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Distribution, variation, and systematics of the Seychelles treefrog, *Tachycnemis seychellensis* (Amphibia: Anura: Hyperoliidae)

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(With 2 plates and 3 figures in the text)

The endemic Seychelles treefrog, *Tachycnemis seychellensis* (Duméril & Bibron), is restricted to four of the granitic islands of the Seychelles: La Digue, Mahé, Praslin and Silhouette. *Megalixalus infrarufus* Günther 1869 is a junior synonym of *Eucnemis* (*Tachycnemis*) *seychellensis* Duméril Bibron, 1841. Significant variation in colour and morphometric characteristics exists within and between island populations. The patterns of geographic variation revealed support the hypothesis that the distribution of *Tachycnemis seychellensis* in the granitic Seychelles reflects vicariance through fragmentation of the Seychelles Microcontinent 10,000 years B. P. by marine transgression. However, the possibility of low rates of postfragmentation dispersal between islands cannot be ruled out. The close relationship of the nearby Mahé and Silhouette populations probably reflects prefragmentation gene flow over relatively short distances and postfragmentation stasis due to large population size and similar environments. The small body size and colour similarities of the Praslin and La Digue populations may result from prefragmentation gene flow between these close populations, but the relatively great differences in morphometric traits suggest rapid divergence in isolation perhaps as a result of genetic drift and strong selection. It is argued that the four island populations represent a single species and that subspecies should not be named.

Contents

Introduction

The islands of the Republic of Seychelles fall into three groups: coralline, raised coral reef and granitic islands. The young, low and relatively dry coralline and raised coral reef islands do not have amphibians, but the ancient granitic islands support an amphibian fauna of 11 species (six caecilians, five frogs), 10 of which are endemic. The Mascarene frog, *Ptychadena mascareniensis*,

widespread in Africa, Madagascar, and other islands of the western Indian Ocean, is the only non-endemic Seychellean amphibian (Nussbaum, 1984, 1985).

The Seychelles treefrog, *Tachycnemis seychellensis*, occurs on the four largest granitic islands in the Seychelles, La Digue, Mahé, Praslin and Silhouette (Nussbaum, 1985). It is the sole representative of the family Hyperoliidae in the Seychelles, and it represents the easternmost limit of the range of the family, which is most diverse in Africa (19 genera, 231 species) and occurs elsewhere only in Madagascar (one genus, seven species). *Tachycnemis* is reportedly monotypic, and its phylogenetic and biogeographic relationships are obscure (Nussbaum, 1980, 1984; Drewes, 1984). Dubois (1981) summarized the nomenclatural history of the Seychelles treefrog. Channing (1989) placed *Tachycnemis* in a monogeneric subfamily, Tachycneminae, of the Hyperoliidae.

Early descriptions of the Seychelles treefrog by Duméril & Bibron (1841), Günther (1859, 1869), and Boulenger (1882) were brief, largely non-comparative and based entirely on preserved material. Reports of dorsal coloration vary from "brun marron" (Duméril & Bibron, 1841: 527), "brown or greyish, marbled with brown" (Günther, 1869: 89) to "uniform green" (Günther, 1859: 485) and "greenish" (Boulenger, 1882: 128). More recent reports (e.g. Honneger, 1966) based on living specimens indicate that these frogs are bright green. The discovery that treefrogs on Mahé are sexually dichromatic, with brown males and green females (Nussbaum, 1984), and that treefrogs on Praslin differ less in coloration between the sexes and have dorsal spotting (unpubl.), raised questions about the taxonomic status of the island populations of Seychelles treefrogs. Furthermore, the status of *Megalixalus infrarufus* Günther, described in 1869 and synonymized with *Tachycnemis seychellensis* by Boulenger (1882) without explanation, needs to be re-evaluated.

In this paper, we assess the taxonomic significance of inter- and intra-island variation in morphometric and colour characters of the Seychelles treefrog and discuss the biogeographic significance of the results.

Methods and materials

Discrete breeding populations were sampled on all 4 islands where treefrogs are known to occur. A single population was sampled on each of the 3 smaller islands, La Digue, Praslin and Silhouette, whereas 2 populations (MGR and MMA) were sampled on Mahé, the largest island, for a total of 5 populations. Two populations were sampled on Mahé to allow us to assess the relative magnitude of intra- versus inter-island variation. The La Digue population occurs on the plateau behind Anse La Réunion, 3–10 m above sea level in highly disturbed marsh habitat. The Praslin population is situated in the drainage of the Nouvelle Decouverte River at 170 m elevation, near the entrance of the Vallée de Mai. The site is an intermittently dry spring head in disturbed palm forest. The MGR population on Mahé occurs at the 400 m contour on the Riviere Grand Bois. The site is a permanent, swift rocky stream with an overstorey of tall rainforest trees. The site is being encroached by tea plantations. The MMA site on Mahé is at Mare aux Cochon, which lies at 400 m elevation. The microhabitat is a slow-moving, sandy bottomed, permanent stream flowing through a highly modified forest of largely introduced tree species. The canopy is low and frequently interrupted by human disturbance. The Silhouette population occurs at Mare aux Cochon (not to be confused with Mare aux Cochon on Mahé, also sometimes known as Scott Vale). The site is a high (375 m) valley once developed for agricultural use, but now abandoned. The original vegetation would have been middle elevation rainforest, but now consists of introduced species including cinnamon, jack fruit and albizzias. The frogs occur along a slow-moving stream and in a system of abandoned irrigation ditches.

Females were exceedingly difficult to find, causing us to pool the females from the 2 Mahé populations along with 5 other females from nearby sites on Mahé for statistical comparisons to females on other islands.

The 2 populations of Mahé males were always treated separately. Individuals were collected mostly at night, killed in chlorotone, fixed in buffered 10% formalin, washed in water to remove the formalin, and transferred to 65% ethanol. Liver and muscle were removed and frozen for molecular studies to be reported elsewhere.

The dorsal colour of live treefrogs was recorded in the field, and lateral and ventral coloration were scored for each preserved specimen.

A few frogs have completely smooth dorsal skin, but most have tubercles variously expressed. We recorded the percentage of individuals in each population with dorsal skin tubercles on the eyelid, head, body and tibial segment.

Longitudinal grooves may occur medially on the finger and toe discs, running from the tip of the disc proximally for one-half to two-thirds the length of the disc. The number of fingers and/or toes that have grooved discs varies from complete absence in some individuals to present on all discs in others; they are most likely to occur on the outer digits. Individuals with at least one disc groove were scored positive for discs present.

Grooves may occur on the subarticular tubercles of the digits of the manus. If they occur, they are restricted to the largest subarticular tubercle on each digit, which is the one at the joint between the 2 proximal phalanges. This large tubercle may be either oval-shaped and entire or oval-shaped and divided with a longitudinal groove. The presence or absence of subarticular grooves was recorded for each individual.

Measurements in millimetres were taken from alcoholic specimens using dial calipers. The following 23 measurements and tooth counts were recorded for each specimen. SVL, snout-vent length, from tip of snout to end of urostyle; PMT, number of premaxillary teeth (right + left); HL, head length, tip of snout perpendicular to line connecting angles of jaw; HW, head width between angles of jaw; INW, internarial width; IOW, interorbital width, shortest distance between eyelids; END, eye to nostril distance, anterior edge of eye to centre of external naris; ED, eye diameter; ELW, upper eyelid width; TW, tympanum width; TH, tympanum height; FAL, forearm length, proximal end of radius to base of internal metacarpal tubercle; ML, manus length, base of internal metacarpal tubercle to tip of third finger; FL1, length of first finger (thumb), from base of first subarticular tubercle to tip of thumb; FL2, length of second finger, base of first subarticular tubercle to tip of third finger; FL3, length of third finger, from base of first subarticular tubercle to tip of third finger; FD3, diameter of disc on tip of third finger; THIL, thigh length, from cloacal opening to knee joint; TIBL, tibia length, from knee joint to tibiotarsal-metatarsal joint; TARL, tarsus length, from tibiotarsal-metatarsal joint to proximal tip of inner metatarsal tubercle; PL, pes length, from proximal tip of inner metatarsal tubercle to tip of fourth toe; TD4, diameter of disc on tip of fourth toe; and MTL, length of metatarsal tubercle.

Males and females were treated separately for statistical comparisons. Both univariate and multivariate comparisons were made. A *t*-test was used to compare body size (snout-vent length) between populations. Because many of the morphometric characters are dependent on body size, univariate comparisons between populations are based on size-adjusted means using snout-vent length as the independent variable in the analysis of covariance. Pearson chi-squared tests were used to compare sexes and populations for categorical variables. Multivariate comparisons of sexes and populations were done using linear discriminant functions and canonical variate analysis. All statistical analyses were done with SYSTAT for IBM compatible microcomputers and with MIDAS, the statistical program of the Computing Center of the University of Michigan.

Attribution of names

There are two names available for Seychellean hyperoliid treefrogs: *Eucnemis seychellensis* Duméril and Bibron, 1841 and *Megalixalus infrarufus* Günther, 1869. Boulenger (1882) synonymized the latter with the former, and since then a single species of treefrog has been

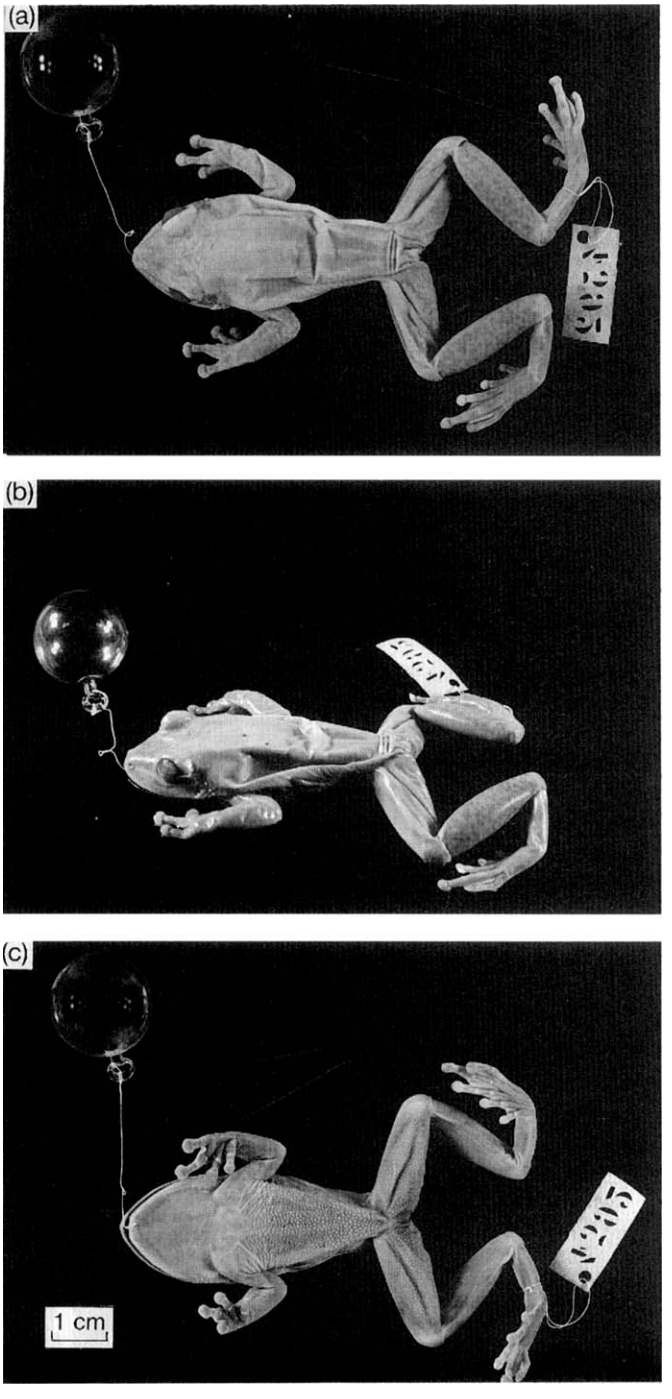

PLATE I. Syntype (MNHNP 4592) of *Tachycnemis* (*Eucnemis*) *seychellensis* (Duméril and Bibron, 1841) in (a) dorsal, (b) lateral and (c) ventral views.

recognized in the Seychelles. However, Boulenger gave no explanation for his actions, and the systematics of Seychellean treefrogs has not been addressed since Boulenger's (1882) treatment. The types of the two nominal species apparently have never been illustrated nor directly compared.

We had the opportunity to compare the available types through the generosity of curators of the British Museum (Natural History) (BM) and the Muséum National d'Histoire Naturelle, Paris (MNHNP). Two syntypes (MNHNP 4592-3) of *Eucnemis seychellensis* are on record, but only one (4592) was available for examination, the other apparently has been lost (pers. comm., D. Payen). The type locality of *E. seychellensis* is "îles Seychelles", and hence the island of origin is unknown. Although Günther (1869) mentioned only one specimen in his description of *Megalixalus infrarufus*, Boulenger (1882) listed two types, a female and a juvenile, for this taxon. These are currently BM 1947.2.9.80-1, both of which we examined. Günther (1869) indicated that the origin of the specimen(s) upon which his description of *M. infrarufus* was based was unknown. But, he later (Günther, 1870) noted that the locality is Mahé, Seychelles.

The remaining syntype of *Eucnemis seychellensis* (MNHNP 4592) is soft and bleached (Plate I). The colour pattern is almost completely lost. Pale lip and upper eyelid lines can still be seen, and some faint mottling (possibly artefactitious) is present on the dorsal surface of the forelimbs and the tibiofibular segment of the hindlimbs. The dorsum is smooth. The ventral surface of the body posterior to the line between the forelimbs is granular as are the lower lateral surfaces of the body and thighs. There is an isolated patch of granular skin at the angle of each jaw. The specimen is a female of mature size (gonads not examined) with the following measurements (mm): snout-vent length, 55·9; snout to angle of jaw, 17·5; head width at angles of jaw, 21·1; interorbital distance, 10·1; internarial distance, 4·3; eye length, 6·9; maximum tympanum diameter, 2·2; length of proximal (humerus) segment of forelimb, 10·7; length of radioulnar segment of forelimb, 12·4; hand length (to tip of longest toe), 15·3; length of proximal (femur) segment of hindlimb, 24·4; length of tibiofibular segment of hindlimb, 28·6; tarsal segment length, 17·6; foot length (to tip of longest toe), 22·5.

The largest of the two syntypes of *Megalixalus infrarufus* (BM 1947.2.9.80) is badly dried with incisions in the left sacral and pectoral areas (Plate II). The dorsum is purplish gray with no spots or tubercles. The ventral surfaces are orange-tan with the chin and throat somewhat lighter in coloration than the body. The ventral surfaces are granular like the syntype of *Eucnemis seychellensis*, but the granulation is less distinct, perhaps because of the dried condition. The margin of the upper jaw is white, the white line extending posteriorly to the insertion of the forelimbs. The upper eyelid has a thin white line. The dorsal surfaces of the digits are orange-tan like the venter. The specimen is a mature female with the following measurements: snout-vent length, 65·4; snout to angle of jaw, 21·9; head width at angle of jaw, 24·2; interorbital distance, 12·9; internarial distance, 5·2; eye length, 8·7; tympanum diameter, 2·8; length of humeral segment of forelimb, 12·1; length of radioulnar segment of forelimb, 13·0; hand length, 17·5; length of proximal segment (femur) of hindlimb, 31·3; length of tibiofibular segment of hindlimb, 30·9; tarsal segment length, 17·3; foot length, 25·5. The second syntype (BM 1947.2.9.81) is a juvenile (svl = 24·5 mm). It conforms in details of morphology to the adult and differs only slightly from the adult in colour. The specimen is similar in every way to other juveniles of this species collected by us.

Detailed direct comparison of these types, including examination of the webbing and other structures of the hands and feet, revealed no significant differences. There is no doubt that the types represent a single species, *Eucnemis* (*Tachycnemis*) *seychellensis* having priority.

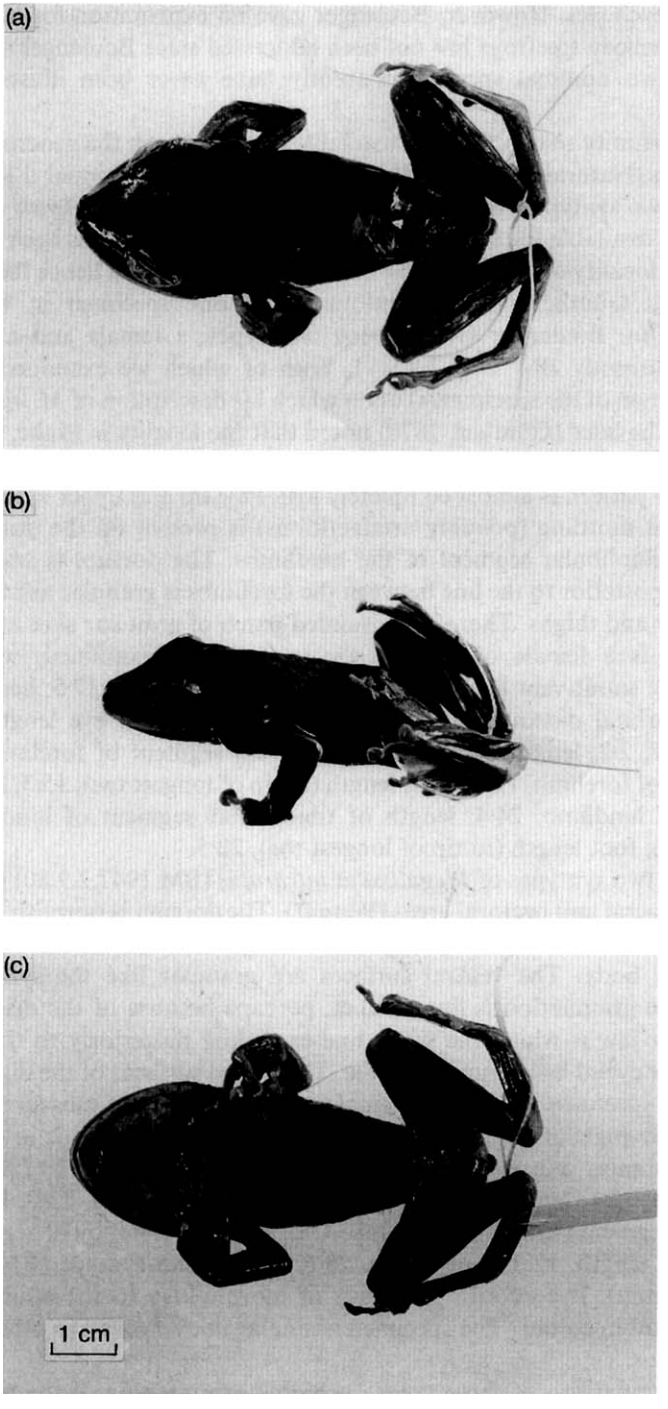

PLATE II. Syntype (BM 1947.2.9.80) of *Megalixalus infrarufus* Günther, 1869 in (a) dorsal, (b) lateral and (c) ventral views.

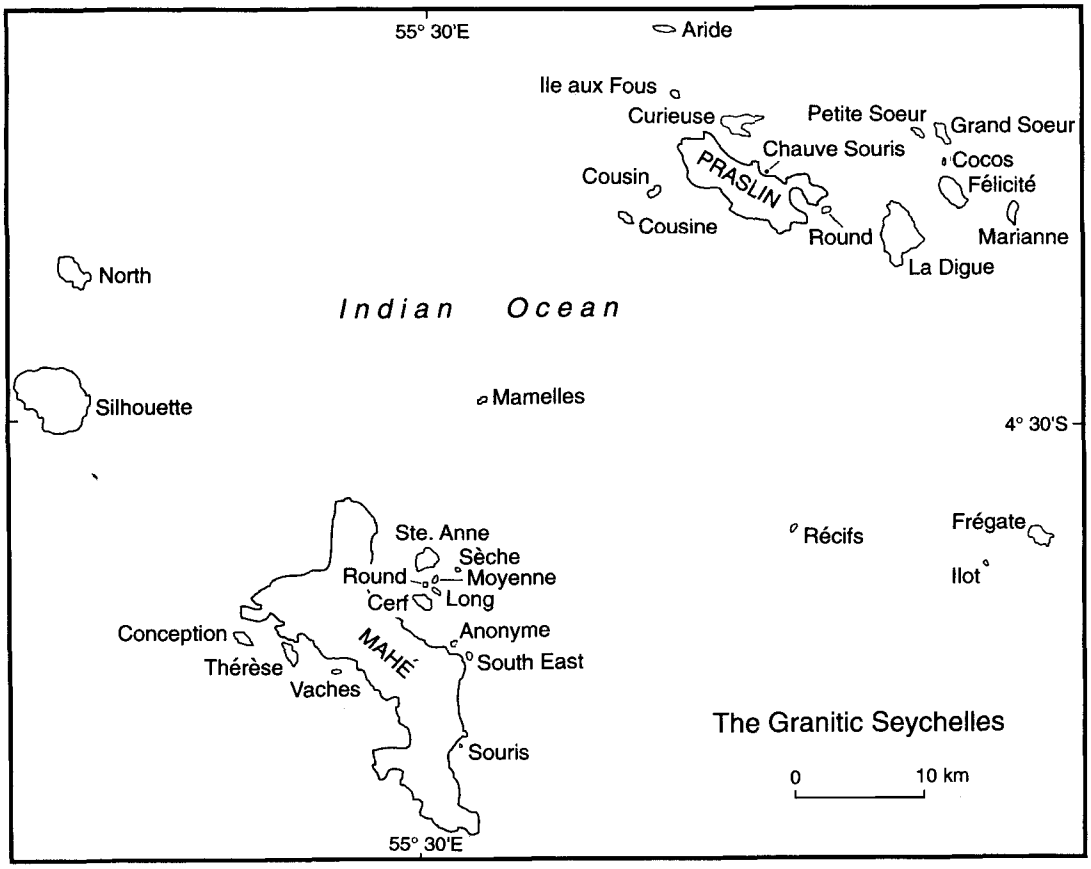

FIG. 1. Map of the granitic islands of the Seychelles Archipelago. *Tachycnemis seychellensis* occurs on only four islands: Mahé and Silhouette (south-western region) and La Digue and Praslin (north-eastern region).

Distribution

The senior author visited the Seychelles 18 times from 1976 through 1991 visiting almost all of the nearly 100 islands at least once. Careful diurnal and nocturnal searching yielded no *Tachycnemis seychellensis* (nor any other amphibian species) on any of the coralline islands, nor on any of the raised coral reef islands. All of the larger granitic islands and most of the smaller granitic islands were thoroughly surveyed for amphibians and reptiles. A few smaller granitic islands were visited only briefly, but these islands consist largely of barren rock with little vegetation, and they have no standing or flowing fresh water. It is highly unlikely that amphibians, especially those with a larval stage such as *T. seychellensis*, could survive on these small, rocky islands. Given the intensity of the herpetofaunal surveys, it is virtually certain that *T. seychellensis* is restricted to the four largest islands of the granitic group. These four islands form two groups: Mahé and Silhouette in the south-western and La Digue and Praslin in the north-eastern portion of the granitic islands (Fig. 1).

Colour variation

Dorsal coloration

Sexual dichromatism of dorsal coloration occurs within populations, and the pattern of sexual colour difference varies between islands. The most striking sexual dichromatism occurs in populations on Mahé. In these populations, living males are brown dorsally without spotting, and living females are bright green dorsally, also without spotting. Frogs in captivity may change colour, with males becoming very light brown, or even light yellowish green, and females lightening to yellowish green. On Silhouette, freshly caught frogs of both sexes are usually green without spots. However, a single male, of more than 100 observed, had pale dorsal spots similar to the pattern observed on most males from Praslin (below). Silhouette females are a darker shade of green than the males. On Praslin, females are bright green without spots, and males vary from brownish green to yellowish green with or without pale yellowish or white dorsal spots. Among a sample of 86 males observed in a breeding aggregation at night, the dorsal coloration of 13 (15%) was brownish green with no or few spots; 33 (38%) were yellowish green with no or few spots; 38 (44%) were yellowish green with many spots: and 2 (2%) were yellowish green with dense spotting. On La Digue, females observed undisturbed at night were green without spots, and males were uniformly light greenish brown to light green. A few males on La Digue had a few pale dorsal spots similar to some Praslin males, but the number of spotted males on La Digue is far fewer than on Praslin.

TABLE I

Variation in lateral coloration of preserved ***Tachycnemis seychellensis****; percentage of individuals in each category*

	Category[1]			Sample size
	1	2	3	
Males				
La Digue	82	18	–	17
Mahé (MGR)	33	30	37	30
Mahé (MMA)	13	40	47	30
Praslin	73	23	3	30
Silhouette	47	40	13	30
Females				
La Digue	100	–	–	4
Mahé	11	22	67	9
Praslin	80	–	20	10
Silhouette	29	43	29	14

[1] Category 1—light yellowish pink lateral stripe from axilla to groin, with irregularly shaped dark greenish brown spots within the stripe forming a more-or-less continuous lateral band within the light stripe.
Category 2—like category 1, but with only a few light brown flecks within the light stripe, never forming a dark lateral band within the light stripe.
Category 3—dark dorsal colour fades gradually to the lateral light brown colour and then to the ventral pale yellowish pink colour.

Lateral coloration

Chi-squared tests indicate there are significant differences in lateral coloration among island populations of both males ($P < 0{\cdot}001$) and females ($P = 0{\cdot}004$). A high percentage of La Digue specimens, both males and females, have a dark band within the lateral, light-coloured stripe (Table I). In this characteristic, the Praslin population is more similar to the La Digue population than it is to the Mahé and Silhouette populations. The latter two populations are similar in lateral coloration, but the Mahé population has a higher frequency of individuals in which the dorsal coloration fades gradually into the ventral coloration. There is no strong tendency for sexual dichromatism in this character.

Ventral coloration

The colour of the gular region varies sexually and, to a lesser degree, geographically (Table II). Males of all populations tend to have a uniformly light yellowish pink gular region, whereas females tend to have more brown spots in the gular region. Although there is some geographic variation in gular coloration within sexes, it is not great, and it is significant only for males ($P < 0{\cdot}001$ for males; $P = 0{\cdot}141$ for females). In addition, the pattern of variation between sexes is not concordant across populations.

Ventral coloration of the body varies sexually and geographically (Table III). However, geographic variation is significant only for males ($P < 0{\cdot}001$ for males; $P = 0{\cdot}295$ for females). Males in all populations tend to have lighter coloured venters and females darker coloured venters, which is consistent with the pattern observed in gular coloration. The La Digue

TABLE II

Variation in coloration of the gular region of preserved ***Tachycnemis seychellensis****: percentage of individuals in each category*

	Category[1]				Sample size
	1	2	3	4	
Males					
La Digue	59	35	6	–	17
Mahé (MGR)	97	3	–	–	30
Mahé (MMA)	100	–	–	–	30
Praslin	83	17	–	–	30
Silhouette	60	37	3	–	30
Females					
La Digue	–	25	50	25	4
Mahé	–	44	–	56	9
Praslin	–	40	10	50	10
Silhouette	–	64	7	29	14

[1] Category 1—gular region uniform light yellowish pink.
Category 2—gular region light yellowish pink with scattered, small, light brown spots irregular in shape.
Category 3—gular region light yellowish pink with large, light brown, irregularly shaped spots some of which are continuous.
Category 4—gular region light brown with only the margin of the lower jaw white or pinkish, in some cases with scattered, small, irregularly shaped darker brown spots.

TABLE III

Variation in ventral coloration of the body of preserved ***Tachycnemis seychellensis****: percentage of individuals in each category*

	Category[1]				Sample size
	1	2	3	4	
Males					
La Digue	6	35	59	–	17
Mahé (MGR)	80	20	–	–	30
Mahé (MMA)	83	7	10	–	30
Praslin	77	23	–	–	30
Silhouette	53	33	10	3	30
Females					
La Digue	–	25	–	75	4
Mahé	22	11	22	44	9
Praslin	20	–	40	40	10
Silhouette	–	21	50	29	14

[1] Category 1—light yellow or pink without spots.
Category 2—light yellow or pink with small brown spots.
Category 3—light yellow or pink with numerous brown spots, which are continuous in some cases.
Category 4—brown.

population is exceptional in that males tend to have more ventral brown spotting than do males of the other populations. Silhouette males are intermediate between the La Digue males and males of Mahé and Praslin in regard to the degree of ventral brown spotting. Although inter-island variation in ventral coloration is evident, there is no clear pattern suggesting inter-island relationships.

Dorsal tubercles

The presence or absence of dorsal tubercles does not depend on the time of year, and hence is independent of the breeding cycle and seasons. Sexual dimorphism is evident: males tend to be more tuberculate than females in all populations (Table IV). Geographic variation is also evident. Among populations of males, geographic variation is significant for tubercles on the dorsum ($P = 0{\cdot}025$), tibia ($P < 0{\cdot}001$), and eyelid ($P < 0{\cdot}001$), but not on the head ($P = 0{\cdot}242$). Females vary significantly for tubercles on the dorsum ($P = 0{\cdot}015$), tibia ($P = 0{\cdot}008$), head ($P = 0{\cdot}001$), and eyelid ($P = 0{\cdot}011$). Silhouette males are more likely to have tubercles on the dorsum, tibial segment of the hindlimb, and dorsal surface of the head than males from all other populations. The overall pattern of variation in this character does not reveal any strong suggestion of relationships between pairs of populations. The two Mahé populations of males, only 1 km apart, are as dissimilar for this trait as are several other pairs of populations that are much further apart and separated by marine barriers.

Grooved discs on digits

Females of every population are more likely to have grooved discs on their fingers and toes than are males (Table V). Geographic variation is significant for males ($P < 0{\cdot}001$ for both

TABLE IV

*Variation in the presence of tubercles in **Tachycnemis seychellensis**: percentage of individuals with tubercles on four body regions*

	Percentage of individuals with tubercles present on				
	dorsum	dorsal surface tibial segment of hindlimb	dorsal surface head	eyelid	Sample size
Males					
La Digue	76	59	65	41	17
Mahé (MGR)	97	93	70	77	30
Mahé (MMA)	83	77	63	33	30
Praslin	93	93	63	97	30
Silhouette	100	100	87	83	30
Females					
La Digue	75	0	25	25	4
Mahé	11	0	0	11	9
Praslin	0	0	20	80	10
Silhouette	29	43	79	64	14

fingers and toes) but not significant for females (fingers, $P = 0{\cdot}354$; toes, $P = 0{\cdot}465$). Silhouette males and females are more likely to have grooved discs than are the respective sexes of other populations. La Digue males have a very low percentage of individuals with grooved discs, and they are similar in this regard to males from Praslin, which is only 4 km distant. However, the two Mahé populations of males are more similar to the La Digue/Praslin male populations, which are 47 km distant, than to the Silhouette males which are only 19 km away. There appears to be no correlation between geographic distance and similarity in percentage of grooved finger and toe discs for the female populations.

TABLE V

*Variation in the percentage occurrence of grooved discs and subarticular tubercles in **Tachycnemis seychellensis***

	Percentage of individuals with grooved			
	discs on fingers[1]	discs on toes[1]	tubercles on manus[2]	Sample size
Males				
La Digue	0	6	82	17
Mahé (MGR)	7	23	90	30
Mahé (MMA)	10	10	53	30
Praslin	7	3	23	30
Silhouette	43	47	33	30
Females				
La Digue	25	25	75	4
Mahé	22	33	33	9
Praslin	40	20	20	10
Silhouette	57	50	43	14

[1] Scored as positive only if more than one finger (or toe) has a grooved disc.
[2] Scored as positive only if one or more of the subarticular tubercles is grooved.

Grooved subarticular tubercles

Males of all populations except Silhouette have a higher percentage of individuals with grooves on the subarticular tubercles compared to females (Table V). Geographic variation is significant for males ($P < 0{\cdot}001$) but not for females ($P = 0{\cdot}269$). As with grooved discs, there appears to be no pattern of geographic variation in the presence of grooved subarticular tubercles that is consistent with geographic distance and the degree of isolation.

Morphometric variation

Body size

Field observations led to the subjective impression that treefrogs from Mahé and Silhouette are larger than those from La Digue and Praslin, and statistics bear this out (Table VI). Pairwise comparisons between populations using *t*-tests show that, among males, only the La Digue and Praslin populations do not differ in body size (at $P \leqslant 0{\cdot}05$). Among populations of females, with much smaller sample sizes, all populations are significantly different in body size except for La Digue and Praslin, Mahé (combined population) and Praslin, and Mahé (combined) and Silhouette). It is also clear that females are the larger sex in all populations (Table VI). Because virtually all morphometric characters are highly correlated with body size (based on correlation coefficients not reproduced here), all morphometric comparisons between sexes and populations were done using analysis of covariance with means adjusted to body size (snout-vent length).

Sexual dimorphism

In addition to body size, the two sexes differ significantly in several morphometric characteristics (Table VII). However, in most cases, these sexual differences are confined to only one or two of the populations per character. For example, females of the Silhouette population have a significantly larger eye (ED) than males, but this relationship does not hold for the other populations. In one character (TW, tympanum width) a pair of populations (Mahé and Silhouette) is sexually dimorphic in the same direction, i.e. females of both populations have

TABLE VI

Body size variation in male and female ***Tachycnemis seychellensis***

	Mean snout-vent length (mm)	Minimum	Maximum	S.D.	Sample size
Males					
La Digue	39·8	33·2	43·9	2·70	17
Mahé (MGR)	46·4	41·3	52·0	2·51	30
Mahé (MMA)	44·5	37·9	50·9	3·26	30
Praslin	42·5	37·6	48·1	2·85	30
Silhouette	44·0	39·7	50·5	2·90	30
Females					
La Digue	51·1	47·6	57·1	4·23	4
Mahé	59·8	47·5	64·7	4·93	9
Praslin	55·9	49·1	65·5	5·05	10
Silhouette	60·8	53·9	77·0	5·29	14

wider tympanums. The height of the tympanum (TH) is not significantly dimorphic for any population, but, in every population, females have a larger mean TH, suggesting that with larger sample sizes of females, statistically significant results would be obtained.

The regression coefficients for males and females are not the same for many characters regressed on body size (Table VII), suggesting male/female differences in growth patterns. Here also the relationships are not consistent between populations. The slope difference does not occur in more than two populations for any character, and in most instances where there are slope differences between sexes, it occurs in only one population. A multivariate analysis using linear discriminant functions, based on all 23 morphometric characteristics, assigned (*a posteriori*) 100 percent of all treefrogs used in this study to the correct sex.

Geographic variation

Geographic variation of morphometric characters by sex is summarized in Table VIII. There are no slope differences for males, but among populations of females, two characters (tarsal segment length, TARL; and pes length, PL) have heterogeneous slopes. Fourteen of 22 characters exhibit significant geographic variation, comparing size-adjusted means, for males; and six of 22 vary for females. Four characters (internarial width, INW; pes length, PL; toe disc length, TD4; length of metatarsal tubercle, MTL) exhibit significant variation for both sexes.

The two Mahé populations (MGR, MMA) are only one linear kilometre apart, but in different drainage systems. A separate analysis of covariance with snout-vent length as the independent variable was done for these two populations to assess the amount of intra-island variation. Only males were analysed, because the sample sizes of the subdivided female populations are too small to allow for tests of equal slopes. Four morphometric traits, the number of premaxillary teeth (PMT), head length (HL), eye diameter (ED), and the length of the metatarsal tubercle (MLT), differ significantly between the two male populations. It is clear that intra-island variation occurs, and for this reason the two male populations were analysed separately in the multivariate analysis.

Multivariate analyses were done to examine the overall morphometric relationships among populations. These included linear discriminant and canonical discriminant functions by sex. For males, five populations (the two Mahé populations separate) were studied, whereas only four island populations of females were analysed (all Mahé females treated together).

A posteriori classification of individuals, using the criterion of equal likelihood of belonging to a population, resulted in all females correctly assigned to their populations of origin and a high percentage of males correctly assigned to their original population (Table IX). Two of 17 La Digue males were assigned to incorrect populations, one to nearby Praslin and one to distant Silhouette. Of the seven incorrectly assigned males from the MGR population from Mahé, two were assigned to the other Mahé population, three to nearby Silhouette, and two to distant Praslin. The MMA population of Mahé has nine of 30 males incorrectly assigned, two to the other Mahé population, four to nearby Silhouette, and two and one, respectively, to the distant islands of La Digue and Praslin. A single male of the 30 Praslin individuals is misassigned to distant Silhouette. Eight of 30 Silhouette males are misclassified, six to the nearby Mahé populations and two to distant La Digue. These data suggest a relatively close relationship among Mahé and Silhouette populations, but give little indication of the affinities of the La Digue and Praslin populations.

The first three canonical variates account for 89·5% of the variance for males in five

TABLE VII

Analysis of covariance of morphometric characters (see ***Methods and materials*** *for definitions) of male and female* ***Tachycnemis seychellensis*** *within populations (means adjusted to snout-vent length, * = significant differences at the 0·95 level, exact probabilities are given only for slopes that are unequal, sample sizes listed in Tables I–VI, the two Mahé populations combined in this analysis)*

	Adjusted means		Exact *P* equal means	Exact *P* equal slopes
	males	females		
PMT				
La Digue	24·9	29·8	0·02*	0·007
Mahé	27·0	29·1	0·17	
Praslin	26·5	26·6	0·96	
Silhouette	26·0	28·1	0·21	
HL				
La Digue	11·7	10·5	0·10	
Mahé	12·6	13·1	0·33	0·006
Praslin	12·4	13·1	0·16	
Silhouette	13·7	13·4	0·55	
HW				
La Digue	14·9	15·2	0·59	
Mahé	17·0	17·6	0·07	0·031
Praslin	16·7	16·9	0·42	
Silhouette	17·9	18·3	0·21	0·006
INW				
La Digue	3·1	3·2	0·54	
Mahé	3·6	3·9	0·08	0·049
Praslin	3·4	3·6	0·37	
Silhouette	3·9	4·1	0·17	
IOW				
La Digue	4·5	5·2	0·06	
Mahé	5·2	5·6	0·15	
Praslin	5·0	4·9	0·86	0·002
Silhouette	5·7	5·3	0·31	
END				
La Digue	4·9	5·2	0·25	
Mahé	5·7	6·0	0·05*	0·003
Praslin	5·6	5·7	0·64	
Silhouette	6·0	6·0	0·78	
ED				
La Digue	6·0	5·6	0·25	
Mahé	6·9	6·9	0·97	
Praslin	6·6	6·9	0·16	
Silhouette	6·9	7·5	0·03*	
ELW				
La Digue	3·4	3·1	0·35	
Mahé	4·2	3·5	0·01*	
Praslin	4·1	3·9	0·56	
Silhouette	4·2	4·2	0·98	
TW				
La Digue	2·0	2·2	0·32	
Mahé	2·1	2·4	0·03*	
Praslin	2·2	2·2	0·86	
Silhouette	2·2	2·6	0·01*	
TH				
La Digue	2·0	2·3	0·09	
Mahé	2·2	2·3	0·92	

TABLE VII
(cont.)

	Adjusted means		Exact *P*	Exact *P*
	males	females	equal means	equal slopes
Praslin	2·4	2·5	0·59	
Silhouette	2·4	2·5	0·70	
FAL				
La Digue	7·7	7·8	0·89	
Mahé	8·6	9·1	0·11	
Praslin	8·1	8·3	0·44	
Silhouette	9·1	9·0	0·70	
ML				
La Digue	11·5	10·8	0·16	
Mahé	12·8	13·2	0·20	0·029
Praslin	12·3	12·4	0·64	
Silhouette	13·3	12·7	0·24	0·007
FL1				
La Digue	3·2	3·4	0·37	
Mahé	3·6	3·7	0·42	
Praslin	3·5	3·6	0·45	
Silhouette	3·9	3·7	0·42	0·023
FL2				
La Digue	3·8	4·2	0·07	
Mahé	4·3	4·6	0·05*	
Praslin	4·1	4·0	0·38	0·004
Silhouette	4·5	4·4	0·48	0·043
FL3				
La Digue	5·9	5·5	0·19	
Mahé	6·7	6·9	0·41	
Praslin	6·4	6·4	0·98	
Silhouette	7·1	6·6	0·04*	0·000
FD3				
La Digue	2·0	2·1	0·74	
Mahé	2·5	2·5	0·94	
Praslin	2·4	2·2	0·37	
Silhouette	2·6	2·6	0·98	0·002
THIL				
La Digue	18·8	19·6	0·48	
Mahé	21·2	22·2	0·09	0·050
Praslin	20·0	20·4	0·60	
Silhouette	22·3	22·8	0·63	
TIBL				
La Digue	21·2	21·8	0·45	
Mahé	22·7	23·6	0·09	0·002
Praslin	21·6	23·0	0·04*	
Silhouette	23·8	23·7	0·94	0·010
TARL				
La Digue	9·5	8·7	0·15	
Mahé	10·2	10·4	0·51	0·013
Praslin	10·0	10·0	0·87	
Silhouette	10·6	10·2	0·42	0·024
PL				
La Digue	17·4	16·7	0·38	
Mahé	18·7	19·3	0·21	0·003
Praslin	18·3	18·1	0·67	
Silhouette	20·2	19·7	0·53	0·021

TABLE VII
(cont.)

	Adjusted means		Exact *P* equal means	Exact *P* equal slopes
	males	females		
TD4				
La Digue	1·5	1·5	0·78	
Mahé	2·0	1·9	0·54	
Praslin	1·8	1·8	0·66	
Silhouette	2·2	2·1	0·36	
MTL				
La Digue	1·8	1·7	0·72	
Mahé	1·9	2·3	0·00*	
Praslin	1·8	1·9	0·44	
Silhouette	2·2	2·2	0·87	

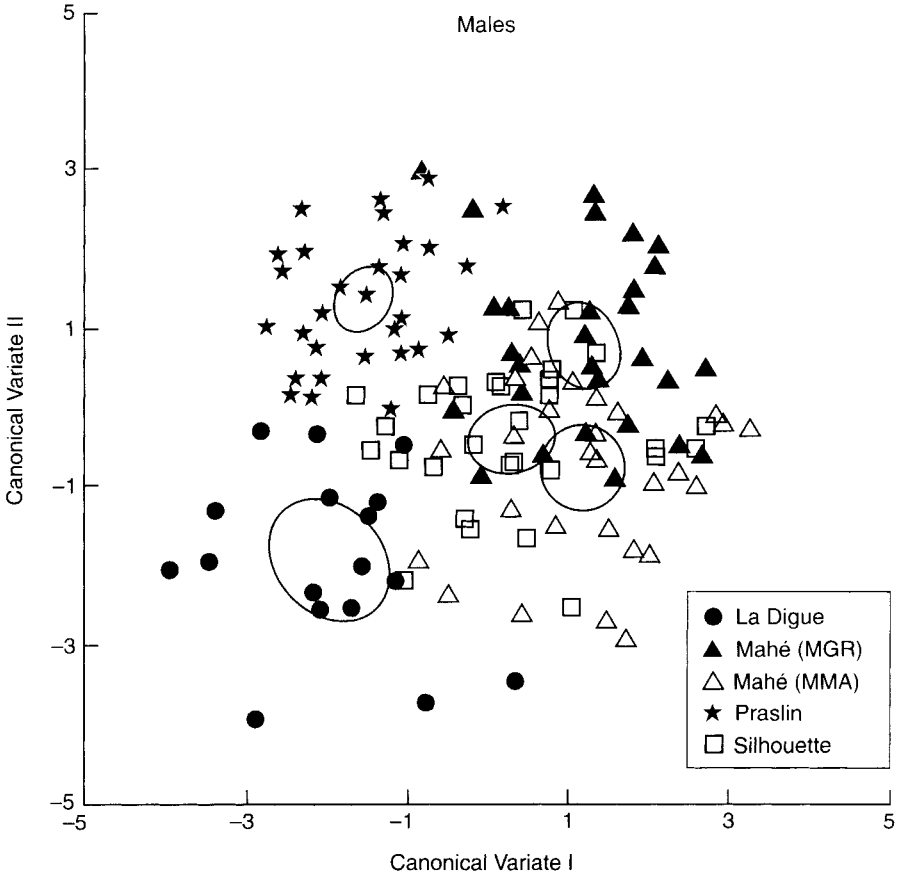

FIG. 2. Distribution of individual males of *Tachycnemis seychellensis* on the first two canonical variates. The first variate accounts for 43·4% and the second variate 30·6% of the variance in the multivariate system. The 95% confidence ellipses for each population are shown.

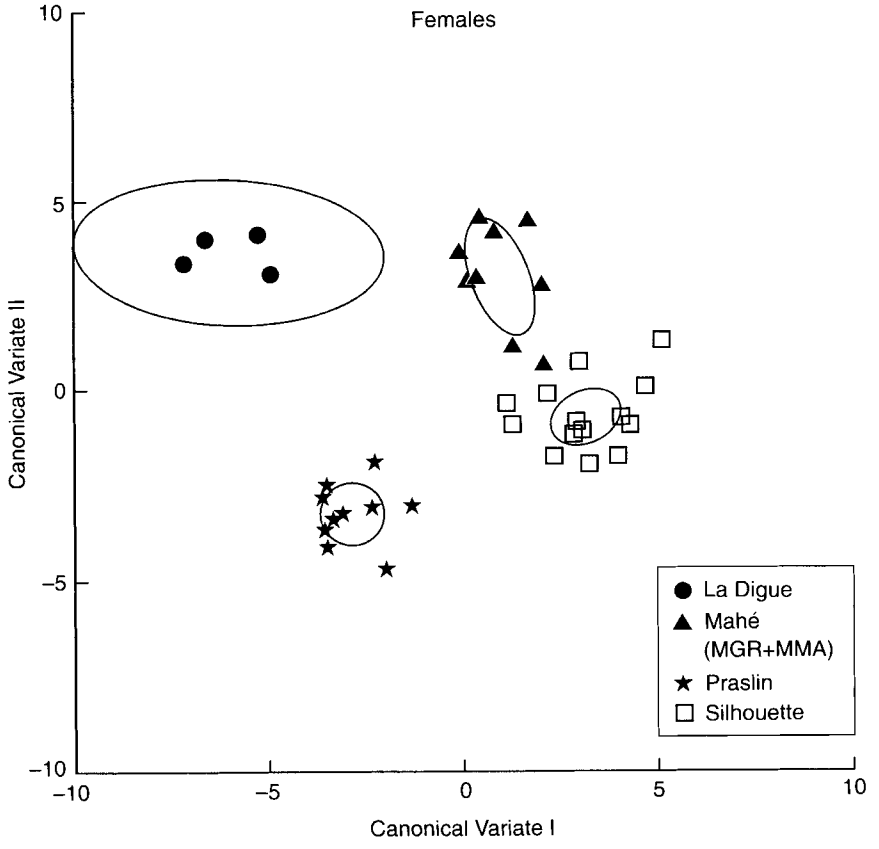

FIG. 3. Distribution of individual females of *Tachycnemis seychellensis* on the first two canonical variates. The first variate accounts for 56·4% and the second variate 37·4% of the variance in the multivariate system. The 95% confidence ellipses for each population are shown.

populations, and the first two canonical variates account for 93·7% of the variance for the four female populations. The distribution of individual males on the first two canonical variates is shown in Fig. 2, and the distances between the centroids (Mahalanobis d^2) are summarized in Table X. Although the distances among the two Mahé populations and the Silhouette population are significant ($P < 0{\cdot}01$), the distances are relatively small. The La Digue and Praslin populations of males are clearly separated from each other and from the cluster of Mahé and Silhouette populations by the first two canonical variates.

The four populations of females are all clearly separated by the first two canonical variates (Fig. 3). The distribution of females among the first canonical variate is similar to that of males (cf. Fig. 2) in that for both males and females the Mahé and Silhouette populations are placed to the right and the La Digue and Praslin populations to the left. The second canonical variate clusters males and females differently in that the positions of the La Digue and Praslin populations are reversed.

As might be expected, the two populations of males on Mahé have the smallest Mahalanobis d^2 (Table X). These two populations lie only one kilometre apart at relatively high elevation

TABLE VIII

Analysis of covariance of morphometric characters of male and female ***Tachycnemis seychellensis*** *by population with means adjusted to snout-vent length (* = $P < 0.05$; ** = $P < 0.01$; sample sizes in Tables I–VI; Mahé populations combined as MGR for females)*

	Males			Females		
	adjusted means	*P* equal slopes	*P* equal means	adjusted means	*P* equal slopes	*P* equal means
PMT						
La Digue	25·5	0·07	0·09	32·2	0·16	0·09
Mahé (MGR)	26·7			31·7		
Mahé (MMA)	25·7			–		
Praslin	25·8			30·0		
Silhouette	25·1			29·5		
HL						
La Digue	12·0	0·31	**	15·3	0·16	0·91
Mahé (MGR)	11·9			15·7		
Mahé (MMA)	11·5			–		
Praslin	12·1			15·7		
Silhouette	12·3			15·7		
HW						
La Digue	15·6	0·10	0·05	21·3	0·15	0·72
Mahé (MGR)	15·7			21·6		
Mahé (MMA)	15·7			–		
Praslin	15·9			21·6		
Silhouette	15·9			21·4		
INW						
La Digue	3·2	0·38	**	4·1	0·17	*
Mahé (MGR)	3·4			4·6		
Mahé (MMA)	3·4			–		
Praslin	3·3			4·3		
Silhouette	3·5			4·6		
IOW						
La Digue	4·6	0·95	*	7·0	0·36	0·49
Mahé (MGR)	4·9			6·6		
Mahé (MMA)	4·7			–		
Praslin	4·7			6·6		
Silhouette	5·0			6·4		
END						
La Digue	5·1	0·18	*	7·1	0·30	0·78
Mahé (MGR)	5·2			7·2		
Mahé (MMA)	5·2			–		
Praslin	5·3			7·0		
Silhouette	5·3			7·2		
ED						
La Digue	6·1	0·56	**	7·5	0·33	0·26
Mahé (MGR)	6·4			7·9		
Mahé (MMA)	6·7			–		
Praslin	6·4			8·1		
Silhouette	6·5			8·0		
ELW						
La Digue	3·5	0·37	*	4·4	0·82	0·67
Mahé (MGR)	3·9			4·6		
Mahé (MMA)	3·8			–		
Praslin	4·0			4·7		
Silhouette	3·9			4·6		
TW						
La Digue	2·1	0·96	0·06	2·9	0·08	0·49
Mahé (MGR)	2·0			2·8		

TABLE VIII
(cont.)

	Males			Females		
	adjusted means	*P* equal slopes	*P* equal means	adjusted means	*P* equal slopes	*P* equal means
Mahé (MMA)	2·0			–		
Praslin	2·1			2·7		
Silhouette	2·0			2·7		
TH						
La Digue	2·2	0·77	**	2·7	0·47	0·50
Mahé (MGR)	2·1			2·8		
Mahé (MMA)	2·1			–		
Praslin	2·3			2·9		
Silhouette	2·2			2·9		
FAL						
La Digue	8·0	0·49	**	10·7	0·73	0·79
Mahé (MGR)	7·7			10·9		
Mahé (MMA)	8·1			–		
Praslin	7·7			10·6		
Silhouette	8·0			10·7		
ML						
La Digue	11·9	0·22	0·08	15·6	0·09	*
Mahé (MGR)	12·0			16·1		
Mahé (MMA)	11·7			–		
Praslin	11·7			16·0		
Silhouette	11·7			15·3		
FL1						
La Digue	3·3	0·35	0·53	4·8	0·27	0·44
Mahé (MGR)	3·3			4·6		
Mahé (MMA)	3·4			–		
Praslin	3·4			4·6		
Silhouette	3·4			4·5		
FL2						
La Digue	3·9	0·87	0·05	5·6	0·41	**
Mahé (MGR)	4·0			5·4		
Mahé (MMA)	4·0			–		
Praslin	3·9			5·2		
Silhouette	4·0			5·2		
FL3						
La Digue	6·1	0·27	0·14	8·1	0·13	*
Mahé (MGR)	6·3			8·4		
Mahé (MMA)	6·2			–		
Praslin	6·1			8·2		
Silhouette	6·2			8·0		
FD3						
La Digue	2·1	0·53	*	3·0	0·55	0·19
Mahé (MGR)	2·3			3·2		
Mahé (MMA)	2·3			–		
Praslin	2·2			3·0		
Silhouette	2·2			3·3		
THIL						
La Digue	19·5	0·81	**	26·1	0·87	0·15
Mahé (MGR)	19·9			26·3		
Mahé (MMA)	19·7			–		
Praslin	19·3			24·8		
Silhouette	20·3			26·1		

TABLE VIII

(cont.)

	Males			Females		
	adjusted means	*P* equal slopes	*P* equal means	adjusted means	*P* equal slopes	*P* equal means
TIBL						
La Digue	21·9	0·08	**	29·2	0·12	0·31
Mahé (MGR)	21·2			28·3		
Mahé (MMA)	21·2			–		
Praslin	21·0			27·7		
Silhouette	21·3			27·9		
TARL						
La Digue	9·8	0·16	0·42	12·4	*	0·20
Mahé (MGR)	9·5			12·5		
Mahé (MMA)	9·5			–		
Praslin	9·6			12·4		
Silhouette	9·5			12·0		
PL						
La Digue	18·0	0·05	**	24·5	*	0·24
Mahé (MGR)	17·2			23·7		
Mahé (MMA)	17·2			–		
Praslin	17·4			23·5		
Silhouette	17·8			23·4		
TD4						
La Digue	1·6	0·06	*	2·3	0·29	*
Mahé (MGR)	1·9			2·5		
Mahé (MMA)	1·8			–		
Praslin	1·8			2·3		
Silhouette	1·9			2·7		
MTL						
La Digue	1·9	0·69	**	2·4	0·09	**
Mahé (MGR)	1·8			2·6		
Mahé (MMA)	1·9			–		
Praslin	1·7			2·4		
Silhouette	1·9			2·6		

TABLE IX

Numbers of male ***Tachycnemis seychellensis*** *correctly assigned to their population of origin and incorrectly assigned to other populations using linear discriminant functions based on 23 morphological characters. The criterion of equal probability of assignment to each population was used for the* ***a posteriori*** *classification*

Original population	Assigned population					Total
	La Digue	Mahé (MGR)	Mahé (MMA)	Praslin	Silhouette	
La Digue	15	0	0	1	1	17
Mahé (MGR)	0	23	2	2	3	30
Mahé (MMA)	2	2	21	1	4	30
Praslin	0	0	0	29	1	30
Silhouette	2	2	4	0	22	30

TABLE X

Mahalanobis d^2 scores for five populations of male and four populations of female ***Tachycnemis seychellensis*** *based on 23 morphometric characters (* $* = P < 0{\cdot}05$, $** = P < 0{\cdot}01$, *otherwise the scores are not significantly different; males above and females below the diagonal, Mahé populations of females combined as MGR)*

	La Digue	Mahé (MGR)	Mahé (MMA)	Praslin	Silhouette
La Digue	–	17·5**	13·5**	12·4**	11·9**
Mahé (MGR)	58·0	–	5·2**	9·7**	6·5**
Mahé (MMA)	xxxx	xxxx	–	12·2**	5·3**
Praslin	62·4	54·1*	xxxx	–	8·9**
Silhouette	102·9**	22·3	xxxx	44·3*	–

(400 m), separated only by low ridges. The island with treefrogs nearest to Mahé is Silhouette, lying 19 km to the north-west. The two Mahé populations of males are nearly as close in morphometric hyperspace to the Silhouette population of males as they are to each other (Table X). The islands of La Digue and Praslin are the closest pair of islands, lying only 4 km apart and separated by relatively shallow seas. However, the multivariate analyses of morphometric characters indicates that the populations of males on these two islands are no more similar to each other than they are to populations on the distant islands of Mahé and Silhouette. La Digue males, for example, have a slightly smaller Mahalanobis d^2, with Silhouette 66 km distant, than they do with Praslin males. Similarly, Praslin males are most similar morphometrically to Silhouette males, the furthest population from Praslin at 52 km, and are least similar to La Digue males.

The Mahalanobis d^2 scores are larger for the female populations, and this may in part reflect the smaller sample sizes of the female populations. Like the males, the greatest similarity for females is between the Mahé and Silhouette populations. Also like the results for males, the La Digue and Praslin females are not as similar morphometrically as would be expected because of their close geographic proximity. The La Digue population of females is most similar to the Mahé population at 47 km, and the Praslin population of females is most similar to the Silhouette population at 52 km.

Discussion

Amphibians are intolerant of salt water and have no special means of dispersing across marine barriers (Myers, 1953; Nussbaum, 1984). This fact is reflected in the distribution patterns of amphibians, which clearly indicate that amphibians seldom cross ocean barriers (Wallace, 1880; Myers, 1953; Darlington, 1957; Nussbaum, 1984). Because the granitic islands of the Seychelles are fragments of a partially submerged, Gondwanan microcontinent that was emergent with all the islands connected by land 10,000 to 16,000 years ago (Davies, 1968; Nussbaum, 1984), it is likely that the island populations of Seychelles treefrogs are of vicariant origin. If there has been no postfragmentation transoceanic dispersal of treefrogs, then the genetic relationships of treefrog populations reflects two factors: prefragmentation similarities and differences due to patterns of gene flow on the Seychellean microcontinent and postfragmentation divergence in isolation. Gene flow before fragmentation should cause closer populations (Mahé and Silhouette; La Digue and Praslin) to be more similar genetically. Postfragmentation divergence patterns could be effected by population size (island size) and ecological differences that impose differential selection pressures.

Mahé and Silhouette are the first and third islands in order of size (14,480 and 1,600 ha) and the first and second islands in order of maximum elevations (905 and 750 m). They are the only islands in the Seychelles with extensive middle elevation wet forests and higher elevation moss forests. In addition, their steep topographies are such that the slight rises in sea level that are believed to have occurred during the past 10,000 years (Geyh & Kudrass, 1979) would not have reduced their areas significantly. Praslin (4,040 ha) and La Digue (960 ha), on the other hand, are much lower in elevation (367 and 333 m maximum) and have more extensive low-elevation, coastal plateaux, such that small rises in sea level certainly would have reduced their areas significantly. In addition, the forests of Praslin and La Digue have always been of a drier aspect dominated by palm associations with no high elevation moss forest (Vesey-Fitzgerald, 1940).

Although there are no quantitative data, it seems certain that *Tachycnemis seychellensis* is far more abundant on Mahé and Silhouette than on Praslin and La Digue. Dense breeding populations of *T. seychellensis* were observed and heard along many mid- and high elevation streams on Mahé and Silhouette. On Praslin there are fewer suitable breeding streams, and only one large population associated with a stream was observed. Treefrogs also breed at one marsh in a valley on Praslin, but otherwise only scattered individuals were observed. There are no permanent streams above the coastal plateaux on La Digue, and breeding aggregations of treefrogs have been observed only in marshes and ditches dug by humans on the large coastal plateau behind Anse La Réunion.

Treefrogs of the Mahé and Silhouette populations are similar in large size, colour and morphometric characters. The simplest explanation for their similarity is that there was gene flow between Mahé and Silhouette populations prior to 10,000 years ago when the two islands were separated by marine transgression. Gene flow may have been relatively high as the two islands are separated by only 19 km. Divergence in isolation has proceeded slowly because large populations occupy nearly identical habitats in relatively extensive rainforests on the two islands.

Prior to separation, the treefrog populations on La Digue and Praslin also should have experienced high levels of gene flow as the two islands are only 4 km apart. The two populations are similar in their smaller size and in some aspects of coloration. However, morphometric analysis indicates that the two populations are no more similar to each other than to the distant Mahé and Silhouette populations, indicating very little if any postfragmentation gene flow between the two populations and relatively rapid divergence in some characteristics after isolation. Two factors may have contributed to rapid divergence in isolation. First, small population sizes may have facilitated genetic drift and selection, and it is highly likely that populations on La Digue and Praslin were subjected to population bottlenecks during the past 10,000 years when sea levels were higher than present (Geyh & Kudrass, 1979). At the time of maximum sea-level stand, La Digue would have been reduced to a very small, steep-sided, rocky island with few if any permanent streams. All of the presently known breeding sites on La Digue were submerged. The effect would have been similar but less dramatic on Praslin. Secondly, strong selection may have been imposed on these relatively small populations because of habitat disturbance. The breeding sites on La Digue and Praslin are more greatly altered by human activities than are those on Mahé and Silhouette. In addition to human disturbance, there is evidence that Praslin suffered extensive fires (Vesey-Fitzgerald, 1940), which would have greatly reduced the amount of habitat suitable for treefrogs.

It is important to note that the perhaps unexpectedly high degree of morphometric divergence between the La Digue and Praslin populations suggests little if any allele exchange, in spite of the proximity of the two islands. It is also important to note that, although the two populations are

divergent from each other, they are also highly divergent from the two distant populations on Mahé and Silhouette, suggesting independent (not influenced by gene flow) evolutionary trajectories both from each other and from the two distant populations. This argues against an origin of the Praslin and/or La Digue populations by dispersal from Mahé or Silhouette. It also argues against all but very low levels of dispersal between these two groups of islands.

The patterns of geographic variation indicate that Seychelles treefrogs consist of a single species presently fragmented into four island populations, each evolving in virtual isolation. That a single species is involved is indicated by the following observations. There is nearly as much variation between the two Mahé populations separated by only 1 km as there is between the Mahé populations and the Silhouette population, which have been separated for about 10,000 years by 19 km of ocean. Although the Praslin and La Digue populations are distinctive, they are as different from each other morphometrically as each is from the distant populations on Mahé and Silhouette, suggesting that their ancestral population was not greatly different from the ancestral population of the two forms on Mahé and Silhouette. The life histories and mating calls are nearly identical across the four islands (Nussbaum, unpubl.).

One could argue that the Mahé/Silhouette group be recognized as a subspecies and the La Digue/Praslin group as another subspecies. But, although the La Digue and Praslin treefrogs are similar in size and some colour traits, they are very distinctive morphometrically, and placing them together at the subspecific level would obscure these differences.

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