphibians.

One of the amphibian families identified as having a higher proportion of threatened species than is expected by chance is the Sooglossidae (Baillie et al., 2004). This family currently comprises four recognized species endemic to the Seychelles islands. These islands are notable for being the most isolated island group to be inhabited by significant and diverse amphibian populations. Other oceanic island populations of amphibians exist, but these are restricted to a small number of species (e.g. Fiji with two endemic frog species). In contrast, the Seychelles are occupied by six species of caecilian, one introduced ranid frog (*Ptychadena mascareniensis*), one endemic hyperoliid (*Tachycnemis seychellensis*) and four species of the endemic frog family Sooglossidae. This family appears to be a Gondwana relict with distant relationships to the Nasikabatrachidae of India (Biju & Bossuyt, 2003), having been isolated on the Seychelles for some 65 million years. Frost et al. (2006) placed *Nasikabatrachus* in the Sooglossidae; however, this obscures the evolutionary history of these taxa and is not followed here, the Sooglossidae being restricted to the Seychelles. These form a monophyletic grouping comprising two genera (redefined in Meijden et al., 2007).

Sooglossid frogs are largely restricted to high forest on the islands of Mahé and Silhouette. Relatively little is known of the ecology of the four species. The first to be described was Sooglossus sechellensis (Boettger, 1896), a high-forest, tadpole-carrying species calling from the leaf litter. Sooglossus gardineri (Boulenger, 1911) is a more widespread species with direct development in terrestrial eggs. This leaf-litter dwelling species is one of the world's smallest frogs, with an adult size of 8.9-16.4 mm snoutvent length (Gerlach & Willi, 2002). Sooglossus thomasseti (Boulenger, 1909) is restricted to boulder fields and mist forest and was suspected to be extinct (Vesey Fitzgerald, 1947) until its relocation in 1976 (Nussbaum, 1984). It has since been recorded as "locally abundant" (Nussbaum, 1984). This is a nocturnal species that calls from boulders and low vegetation. It also has terrestrial eggs (Boistel, pers. comm.). The most recently described species, Sooglossus pipilodryas (Gerlach & Willi, 2002) is arboreal; nothing is known of its reproductive biology. Much of the literature discusses the phylogenetic relationships (Boettger, 1896; Boulenger,

Correspondence: Justin Gerlach, 133 Cherry Hinton Road, Cambridge CB1 7BX, U.K. E-mail: jstgerlach@aol.com 1906, 1909, 1911; Noble, 1926, 1931; Griffiths, 1959; Gorham, 1974; Duellman, 1975; Laurent, 1975; Biju & Bossuyt, 2003; Meijden et al., 2007) of the Sooglossidae, but only a small number of publications relate to their behaviour or ecology (Brauer, 1898; Honegger, 1966; Nussbaum, 1980, 1984; Nussbaum et al., 1982; Michell & Altig, 1983; Dodd, 1984; Gerlach, 2001) and none have addressed population size. The Global Amphibian Assessment categorized all sooglossids as Vulnerable (D2) on the basis of restricted ranges (IUCN et al., 2004) in the absence of any population or trend data. Since 1990 the distribution and populations of sooglossids have been investigated; the results of these studies are reported here with an evaluation of monitoring approaches for the family.

METHODS

Surveys were carried out between 1990 and 2006. Until 2000 surveys were opportunistic, recording frog populations during field work for other projects. In 2000–2005 a large number of field sites were visited during the Indian Ocean Biodiversity Assessment 2000–2005, for which frogs were recorded as part of a comprehensive biodiversity assessment of all Seychelles islands. Specific research on Sooglossidae was carried out from 1997 on Silhouette island. This forms the basis of monitoring method evaluations.

Distribution

Between 1990 and 2005 all localities where Sooglossidae had been reported were visited. In each locality records were kept of frog identifications from calls or from capture. In addition, searches were made for frogs outside these areas. All four species are easily identified by call (Nussbaum et al., 1982), with a single high-pitched note being produced by *S. gardineri*, *S. pipilodryas* producing a similar call but repeated 4–6 times, *S. sechellensis* having a deep croak with four rapid repeats, and a similar but more prolonged call being produced by *S. thomasseti* – this has the lowest dominant frequency and longest duration.

On Silhouette island the distribution of sooglossids was mapped on to a grid of 250×250 m squares. Within each of the 300 grid squares the following ecological variables were recorded: altitude, habitat type (categorized after Gerlach, 1998), estimated canopy cover, leaf-litter depth (measured to the nearest 5 mm at 10 random points), rock cover (estimated percentage) and vegetation. The habitat categories relevant to this study were mid-altitude forest (closed canopy forest at 100-350 m altitude), highaltitude forest (350-550 m), degraded high-altitude forest (as high-altitude forest but with invasive plant species forming at least 50% of mature trees), Pisonia forest (dominated by the tree Pisonia sechellarum) and moss forest (a hygrophilic forest type found above 550 m). Vegetation composition was quantified by random placement of ten 5×5 m quadrats in which all trees over 2 m were identified and recorded. Annual rainfall and temperature data were derived from meteorological office data for Mahé and unpublished data for Silhouette.

Comparisons were made between frog abundance and the density of different animal taxa in the leaf litter. Data for invertebrate abundance were collected as part of the Indian Ocean Biodiversity Assessment 2000–2005; collection methods are described in Gerlach (2003). All data were analysed as described below.

Calling behaviour

As sooglossids can be identified easily by their calls and this facilitates distribution mapping, the rate of calling (in this context the number of frog calls detectable in a given time period) is potentially useful in population estimation. This requires data on the frequency and variability of calling rates, and temporal and spatial variation. From July to September 1990 data on frog calls were recorded on Silhouette island at upper Jardin Marron during the Oxford University Silhouette Expedition 1990, and at the lower part of this site, and at Gratte Fesse, several times a year since 1997. The upper Jardin Marron and Gratte Fesse sites are 450 m above sea level and have constantly high humidity levels. In contrast the lower Jardin Marron site is 390 m above sea level and experiences strong seasonal changes in rainfall and humidity. The average number of calls of each species audible in 20 one-minute time periods was recorded at each site on five separate days. As S. pipilodryas and S. gardineri were not recognized as a distinct species until 2003, the 1990 data represent a combination of both species. At upper Jardin Marron the available data cover different times of day and night. Data were recorded separately for periods of rain and dry weather.

Population estimates

As sooglossids are small and cryptic in habits, populations were estimated using three approaches: quadrats, palm tree searches and acoustic survey. For direct estimation by quadrats, 1×1 m sample areas were used in all habitats occupied by Sooglossidae. Leaf litter was removed from a 10 cm band around the quadrat perimeter, and then each leaf was removed, starting from one corner. This systematic approach ensured that no frogs were overlooked or escaped from the quadrat before being detected. Twenty quadrats were used at each site. This method only sampled leaf-litter species and was supplemented by searches of trees. Arboreal sooglossids have only been located in the leaf axils of palms, and at each site 20 palms of each species (Nephrosperma vanhouetteana, Pheonicophorium borsigianum, *Verschaffeltia splendida* and *Roscheria melanochaetes*) were searched. Each interstice was examined by careful pulling down the leaf rachis. Quadrats provide a direct estimate of population density; for palm axils the number of frogs per palm could be converted to a density estimate by combination with the quantified habitat data.

Acoustic surveys were carried out using both line transect and fixed point methods. In line transects, all frogs heard along a path were recorded in 100 m sections, recording in each section lasting 5 mins. For the fixed point method, 10 fixed points were used at each site and the number of frogs heard in 10 one-minute sample periods recorded. In order to avoid over-estimation, frogs





Fig.1. Distribution of Sooglossidae overlaid on annual rainfall distribution (from Seychelles Meteorological Office and unpublished data). Light shading: 2000–2500 mm of rain; mid-shading: 2500–3500 mm; dark shading: >3500 mm. a) Sooglossus thomasseti; b) S. sechellensis; c) S. gardineri; d) S. pipilodryas.

Fig. 2. Distribution of Sooglossidae on Silhouette island. 100 m contour lines shown. a) Sooglossus thomasseti; b) S. sechellensis; c) S. gardineri; d) S. pipilodryas.

calling from approximately the same point were considered to represent a single individual unless calls overlapped or followed within 5 secs. Locating calling Sooglossidae in leaf litter is not practical as calling ceases when the area is approached or the leaf litter is disturbed, so no attempt was made to determine audible distance. Surveys were carried out in different months, allowing seasonal effects to be evaluated. Acoustic survey points were investigated at Jardin Marron and Mon Plaisir, Silhouette.

In order to determine the number of samples of the different survey methods required to produce consistent results a large number of quadrats and acoustic survey points were used at Mon Plaisir, Silhouette in July 2000. Two hundred acoustic survey points were used but due to the time investment required for quadrat sampling the sample size was limited to 40 quadrats.

Microhabitat selection

Microhabitat selection was investigated at Morne Blanc, Mahé by examining 10 randomly placed 5×5 m quadrats. These were divided into 25×25 cm squares and each subsample examined for sooglossids. The number of sooglossids in each subsample was recorded, producing a map of frog distribution in each quadrat. The plants and leaf-litter depth in each subquadrat were also recorded.

Population density (per hectare) in occupied forest habitats						
Mid-altitude forest	High-altitude forest	Degraded high- altitude forest	Pisonia forest	Moss forest	Altitude or range (m)	Area of occupancy (ha)
0	291.66±50.2	0	-	333.33±57.7	400–994	325
0	708.34±142.5	0	-	2040.82±498.0	450-950	696
166.67±45.7	3333.33±201.5	4285.71±1124.3	-	3040.81±455.0	200–900	1995
+	+	-	78.13±12.5	+	80-771	325
0	466.67±88.9	-	666.67±52.0	1800.00±181.2	250-771	417
454.45±33.2	888.89±329.3	-	166.67±21.5	844.45±316.4	200-771	603
1888.89±127.6	2000.00±356.6	-	0	83.34±42.0	125-600	418
	Populati Mid-altitude forest 0 0 166.67±45.7 + 0 454.45±33.2 1888.89±127.6	Population density (per Mid-altitude forest High-altitude forest 0 291.66±50.2 0 708.34±142.5 166.67±45.7 3333.33±201.5 + + 0 466.67±88.9 454.45±33.2 888.89±329.3 1888.89±127.6 2000.00±356.6	$\begin{array}{c c c c c c c c c c c c c c c c c c c $	Population density (per hectare) in occupied forest habMid-altitude forestHigh-altitude forestDegraded high- altitude forestPisonia forest0291.66±50.20-0708.34±142.50-166.67±45.73333.33±201.54285.71±1124.3-++-78.13±12.50466.67±88.9-666.67±52.0454.45±33.2888.89±329.3-166.67±21.51888.89±127.62000.00±356.6-0	$\begin{array}{c c c c c c c c c c c c c c c c c c c $	Population density (per hectare) in occupied forest habitatsMid-altitude forestHigh-altitude forestDegraded high- altitude forestPisonia forestAltitude o range (m)0291.66 \pm 50.20-333.33 \pm 57.7400–9940708.34 \pm 142.50-2040.82 \pm 498.0450–950166.67 \pm 45.73333.33 \pm 201.54285.71 \pm 1124.3-3040.81 \pm 455.0200–900++-78.13 \pm 12.5+80–7710466.67 \pm 88.9-666.67 \pm 52.01800.00 \pm 181.2250–771454.45 \pm 33.2888.89 \pm 329.3-166.67 \pm 21.5844.45 \pm 316.4200–7711888.89 \pm 127.62000.00 \pm 356.6-083.34 \pm 42.0125–600

Table 1. Altitude ranges, habitat associations and population density estimates from quadrats. + represents species presence but without quantification.



Fig. 3. Temporal variation of the number of frog calls (mean in 5-minute periods with standard error bars) and the effects of rainfall. a) Days with rain; b) days without rain. Bars represent 2-hour periods starting from midnight; black bars: night, grey: dawn and dusk, white: daylight.

Statistical analysis

Population densities were calculated directly from quadrat data. These were compared to call rates and to environmental variables by stepwise multiple linear regression. Microhabitat selection was evaluated by calculation of the negative binomial coefficient of aggregation. Correlation analysis was carried out for the location of clusters of frogs with leaf-litter depth and plant distribution.

RESULTS

Distribution and habitat

Distributions of the four species are shown in Figures 1 and 2. Altitude ranges and habitat associations are summarized in Table 1.



Fig. 4. Number of sooglossid frog calls per 5-minute period along two representative transects.

Microhabitat selection

Only *S. gardineri* was encountered in sufficient numbers in quadrats for aggregation to be investigated. They were not distributed randomly in the quadrats (χ^2 =583.029; P_{419} <0.001), the coefficient of aggregation indicates a high degree of aggregation (negative binomial coefficient of aggregation *k*=0.051). These aggregations were small (a maximum of four individuals in a 25 × 25 cm subquadrat) and clustering in patches of deeper leaf litter (*r*=0.865, $t_{0.05,419}$ =2.228, *P*<0.001). This patchy distribution was also apparent in the broader distribution of calling frogs (Fig. 2), associated with topographical features.

Calling behaviour

Calling rates are shown in Figure 3. All species call more frequently in wet weather, even in the upper Jardin Marron site where humidity remains above 85% at all times. All species are active at all times of day and night, but *S. gardineri* and *S. pipilodryas* are predominantly diurnal, with early morning peaks in activity. *Sooglossus sechellensis* is largely crepuscular and *S. thomasseti* nocturnal. Local factors had a strong effect on call rates as indicated by variation along transects; examples of this are shown in Figure 4.

Population estimation

Data from direct estimation by quadrats are summarized in Table 1. Repeat sampling at the same site in different months produced no significant differences in population estimates in high-forest sites (over 450 m above sea level). Lower altitudes showed seasonal variations; seasonal and annual changes in population density estimates are shown in Figure 5. Repeat audio sampling resulted in clear differences, corresponding to rainfall levels (Fig. 3). The effects of sample size on frog density in quadrats and call rates are shown in Figure 6.

Relationship to other factors

The significant results of multiple regressions are shown in Table 2.

DISCUSSION

An important aspect of the present study was the evaluations of different monitoring methods. Such investigations are essential prerequisites for the development of reliable long-term monitoring (Corn et al., 2000; Hsu et al., 2005). The quadrat method employed in this study provided direct estimation of population densities. These are considered to be effective for sooglossids in leaf litter and in palms. Most of the seasonal changes in abundance detected at low-altitude sites probably do not reflect real changes in abundance but rather frogs moving from easily sampled leaf-litter layers into the more climatically stable root-mat, and for the lower-altitude sites survey data from the wet season of December-March are considered most reliable. Most S. thomasseti occur under boulders and could not be sampled directly; this species remains under-sampled due to its behaviour and microhabitat preferences. Audio transects provide a method of assessing abundance of inaccessible frogs over a large area and in all habitats. In the absence of data on audible

Table 2. Significant stepwise multiple regression results of the effects of habitat (tree abundance) or invertebrate abundance on the population density of sooglossids. Only significant results are shown (most plant and invertebrate species had non-significant associations with frog abundance).

HABITAT						
Island	Species	Factor	Coefficent	Standard deviation	<i>t</i> (1)	Р
Mahé	S. sechellensis	K	-306.770	152.022	-2.018	0.083
		Colea	1375.952	186.983	7.359	< 0.001
		altitude	1.443	0.403	3.577	0.009
Silhouette	S. thomasseti	Κ	-16.194	14.990	-1.080	0.316
		Glionnetia	3.490	0.434	8.047	< 0.001
		palms	9.768	2.347	4.162	0.004
	S. sechellensis	Κ	-820.220	385.220	-2.129	0.066
		altitude	3.755	0.855	4.394	0.002
	S. pipilodryas	Κ	-487.104	123.315	-3.950	0.005
		palms	258.595	20.185	12.811	< 0.001
INVERTEBRA	TES					
Mahé S. tho.	S. thomasseti	Κ	2.185	11.856	0.184	0.859
		Amphipoda	1.245	0.120	10.408	< 0.001
		Hirudinea	21.754	4.248	5.121	0.001
	S. sechellensis	Κ	99.654	226.411	0.440	0.671
		Mollusca	56.293	17.396	3.236	0.012
	S. gardineri	K	248.677	121.638	2.044	0.080
		Amphipoda	12.847	1.227	10.470	< 0.001
		Hirudinea	128.043	43.579	2.938	0.022
Silhouette	S. thomasseti	Κ	12.754	22.503	0.567	0.586
S. S.		Hirudinea	17.993	6.125	2.938	0.019
	S. gardineri	Κ	68.368	125.476	0.545	0.603
	0	Hirudinea	155.785	30.503	5.107	0.001
		Lepidoptera	5.262	1.914	2.750	0.029
	S. pipilodryas	К	-266.571	119.835	-2.224	0.061
		Chelicerata	12.998	2.122	6.125	< 0.001
		Hymenoptera	4.767	0.785	6.076	< 0.005

distance, acoustic sampling does not provide a density estimate, but may act as a useful index of abundance or activity for sooglossids (Nussbaum et al., 1980). The reliability of audio methods of detection or population estimation depends on frogs calling at a constant rate whenever surveys are carried out. Reproduction (and hence, it can be assumed, calling) occurs throughout the year in all the species (as indicated by date of breeding cited in Brauer, 1898 and Nussbaum, 1980, 1984). As previously noted (Nussbaum, 1984), calling rates increase during rainy weather; they are highly dependent on weather conditions, with too much temporal variation to allow reliable evaluation. Use of an audio monitoring system based on fixed points could be practical with certain limitations. Due to the great temporal variation in call rate, monitoring fixed points would have to cover a wide time range. Firstly each data point would have to be based on an automated recording system over at least a 24-hour period and sampling points would have to be spread over several days across the seasonal range. Alternatively, sampling could focus on the peak of breeding activity in the normal wet season (December-March). Further limitations to auditory recording are imposed by the microhabitat preferences of all the species. The highly

patchy distribution of sooglossids requires all sampling methods to cover a high number of samples, distributed over a wide area. The large number of samples used in the present study indicates that in order to produce reliable indices at least 70 audio points would be required at each field site. This approach appears to be the most reliable for use with these non-aquatic frogs, the Sooglossidae being completely independent of standing or running water, requiring only damp habitats for survival and reproduction. Whilst these methods are effective in an environment with only a small number of easily identifiable species they may prove unreliable in regions where there are identification issues or highly patchy distributions (such as in species with stream or pond breeding congregations).

Sooglossus thomasseti has been considered to be the rarest sooglossid species, restricted to "the moist, middle and high elevation forests" (Nussbaum et al., 1980). The present study found the species to be widespread above 400 m, although most abundant over 600 m. There is an exceptional low altitude locality at 80 m above sea level (Boistel, pers. comm.). This is a boulder field connected to the main high-altitude range for the species. *S. thomasseti* is found at moderately high densities in high-altitude and

Species	Population estimate		А		
	Mahé	Silhouette	Mahé	Silhouette	Total
S. thomasseti	?	25,422±4063	325	325	650
S. sechellensis	?	34,256±5514	696	417	1113
S. gardineri	?	424,679±110,699	1995	603	2598
S. pipilodryas	-	636,637±33,381	-	418	418

Table 3. Population estimates and distribution ranges for Sooglossidae based on population density calculations and the area occupied by each species.

moss forests on Mahé (Table 1); it has not been found in degraded habitats. Although a greater altitude range has been found on Silhouette than on Mahé, recorded population density is lower. The population estimates for this species are probably unreliable due to its nocturnal habits and boulder associations.

S. sechellensis was considered by Nussbaum et al. (1980) to be more widespread and abundant than *S. thomasseti*, although there is little difference in their ranges. Most localities for this species are above 500 m above sea level. It can occur at lower altitudes in suitable habitat patches. *Sooglossus sechellensis* is recorded at higher densities than *S. thomasseti*; population densities on Mahé and Silhouette are not significantly different.

Sooglossus gardineri has always been reputed to have the greatest altitude range, being found above 200 m (Nussbaum et al., 1980) on Mahé and Silhouette islands (although this is contradicted by the exceptional low-altitude *S. thomasseti* record). All reports of *S. gardineri* calls below 200 m appear to be attributable to superficially similar sounding crickets. On Mahé this species appears

to be tolerant of a wide range of habitats and high population densities are found in all forest habitats; it is the only species present in degraded habitats. On Silhouette there appears to be a preference for mid-altitude forest, with comparatively low densities at higher altitudes. A similar altitude range is found in S. pipilodryas but this species is closely associated with palm trees and is restricted to sites with high palm densities. On current data this is the only single-island endemic sooglossid, being restricted to Silhouette. It is largely found in palm axils and its distribution correlates with the distribution of humid palm rich habitat. This habitat is widespread on Silhouette, but palms are comparatively scarce on Mahé. It is possible that the species was present on Mahé before palms were displaced by invasive plants and that a relict population may exist undetected on the island.

Altitude is probably only an approximate indicator of factors controlling the distribution of these species, with microclimate and microhabitat effects being more important. This would explain how *S. sechellensis* is able to occur in bracken habitat at 300 m above sea level on Sil-



Fig. 5. Population densities at Jardin Marron (390 m) and Mon Plaisir (500 m), Silhouette, in dry and wet seasons from 1995 showing the seasonal and annual variation at the lower-altitude site. Wet season rainfall is 179–610 mm per month, dry season 50–250 mm (except 1997–1999 when dry season rainfall was 12–32 mm). Bold line: dry season; thin line: wet season.



Fig. 6. The effect of sample size on population estimation and call rates. a) Call rate; b) density estimates from quadrats.

houette in sheltered, highly humid river valleys, while S. thomasseti occurs as low as 80 m in one boulder field. Sooglossus thomasseti abundance does not correlate with any of the habitat factors measured (being associated with boulder fields, which were not quantified) on Mahé, although it is associated with palms and the tree Glionnetia sericea on Silhouette. The latter is a mist forest species and this association may be due to a preference for mist-forest habitats, whilst palms are particularly abundant in boulder fields (pers. obs.). Sooglossus sechellensis is correlated with altitude and Colea seychellarum trees, although this is probably an artefact of the high-altitude distribution of this plant. C. seychellarum is very scarce on Silhouette, and no significant association was detected other than altitude on that island. Sooglossus gardineri is widespread with a wide habitat and altitude tolerance; accordingly it is to be expected that no clear habitat correlation would be detected. Sooglossus pipilodryas has a similarly predictable strong association with palms.

Population densities were correlated with the abundance of leeches for *S. thomasseti* and *S. gardineri*. On one occasion the normally molluscivorous leech *Mahebdella miranda* was observed on a *S. gardineri* (Congo Rouge, Mahé – pers. obs.), and the leech population may be partly associated with frog abundance. The abundances of these two frog species and amphipods were also correlated; amphipods have been found in the diet of *S. gardineri* (Mitchell & Altig, 1983). As the introduced talitrid amphipod *Talitorides alluaudi* is restricted to Mahé, at present no such association occurs on Silhouette. *Sooglossus sechellensis* is associated with Mollusca, but again this may be due to peaks of mollusc abundance in the altitude zone occupied by *S. sechellensis* rather than any dietary connection. Associations between *S. gardineri* on Silhouette and moth larvae abundance, and between *S. pipilodryas* and spiders and ants, may have a dietary basis; there is some evidence in support of this from dietary studies of the former (Mitchell & Altig, 1983; Gerlach, 2001).

The main habitats in which sooglossids are found are relatively stable climatically. The lower altitude areas are affected by seasonal changes in rainfall and these populations may be under pressure in extremely dry years. This was reflected in the absence of calling sooglossids in mid-altitude forests in the dry season of 1997–1999. It has been noted that during the wet season normal activity levels of *S. gardineri* were recorded in all areas, but *S. sechellensis* was slower to recover (Gerlach, 2000). This is reflected in the population monitoring reported here for *S. gardineri* and *S. sechellensis* at Jardin Marron, Silhouette. Only long-term monitoring will identify whether these are natural periodic fluctuations or indicators of vulnerability to climate change.

The population densities estimated in the present study indicate that substantial populations of all species are present. Total population sizes cannot be estimated directly from the data as the high forests on Mahé represent mosaics of high quality and degraded habitat. Thus, although the range of S. sechellensis includes 14 hectares of contiguous high forest in the Morne Blanc area of central Mahé, it is actually present in quantifiable numbers in only 4.5 hectares. The precise distribution of significant populations could be determined from mapping at a 250 m scale or approximated from the distribution of primary high-forest habitat, determined from high resolution aerial surveys or satellite imagery. The necessary mapping has not been carried out to date. The fine-resolution surveys on Silhouette allow more precise population estimates (given in Table 3).

Despite the high population densities all sooglossids can be categorized as Vulnerable due to their restricted ranges (IUCN et al., 2004). The widest range is that of S. gardineri; although this is greater than the 20 km² criterion of the IUCN Red List (IUCN, 2001), at only 26 km² and only two separate populations, the species can still be considered Vulnerable (criterion D2). The other sooglossids all qualify for Vulnerable status on the basis both of numbers of populations and ranges (the greatest area of occupancy being S. sechellensis at 11 km²). Being a single island endemic, S. pipilodryas is the most restricted, with an extent of occurrence and area of occupancy of only 4.2 km². The preservation of the endemic species of the family Sooglossidae requires the protection of their forest habitats. Substantial parts of the range of the Mahé Sooglossidae receive legal protection within the Morne Seychellois National Park. However, in this area habitat degradation due to invasive plant species is increasing (pers. obs.). This poses a threat to S. sechellensis and S. thomasseti and active habitat management is required in order to safeguard these species. Monitoring of habitat change and sooglossid fine-scale distribution is required before the impacts of habitat change can be fully quantified. Habitats are more stable on Silhouette island (Gerlach, 2004), but the island currently receives no legal protection.

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