

Habitat use by stream-breeding frogs in south-east Sulawesi, with some preliminary observations on community organization

Graeme R. Gillespie*¹, David Lockie†, Michael P. Scroggie* and Djoko T. Iskandar‡

* Arthur Rylah Institute for Environmental Research, P.O. Box 137, Heidelberg 3084, Victoria, Australia

† Lark Rise, Franks Field, Peaslake, Guildford, Surrey, GU5 9SS, UK

‡ Department of Biology, Faculty of Mathematics and Natural Sciences, Institute of Technology Bandung, Jl. Ganesha 10, Bandung 40132, Indonesia
(Accepted 16 June 2003)

Abstract: The habitat associations of stream-breeding frogs were examined along a series of stream transects on Buton Island in south-east Sulawesi, Indonesia. Of the eight frog species located along streams, four were observed breeding in stream habitats. We examined spatial habitat partitioning among these species. Three of the four species were found to be associated with a non-random selection of the available perch sites. Strong partitioning between species in habitat associations was found; partitioning of the available habitat space was primarily associated with differences in proximity to stream features, and in the height of perch sites. General observations indicated that oviposition sites of most species were associated with the microhabitats in which the adult frogs were found. All four stream-breeding species appear to have synchronous breeding phenologies and the spatial relationships of these species within the habitat space appear to reflect partitioning of calling sites and oviposition sites. The stream-breeding frog community in this region of Sulawesi has much lower species richness and less specialized habitat use compared with other tropical stream-breeding frog communities in the region.

Abstrakt (Bahasa Indonesia): Asosiasi habitat antara katak dengan lingkungan diteliti pada jenis-jenis amfibi riparia sepanjang transek sungai di pulau Buton, Sulawesi Tenggara, Indonesia. Dari delapan jenis katak yang ditemukan sepanjang sungai, empat jenis di antaranya berkembang biak pada waktu penelitian ini berlangsung. Telah diamati pula pola pemisahan habitat antar jenis-jenis yang diamati. Tiga dari empat jenis ditemukan secara acak pada semua macam tempat hinggap. Pemisahan habitat antar jenis mempunyai korekasi yang sangat kuat terhadap jarak dari sungai dan ketinggian tempat hinggap. Walaupun demikian tempat peneluran sangat erat berasosiasi dengan iklim mikro masing-masing jenis. Keempat jenis yang diamati, masing-masing mempunyai musim peneluran yang relatif sinkron dan mencerminkan pemisahan habitat sesuai dengan tempat melakukan panggilan kawin dan tempat bertelur. Pola yang diamati dibandingkan pula dengan data yang terdapat dari Borneo. Disimpulkan bahwa katak yang berkembang biak di sungai-sungai di Buton, Sulawesi mempunyai keanekaragaman jenis yang rendah dan juga relatif tidak terspesialisasi dalam penggunaan habitat.

Key Words: amphibian, resource partitioning, South-East Asia, tropical anuran community

INTRODUCTION

Knowledge of habitat use, and how it and other resources are partitioned by species, is necessary for understanding the factors determining the distribution and abundance of organisms, and hence the organization of communities (Toft 1985). Community organization of amphibians is

complicated by their complex life cycle (Wilbur 1980). Factors that influence the availability of suitable larval habitats may differ substantially from those affecting availability of adult habitat. Relationships among species may thus differ at different life stages. In general, habitat is the primary resource partitioned by adult amphibians, whereas aquatic larvae primarily partition seasonal time (Toft 1985). Spatial or/and temporal partitioning of reproductive resources are thought to be important mechanisms enabling syntopic taxa to avoid competition (Crump 1971, Donnelly & Guyer 1994, Maiorana 1976).

¹ Corresponding author. Email: Graeme.Gillespie@dse.vic.gov.au

Despite the high diversity of anuran communities in the tropics, basic information on habitat use and reproductive patterns are available for relatively few tropical anuran assemblages (Aichinger 1987, Berry 1964, Crump 1974, Donnelly & Guyer 1994, Gascon 1991, Heyer 1973, Inger 1969, Trennery 1991). Much of our understanding of ecology of tropical anuran communities is derived from studies in the neotropics (Aichinger 1987, Crump 1971, 1974; Donnelly & Guyer 1994, Duellman 1978, 1988, 1989; Gascon 1991). Relatively few studies have been undertaken in South-East Asia (Berry 1964, Emerson & Inger 1992, Heyer 1973, Inger 1969) or tropical Australasia (Trennery 1991, Williams & Hero 1998). Furthermore, patterns of habitat use and community organization in stream-breeding frog assemblages has received relatively little attention worldwide (Emerson & Inger 1992, Eterovick & Sazima 2001, Inger 1969, Inger & Voris 1993, Lips 1996, 1998; Parris & McCarthy 1999, Ovaska 1991, Utsunomiya *et al.* 1983, Williams & Hero 1998). This focus upon pond-breeding communities possibly reflects the bias towards studies of lowland neotropical assemblages, where there is a predominance of non-stream breeding species (Crump 1971). Inger (1969) and Inger & Voris (1993) have reported the only detailed studies of a stream-breeding frog community in South-East Asia. They documented various aspects of the ecology of each species and habitat associations of different life stages, which enabled characterization of the niches of each species in a Bornean community. It remains to be seen how well the patterns observed in neotropical anuran communities apply to South-East Asian communities and specifically to stream-breeding assemblages.

Sulawesi is a large equatorial island in the Indonesian archipelago. Its biogeographic significance, with high levels of endemism across many vertebrate groups, has been well-documented (Cranbrook 1981, Whitten *et al.* 1987). However, knowledge of the ecology of the fauna of this region remains poor (Brown & Iskandar 2000, Whitten *et al.* 1987). Information on amphibians is especially limited. Many taxa remain undescribed (Cranbrook 1981, Iskandar & Tjan 1996, Inger & Voris 2001). Apart from one study documenting aspects of the reproductive biology of *Rana arathoani* in south-west Sulawesi (Brown & Iskandar 2000), virtually nothing is known about the ecology of any Sulawesi frog species.

In south-east Sulawesi several species of frog occur sympatrically along streams. The goals of our study were to describe this stream-breeding assemblage, to examine patterns of habitat use, and to make preliminary comparisons between the organization of this and other stream-breeding anuran communities.

METHODS

Study area

The study was conducted on central Buton Island, south-east Sulawesi (Figure 1). The region is characterized by limestone karst geology, with a maximum elevation of 760 m. The climate is tropical and monsoonal with a mean annual rainfall of approximately 1500–2000 mm (Fontanel & Chantefort 1978). A pronounced dry season occurs from August to October, followed by the wet season from November to April. Variable rainfall occurs from May to July. Much of central Buton Island remains covered in monsoon rain forest (see Whitmore 1986), the condition of which ranges from intact to young secondary forest (following agricultural use). Coastal plains, valley floors and some hill slopes have been cleared for agriculture. Remaining forest areas are subject to varying levels of human disturbance from selective timber cutting, rattan harvesting and hunting.

Study animals

General observations of frogs were made throughout the forest, streams and other aquatic habitats, such as rice paddies, ditches and pools in plantations, from June to September 2000. Standard sampling techniques were used, such as visual encounter surveys with headlamps, and dip-net sampling for larvae (Heyer *et al.* 1994). Preliminary surveys revealed eight frog species along streams, comprising five ranid, one bufonid and two rhacophorid species. Voucher specimens of all species have been lodged at the Museum Zoologicum Bogorinse, Indonesia (Appendix 1).

The systematics of Sulawesi anurans requires extensive revision (Iskandar & Tjan 1996) and the nomenclature herein is based on that of Iskandar & Tjan (1996) and Iskandar & Colijn (2000).

Sampling strategy

Eleven streams were selected for the study, incorporating a range of small and larger watercourses, ranging from sea level to an elevation of 435 m, with varying degrees of human disturbance (Figure 1; Table 1). Transects, 100 m long, were established along the streams and were marked with coloured flagging tape at intervals of 5 m. Where possible, transects were placed on sections of stream such that the broad habitat type (i.e. undisturbed forest, secondary forest or plantation) did not change substantially along the transect.

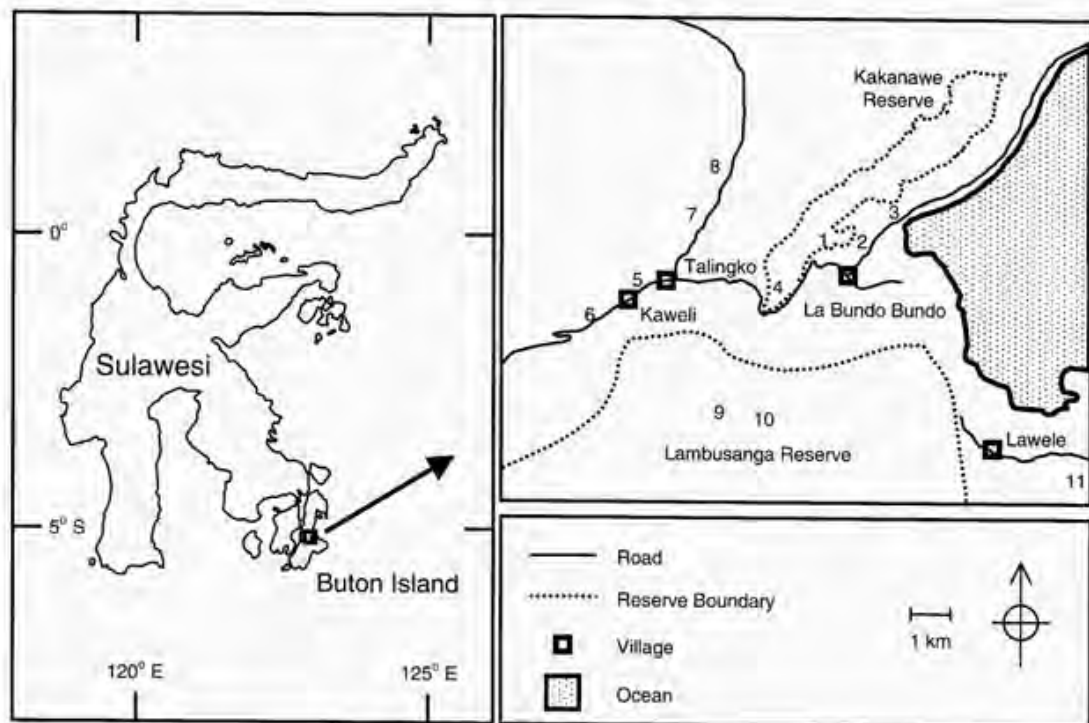


Figure 1. Map of the study area, showing the location within Sulawesi, and locations of the study sites in central Buton Island. See Table 1 for precise locations of the study sites.

Visual censuses were conducted on each transect between 19h00 (approximately 90 min after sunset) and 23h00 (see Crump & Scott 1994). Prior to commencing

each census, meteorological conditions were recorded, including wet bulb and dry bulb air temperatures, water temperature, cloud cover, precipitation, moon phase and

Table 1. Location and description of streams examined during the study, and occurrence of various frog species on each transect.

Site	Latitude (°S)/ Longitude (°E)	Altitude (m asl)	General habitat type	Mean stream width (m)	<i>Bufo</i> <i>celebensis</i>	<i>Limnonectes</i> <i>cf. grunniens</i>	<i>Limnonectes</i> <i>cf. modestus</i>	<i>Rana</i> <i>chalconota</i>	<i>Rhacophorus</i> <i>cf. monticola</i>
1	05°10'50"/122°54'05"	60	Forest, moderate disturbance	4.1	*	*	*	*	*
2	05°11'55"/122°54'35"	10	Plantation	4.9	*	*	*	*	*
3	05°10'30"/122°55'00"	20	Forest, limited disturbance	9.3	*	*	*	*	*
4	05°11'20"/122°52'50"	330	Forest, moderate disturbance	3.1	*	*	*	*	*
5	05°11'35"/122°51'20"	225	Forest, moderate disturbance	3.1	*	*	*	*	*
6	05°11'45"/122°51'05"	220	Forest, moderate disturbance	3.4	*	*	*	*	*
7	05°10'40"/122°52'25"	430	Forest, limited disturbance	2.2	*	*	*	*	*
8	05°10'35"/122°52'30"	435	Forest, limited disturbance	2.4	*	*	*	*	*
9	05°12'45"/122°52'35"	200	Forest, undisturbed	10.9	*	*	*	*	*
10	05°12'35"/122°52'35"	200	Forest, extensive disturbance	5.5	*	*	*	*	*
11	05°13'45"/122°58'10"	130	Forest, limited disturbance	1.7	*	*	*	*	*

wind speed. Censuses were conducted by two observers walking slowly upstream searching for frogs (with the aid of headlamps). The search area also included adjacent stream banks and terraces up to a distance of 3 m from the water's edge, and to a height of 3 m. This search area encompassed the environment that we felt could be effectively searched for frogs, and helped to ensure consistency in search effort between sites.

When located, each frog was identified to species and its position, perch type, activity and distance along the transect were recorded. Distances from the exact position at which the frog was found to various nearby habitat features were then measured with a tape measure as follows: distances to water, nearest rock, pool, riffle, log (> 6 cm diameter), litter, nearest tree > 50 cm diameter at 1.5 m above ground, nearest tree < 50 cm diameter, and height above ground.

Where possible, frogs were captured, placed in a plastic bag, and weighed (± 0.1 g) and measured (snout-urostyle length, ± 0.1 mm). Sex and reproductive condition were assessed if possible. Frogs were classified as adult males if nuptial pads were visible, or as adult females if eggs were visible within the abdominal cavity. The sex of *Limnonectes* spp. could not be determined in most cases, because these frogs lack nuptial pads, and because the female body wall is too opaque for reliable detection of eggs. All frogs were released at their points of capture.

All transects were revisited during daylight hours in order to assess the spatial distribution of microhabitat features. Random locations in the three-dimensional space along each transect were obtained by using a random number table to generate sets of three-dimensional Cartesian coordinates. The nearest available perch site (i.e. rock, log, leaf, ground surface etc.) to each random location was then located. The habitat characteristics of these randomly selected perch locations were measured in the same way as were the perch sites used by the frogs. For each transect, the number of random locations surveyed was equal to the number of actual frog locations that were surveyed.

General observations were made during the day and during nocturnal censuses of oviposition sites and the habitat associations of tadpole species, by visual searches and with the aid of a dip-net. Eggs and tadpoles were reared to metamorphosis in buckets of stream water to confirm species identification.

Data analysis

Habitat variables were transformed to natural logarithms and standardized to zero mean and unit variance (z -scores). A matrix of pair-wise dissimilarities between the habitat variables of each measured location (both frog locations and random locations) was constructed,

with Euclidean distance as the dissimilarity metric. Ordination of the original 9-dimensional habitat data was carried out on the dissimilarity matrix using non-metric multidimensional scaling (NMDS; Kruskal 1964). The NMDS procedures were carried out using the R statistical package, version 1.3.1 (Ihaka & Gentleman 1996). Following NMDS ordination, linear vectors related to underlying variation in the original 9-dimensional space were fitted to the ordination space by finding directions within the ordination space which had maximal correlation with each of the nine original habitat variables. Fitting of environmental vectors to the ordination configuration was carried out using the R add-in package *vegan* (J. Oksanen, University of Oulu, Finland), following the methodology originally proposed by Minchin (1991). Community ecologists have found the use of vector-fitting procedures to be a powerful method for relating the results of ordination procedures to underlying variables (Minchin 1991, Siira-Pietikäinen *et al.* 2001, Tolotti 2001, Zimmer *et al.* 2000).

Habitat use of each frog species was compared with the range of available habitats (based on the samples of randomly selected sites) by using analysis of similarities (ANOSIM; Clarke 1993) with the software package *PRIMER*. Due to the large sample sizes, complete enumeration of all possible permutations was not feasible. Therefore the distributions of dissimilarities within and between groups for each ANOSIM test were based on random samples of 1000 pair-wise dissimilarities.

RESULTS

General observations of habitat associations

Four species of frog were commonly found along streams (Table 1). With the exception of *Limnonectes* cf. *grummiens*, which may be a 'voiceless' species (see Emerson & Berrigan 1993), all these species were heard calling from June to August. Eggs and tadpoles of the four species were also found along most transects during the study. These four species were therefore included in the subsequent analyses of stream habitat use. With the exception of *Limnonectes* cf. *modestus*, no evidence of reproduction (egg masses, tadpoles, calling males, amplexant pairs) was found in non-stream habitats by these species, suggesting that most are obligate stream-breeders. Tadpoles of *L.* cf. *modestus* were also observed in lentic rain pools in the forest (Table 2).

Four other species were encountered infrequently along streams (Table 2). Calling *Bufo celebensis* were encountered along two of the streams during preliminary surveys, but not during the transect censuses. Egg masses and tadpoles of this species were encountered in two streams (but not on transects) during the study (Table 2).

Table 2. General observations of habitat associations of frog species found near streams in the study area. A = adults; J = juveniles or immature frogs; T = tadpoles.

Species	Streams	Pond habitats	Undisturbed forests	Disturbed or secondary forests	Plantation
<i>Bufo celebensis</i>	A, J, T	A	A, J	A, J	A, J
<i>Fekervaryia cancrivora</i>	A	A, J, T		A, J	A, J
<i>Limnonectes cf. grunniens</i>	A, J, T		J		
<i>L. cf. modestus</i>	A, J, T	A, J, T	A, J	A, J	
<i>Rana chalconota</i>	A, T		A	A	
<i>R. celebensis</i>	A	A, T	A	A	A
<i>Polypedates leucomystax</i>	A	A, T	A	A	A, J
<i>Rhacophorus cf. monticola</i>	A, J, T		A		

suggesting that this species also uses streams for reproduction. The few individuals observed were perched either on the ground, logs or rocks, or on the banks of streams near slow-flowing pool sections.

No evidence of reproduction in streams by the other three species was recorded. All three were observed reproducing in lentic habitats, such as forest rain pools, swamps or rice paddies elsewhere in the region (Table 2).

Morphological characteristics

Of the five stream-breeding species, only *Limnonectes cf. grunniens* had morphological characteristics consistent with a stream-dwelling or lotic habit, such as complete digital webbing and reduced toe discs (Table 3). *Rana chalconota* and *R. cf. monticola* are both slender-bodied species with only moderate toe webbing but well-developed digital discs on both hind and forelimbs, consistent with arboreal habits. *Limnonectes cf. modestus* and *B. celebensis* had morphologies consistent with other

terrestrial species from these genera, with moderate toe webbing and small or absent digital discs respectively.

Oviposition sites and tadpole habitat

Egg clutches of *L. cf. grunniens* were found in shallow gravel depressions constructed by the adults (G. Gillespie, pers. obs.) or natural depressions on flat rock shelves in the middle of the stream, near riffle sections or cascades (Table 3). Oviposition sites of *L. cf. modestus* were found amongst leaf litter along the edge of pools. *Rhacophorus cf. monticola* deposited eggs on the surface of flat leaves overhanging pools. *Rana chalconota* deposited a floating raft of eggs on the surface of pools. *Bufo celebensis* deposited strings of eggs wrapped around woody debris or root mats below the water surface of slow-flowing or still pools in streams.

Tadpoles of all species were typically found in still pools in the main channels of streams or connected side pools (Table 3). Tadpoles of *L. cf. grunniens* were the only species

Table 3. Summary of adult morphological characteristics and habitat characteristics of oviposition sites and tadpoles for stream-breeding frogs recorded in this study. m = males; f = females; C = complete; M = moderate, penultimate phalange of longest toe free; B = basal webbing only; N = none; S = small, marginally wider than phalanges; L = large, at least twice as wide as phalange.

	<i>Bufo celebensis</i>	<i>Limnonectes cf. grunniens</i>	<i>Limnonectes cf. modestus</i>	<i>Rana chalconota</i>	<i>Rhacophorus cf. monticola</i>
Adult morphology					
Snout-vent length (mm)	48.6–58.9 (m) 67.7–80.0 (f)	24.0–170.0	18.0–58.3	31.7–49.3 (m) 67.0–78.9 (f)	28.0–36.7 (m) 36.0–39.9 (f)
Mass (g)	10.6–18.6 (m) 30.0–42.0 (f)	2.1–620.0	2.0–21.0	2.9–7.1 (m) 18.0–35.5 (f)	1.5–2.1 (m) 2.5–3.5 (f)
Extent of toe webbing	M	C	M	M	M
Digital discs	N	S	S	L	L
Oviposition sites					
Environment	aquatic	aquatic	aquatic/terrestrial	arboreal	aquatic
Substrate	woody debris	rock/sand	sand/leaf litter	leaf	water surface
Tadpole habitat associations					
Slow-current pools		*			
Connected side-pools	*	*	*	-	*
Isolated side-pools			*		

recorded in habitats with observable flow. Tadpoles of *L. cf. modestus* were the only species recorded in pools not connected to the stream.

Ordination of adult habitat

Habitat measurements were recorded for 123 *Limnodynastes cf. grunniens*, 184 *L. cf. modestus*, 130 *Rana chalconota*, 107 *Rhacophorus cf. monticola* and a corresponding 546 random sites. The stress of the final three-dimensional NMDS configuration was 0.216, indicating good concordance between the dissimilarity matrix and ordination configuration. A plot of the first and second NMDS axes shows clear differentiation between the species in habitat utilization (Figure 2). Consideration of the fitted environmental vectors associated with the scatterplot of the first and second NMDS axes allows interpretation of the nature of the differences in habitat utilization between the species.

Limnodynastes cf. grunniens was well separated from the other three species on the basis of its position along the three environmental gradients associated with use of the aquatic habitat (distances to riffle, pool and water). In contrast to the other three species, *L. cf. grunniens* was usually found in, or near the water.

Limnodynastes cf. modestus was separated from *L. cf. grunniens* on the basis of use of the aquatic habitat, and from *Rhacophorus cf. monticola* on the vectors associated with height, and distance from litter and rocks. In contrast to *L. cf. grunniens*, *L. cf. modestus* was usually found on stream banks, rather than in the water, and was rarely found more than 15 cm above ground, unlike *R. cf. monticola*, which was usually found in trees. By contrast, *Rana chalconota* was found across all of the habitats occupied by the other species, and showed no obvious separation from them.

Analysis of similarities

The results of ANOSIM tests, comparing the available habitat as represented by the sample of random locations, to the habitat occupied by each of the four species of frogs are presented in Table 4. The range of habitats occupied

Table 4. Results of ANOSIM tests, comparing the range of habitats occupied by each of the four stream-breeding frog species with the randomly selected sample of available habitat.

Species	R-statistic	Permutations	Approximate P value
<i>Limnodynastes cf. grunniens</i>	0.606	1000	< 0.001
<i>Limnodynastes cf. modestus</i>	0.282	1000	< 0.001
<i>Rana chalconota</i>	0.013	1000	0.339
<i>Rhacophorus cf. monticola</i>	0.192	1000	< 0.001

by all species differed significantly from the overall set of available habitat, except for the habitat-space used by *Rana chalconota*, which did not differ significantly from the random habitat sample.

DISCUSSION

Three of the stream-breeding frog species examined in this study showed strong partitioning of the available riparian habitat. *Limnodynastes cf. grunniens* was strongly associated with in-stream habitats, typically found perched on rocks within the margins of the watercourse, and usually close to riffles or cascades. *Limnodynastes cf. modestus* occurred on the ground, usually along the banks of streams or several metres away from watercourses, in the vicinity of slow-flowing stream sections. *Rhacophorus cf. monticola* was found perched exclusively on vegetation along the banks, or overhanging streams. *Rana chalconota* was distributed throughout the habitat space occupied by the other three species and showed no significant associations. These differences in habitat use are explained primarily by proximity to the stream, and height above the water, which is correlated with distance to rocks, water, ground litter and logs. Structural components of the riparian microhabitat appear to be much more important influences on habitat suitability for these species than broader structural characteristics of the surrounding forest. In south-east Queensland, Australia, Parris & McCarthy (1999) also found that local stream structure and understorey vegetation characteristics had greater influence on the composition of frog assemblages along streams than structure of surrounding forest overstorey.

Limnodynastes cf. grunniens, *L. cf. modestus* and *R. cf. monticola* used a non-random selection and narrow range of positions within the available habitat space. With the exception of *L. chalconota*, oviposition sites were associated with the microhabitats in which the frog species were found. Calling and oviposition site selection are important determinants of reproductive success, and therefore fitness, in anurans (Lips 1996, Resetarits & Wilbur 1991). Given that all four species were breeding at the time of this study the spatial relationships of these species within the riparian habitat probably reflects partitioning of calling sites and oviposition sites, as well as more general partitioning of the habitat space. This strong spatial habitat partitioning by adults is generally consistent with studies of other anuran communities (Toft 1985). Inger (1969) observed extensive spatial overlap of niches by stream-breeding frogs in Sarawak; however, he measured habitat associations on a relatively coarse scale.

We have only examined this anuran community during one 4-mo period, coinciding with the end of the monsoon season and the following dry season. Nevertheless the four stream-breeding species we studied

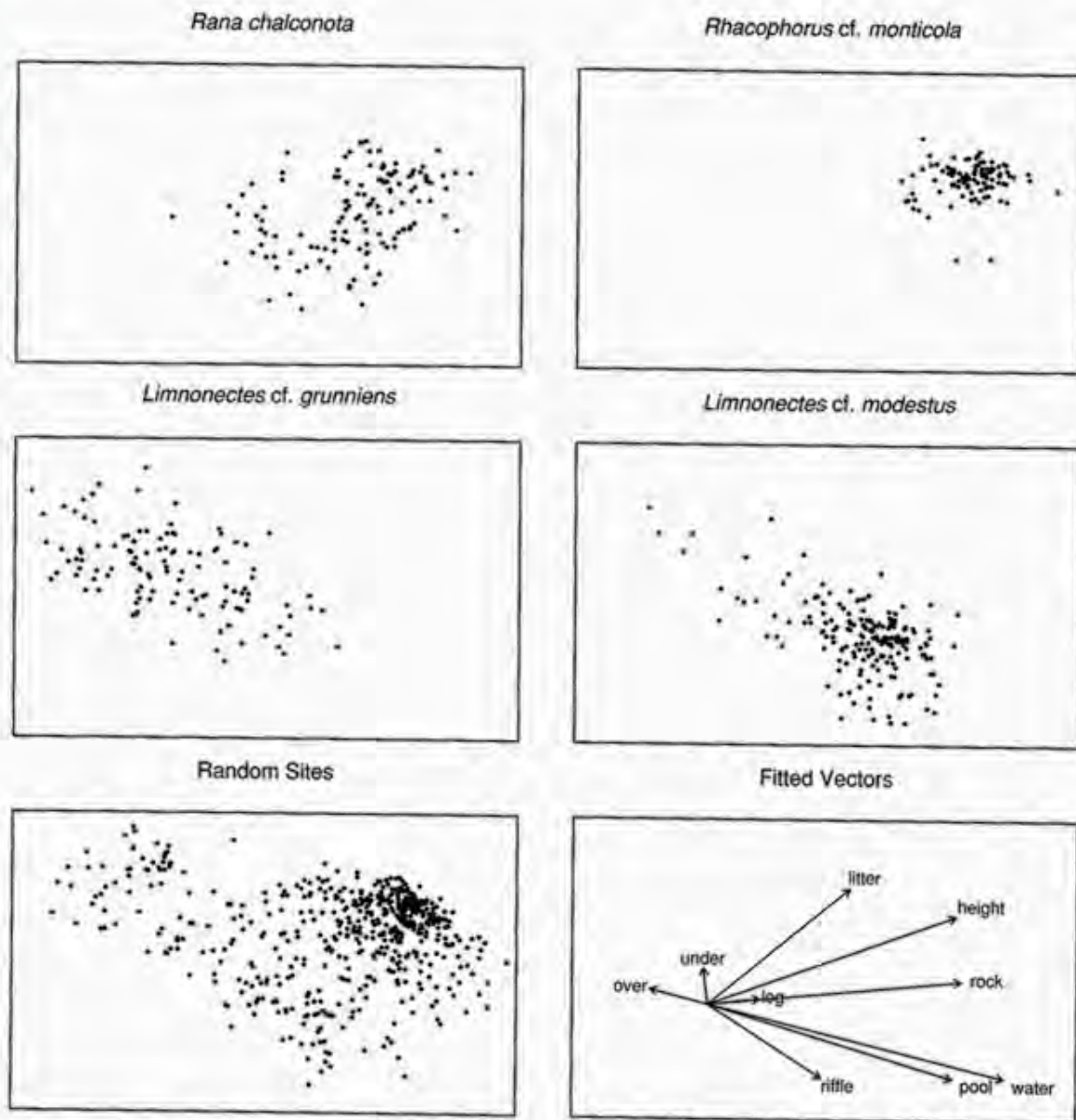


Figure 2. Plots of the first and second NMDS axes for the four frog species and the randomly selected sites. The plot at bottom-right shows the directions and strength of the fitted environmental variables within the ordination space. The lengths of the vectors are proportional to the correlations between the underlying environmental variables and the direction in the ordination space. The environmental vectors are labelled as follows: water = distance to nearest water; rock = distance to nearest rock; pool = distance to nearest pool; riffle = distance to nearest riffle; log = distance to nearest log; litter = distance to nearest leaf litter; over = distance to nearest tree > 50 cm diameter at 1.5 m above the ground; under = distance to nearest tree < 50 cm diameter; and height = height above ground.

appear to have synchronous breeding seasons. Many riverine frog communities in seasonal environments have relatively synchronous breeding seasons (Heyer 1973, Tsuji & Kawamichi 1996), possibly reflecting abiotic constraints on timing of breeding, such as seasonal drying or flooding. Many of the streams in

our study area dry up completely by September (G. Gillespie, *pers. obs.*), becoming unsuitable for aquatic anuran reproduction, thus constraining the breeding phenologies of stream-breeding frogs in the region. It is not known what other habitats these species may use outside the study period. However, general

observations on the non-riparian distribution of frogs collected throughout the study area suggest different levels of post-breeding dispersal or use of non-stream habitats. *Limnonectes cf. modestus* was frequently found throughout the surrounding rain forest, far from streams; however, most of these individuals were immature or recently metamorphosed. *Limnonectes cf. grunniens* were rarely found away from streams, all of which were immature. Furthermore, immature *L. cf. grunniens* were frequently found along streams. On only one occasion was *R. cf. monticola* found away from the riparian zone. Adult *Rana chalconota* were recorded frequently throughout the forest away from streams. *Rana chalconota* may be a habitat generalist or only a seasonal stream inhabitant, rather than an obligate stream-dweller. This could explain its strong overlap in habitat use with the other stream breeders.

Inger (1969) also recorded *R. chalconota* along streams in Sarawak. However, he described this species as strictly riparian. Males and females of *R. chalconota* in Borneo are much smaller (33–44 mm and 46–59 mm respectively; Inger & Stuebing 1997) than those at our study site (Table 3). Inger & Stuebing (1997) also describe the tadpole as having elongate patches of small distinctive glands on the ventral surface of the body, which are absent on tadpoles from Buton Island (G. Gillespie, *pers. obs.*). The taxonomic status of *R. chalconota* is unclear and future work should resolve the status of Sulawesi populations.

Bufo celebensis also breeds in streams in the study area. Although frequently encountered throughout the forest and plantations, adults were found along streams infrequently. *Bufo celebensis* has been reported breeding in pond habitats in northern Sulawesi (Leong & Chou 2000). Our data do not allow definite conclusions to be drawn as to whether *B. celebensis* is an obligate or facultative stream breeder. It may have a different phenological pattern from the other species that we could not detect in our 4-mo study. All other frog species found in the vicinity of streams at our study site breed in lentic pools (Inger & Stuebing 1997, G. Gillespie, *pers. obs.*).

There are distinctive differences in size and body form of the species in this community related to their microhabitat associations. Size and morphology are potentially also important factors in resource partitioning within amphibian communities (Inger 1969, Toft 1985). Based upon their stream habitat associations, occurrence of various life history stages in other habitats, and morphological characteristics of each species, frog species in the Buton stream community may be assigned to similar ecological types to those identified by Inger (1969). These types are: large size, strictly terrestrial, riparian (*Limnonectes cf. grunniens*); medium size, strictly terrestrial, not strictly riparian (*Limnonectes cf. modestus* and possibly *Bufo celebensis*); medium size, partially arboreal, not strictly riparian (*Rana chalconota*); small,

arboreal, riparian (*Rhacophorus cf. monticola*). *Limnonectes cf. grunniens* appears to be the only 'stream-dwelling' species.

Stream communities in Sarawak have higher species richness than in Sulawesi (Brown & Iskandar 2000, Inger 1969, Inger *et al.* 1986). Inger (1969) recorded 24 species breeding in streams compared with four or five species at our study site in Sulawesi, however there were a similar number of ecological types present. Brown & Iskandar (2000) recorded similarly low numbers of stream-breeding species in the Cikoro Desa region of south-western Sulawesi. We found little variation in niche partitioning amongst stream-dwelling tadpoles on Buton Island. Tadpoles of all species were found in connected pools or slow-flowing runs and have typical lotic/lotic-clasping morphologies (see Altig & Johnson 1989). Inger (1969) and Inger *et al.* (1986) recorded tadpoles of various species in a diversity of stream habitats, such as rock pot-holes and torrents. A greater diversity of morphological types of anuran larvae were also present, including specialized suctorial forms (Inger *et al.* 1986, Inger & Stuebing 1997). In the wet tropics of Australia, the species richness of stream-breeding anuran communities is intermediate between Sarawak and south-east Sulawesi (Richards *et al.* 1993, Trennery 1991, Williams & Hero 1998), but the diversity of ecological types of both adults and larvae is similar to Sarawak (Richards 1992, Trennery 1991, Williams & Hero 1998).

Borneo has a humid tropical environment with higher rainfall and a less pronounced seasonality than south-east Sulawesi (Inger 1969, Whitmore 1986). In contrast with south-east Sulawesi, Sarawak has year-round rainfall (Inger 1969). Climatic stability and higher rainfall have been shown to contribute to increased species richness through increased potential for diversity of reproductive modes (Duellman 1978). The Bornean climate may provide greater opportunities for temporal patterning in timing and duration of reproduction, and availability of a greater diversity of breeding habitats, than are available to anurans on Sulawesi.

Sulawesi is geologically younger than Borneo and has been isolated from continental Asia for at least 25 million years (Audley-Charles 1981, Voris 2000), whereas Borneo has been connected to continental Asia during successive Pleistocene glacial periods (Inger & Voris 2001, Morley & Fenley 1987). Consequently there may have been less time for evolution of the frog fauna in Sulawesi, and less opportunity for colonization by continental species.

The stream-breeding community of Buton is relatively simple compared with other tropical anuran communities (Crump 1971, Donnelly & Guyer 1994, Gascon 1991, Inger 1969, Inger & Voris 1993, Williams & Hero 1998). As in other anuran communities, habitat appears to be a major resource partitioned by adults (Toft

1985). In contrast to many other tropical anuran communities, our observations suggest little or no temporal partitioning of reproductive resources. This pattern is more similar to communities in non-tropical seasonal environments, where there are abiotic constraints on temporal availability of breeding habitats. However, further investigation is required to fully ascertain the temporal characteristics of this community and how resources are partitioned among species at the larval stage.

ACKNOWLEDGEMENTS

Funding and support for this research was provided by Operation Wallacea, Lincolnshire, UK and the Arthur Rylah Institute for Environmental Research, Victoria, Australia. Permission for this study was provided by a Memorandum of Understanding between Lembaga Ilmu Pengetahuan Indonesia (Indonesian Institute of Sciences), Departemen Kehutanan Direktorat Jenderal Perlindungan dan Konservasi Alam (Department of Forestry Directorate General of The Natural Protection and Conservation), and the Wallacea Development Institute, Jakarta. Additional assistance and support were provided by Pusat Penelitian Pengembangan Biologi (Research and Development Centre for Biology); Forestry Department South East Sulawesi, Natural Resources Conservation Unit of South East Sulawesi, Muna and Buton Section; Government of Buton Regency Culture and Tourism Department; Bidang Zoologi, Puslit Biologi-LIPI (Museum). We thank K. Morrison, S. Howard, D. Halligan, J. Fry, B. Wilson, A. White, S. Hopper and L. Perrett for assistance in the field. We also thank G. Newell for providing assistance with PRIMER and A. Webb for helpful statistical discussions. Helpful comments improving the manuscript were provided by R. Brown, R. Inger, M. Donnelly, J.-M. Hero, D. Lucas, S. Nicol and one anonymous reviewer.

LITERATURE CITED

- AICHINGER, M. 1987. Annual activity patterns of anurans in a seasonal Neotropical environment. *Oecologia* 71:583–592.
- ALTIG, R. & JOHNSON, G. F. 1989. Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. *Herpetological Monographs* 3:81–109.
- AUDLEY-CHARLES, M. G. 1981. Geological history of the region of Wallace's Line. Pp. 24–35 in Whitmore, T. C. (ed.). *Wallace's line and plate tectonics*. Clarendon Press, Oxford.
- BERRY, P. Y. 1964. The breeding patterns of seven species of Singapore Anura. *Journal of Animal Ecology* 33:227–243.
- BROWN, R. M. & ISKANDAR, D. T. 2000. Nest site selection, larval hatching, and advertisement calls, of *Rana arathooni* from southwestern Sulawesi (Celebes) Island, Indonesia. *Journal of Herpetology* 34:404–413.
- CLARKE, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117–143.
- CRANBROOK, Earl of 1981. The vertebrate faunas. Pp. 58–70 in Whitmore, T. C. (ed.). *Wallace's line and plate tectonics*. Clarendon Press, London.
- CRUMP, M. L. 1971. Quantitative analysis of the ecological distribution of a tropical herpetofauna. *University of Kansas Museum of Natural History Occasional Papers* 3:1–62.
- CRUMP, M. L. 1974. Reproductive strategies in a tropical anuran community. *University of Kansas Museum of Natural History Miscellaneous Publications* 61:1–67.
- CRUMP, M. L. & SCOTT, N. J. 1994. Visual encounter surveys. Pp. 85–92 in Heyer, W. R., Donnelly, M. A., McDiarmid, R. W., Hayek, L. C. & Foster, M. S. (eds). *Measuring and monitoring biological diversity – standard methods for amphibians*. Smithsonian Institution Press, Washington, DC.
- DONNELLY, M. A. & GUYER, C. 1994. Patterns of reproduction and habitat use in an assemblage of Neotropical hyliid frogs. *Oecologia* 98:291–302.
- DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. *Miscellaneous Publications of the Museum of Natural History University of Kansas* 65:1–352.
- DUELLMAN, W. E. 1988. Patterns of species diversity in anuran amphibians in the American tropics. *Annals of the Missouri Botanical Garden* 75:79–104.
- DUELLMAN, W. E. 1989. Tropical herpetofauna communities: patterns of community structure in Neotropical rainforests. Pp. 61–68 in Harmelin-Vivien, M. & Bourlière, F. (eds). *Vertebrates in complex tropical systems*. Springer, New York.
- EMERSON, S. B. & BERRIGAN, D. 1993. Systematics of Southeast Asian ranids: multiple origins of voicelessness in the subgenus *Limnoneustes* (Fitzinger). *Herpetologica* 49:22–31.
- EMERSON, S. B. & INGER, R. F. 1992. The comparative ecology of voiced and voiceless Bornean frogs. *Journal of Ecology* 26:490–495.
- ETEROVICK, P. C. & SAZIMA, I. 2001. Structure of an anuran community in a montane meadow in southeastern Brazil: effects of seasonality, habitat, and predation. *Amphibia-Reptilia* 21:439–461.
- FONTANEL, J. & CHANTEFORT, A. 1978. *Bioclimates of the Indonesian Archipelago*. Institut Française de Pondicherry, Pondicherry. 104 pp.
- GASCON, C. 1991. Population- and community-level analyses of species occurrences of Central Amazonian rainforest tadpoles. *Ecology* 72:1731–1746.
- HEYER, W. R. 1973. Ecological interactions of frog larvae at a seasonal tropical location in Thailand. *Journal of Herpetology* 7:337–361.
- HEYER, W. R., DONNELLY, M. A., MCDIARMID, R. W., HAYEK, L. C. & FOSTER, M. S. (eds), 1994. *Measuring and monitoring biological diversity – standard methods for amphibians*. Smithsonian Institution Press, Washington, DC. 364 pp.
- IHAKA, R. & GENTLEMAN, R. 1996. R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics* 5:299–314.
- INGER, R. F. 1969. Organization of communities of frogs along small rain forest streams in Sarawak. *Journal of Animal Ecology* 38:123–148.

- INGER, R. F. & STUEBING, R. B. 1997. *A field guide to the frogs of Borneo*. Natural History Publications, Sabah, Malaysia, 205 pp.
- INGER, R. F. & VORIS, H. K. 1993. A comparison of amphibian communities through time and from place to place in Bornean forests. *Journal of Tropical Ecology* 9:409–433.
- INGER, R. F. & VORIS, H. K. 2001. The biogeographical relations of the frogs and snakes of Sundaland. *Journal of Biogeography* 28:863–891.
- INGER, R. F., VORIS, H. K. & FROGNER, K. J. 1986. Organization of a community of tadpoles in rain forest streams in Borneo. *Journal of Tropical Ecology* 2:193–205.
- ISKANDAR, D. T. & COLIJN, E. 2000. Preliminary checklist of Southeast Asian Herpetofauna I. Amphibians. *Treubia* 31 (Supplement):1–133.
- ISKANDAR, D. T. & TJAN, K. N. 1996. The amphibians and reptiles of Sulawesi, with notes on the distribution and chromosomal number of frogs. Pp.39–46 in Kitchener, D. A. & Suyanto, A. (eds). *Proceedings of the First International Conference on Eastern Indonesian-Australian Vertebrate Fauna*. Western Australian Museum for Lempaga Ilmu Pengetahuan Indonesia, Perth.
- KRUSKAL, J. B. 1964. Non-metric multidimensional scaling: a numerical method. *Psychometrika* 29:115–129.
- LEONG, T. M. & CHOU, L. M. 2000. Tadpole of the Celebes toad *Bufo celebensis* Günther (Amphibia: Anura: Bufonidae) from northeast Sulawesi. *Raffles Bulletin of Zoology* 48:297–300.
- LIPS, K. R. 1996. New treefrog from the Cordillera de Talamanca of Central America with a discussion of systematic relationships in the *Hyla lancasteri* group. *Copeia* 1996:615–626.
- LIPS, K. R. 1998. Decline of a tropical montane amphibian fauna. *Conservation Biology* 12:106–117.
- MAIORANA, V. C. 1976. Predation, submergent behaviour, and tropical diversity. *Evolutionary Theory* 1:157–177.
- MINCHIN, P. 1991. *DECODA: database for ecological community data*. (Computer Software) Australian National University, Canberra.
- MORLEY, R. J. & FENLEY, J. R. 1987. Late Cainozoic vegetational and environmental changes in the Malay archipelago. Pp. 50–59 in Whitmore, T. C. (ed.). *Biogeographical evolution of the Malay Archipelago*. Clarendon Press, Oxford.
- OVASKA, K. 1991. Reproductive phenology, population structure, and habitat use of the frog *Eleutherodactylus johnstonei* in Barbados, West Indies. *Journal of Herpetology* 25:424–430.
- PARRIS, K. M. & MCCARTHY, M. A. 1999. What influences the structure of frog assemblages at forest streams? *Australian Journal of Ecology* 24:495–502.
- RESEKARTIS, W. J. & WILBUR, H. M. 1991. Calling site choice by *Hyla chrysocelis*: effect of predators, competitors, and oviposition sites. *Ecology* 72:778–786.
- RICHARDS, S. J. 1992. The tadpole of *Litoria nyakalensis* (Anura, Hyidae), and a key to the torrent tadpoles of northern Queensland. *Allytes* 10:99–103.
- RICHARDS, S. J., McDONALD, K. R. & ALFORD, R. A. 1993. Declines in populations of Australia's endemic tropical rainforest frogs. *Pacific Conservation Biology* 1:66–77.
- SIIRA-PIETIKÄINEN, A., PIETIKÄINEN, J., FRITZE, H. & HAIMI, J. 2001. Short-term responses of soil decomposer communities to forest management: clear felling versus alternative forest harvesting methods. *Canadian Journal of Forest Research* 31:88–99.
- TOFT, C. A. 1985. Resource partitioning in amphibians and reptiles. *Copeia* 1985:1–21.
- TOLOTTI, M. 2001. Phytoplankton and littoral epilithic diatoms in high mountain lakes of the Adamello-Brenta Regional Park (Trentino, Italy) and their relation to trophic status and acidification risk. *Journal of Limnology* 60:171–188.
- TRENNERY, A. D. 1991. Observations on species diversity and habitat compartmentalisation of the frogs of Mt Lewis rainforests, Carbine Tableland, northern Queensland. Pp.325–334 in Werren, G. & Kershaw, P. (eds). *The rainforest legacy. Volume 1, Flora and fauna of the rainforests*, Australian Government Publishing Service, Canberra.
- TSUJI, H. & KAWAMICHI, T. 1996. Breeding habitats of a stream-breeding toad, *Bufo torenticola*, in an Asian mountain torrent. *Journal of Herpetology* 30:451–454.
- UTSUNOMIYA, Y., UTSUNOMIYA, T. & KATSUREN, S. 1983. Habitat segregation observed in the breeding of five frog species dwelling in a mountain stream of Okinawa Island. *Annotated Zoology of Japan* 56:149–153.
- VORIS, H. K. 2000. Maps of Pleistocene sea levels in southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography* 27:1153–1167.
- WHITMORE, T. C. 1986. *Tropical rain forests of the Far East*. (Second Edition). Oxford University Press, Oxford, 352 pp.
- WHITTEN, A. J., MUSTAFI, M. & HENDERSON, G. S. 1987. *The ecology of Sulawesi*. Gadjah Mada University Press, Yogyakarta, 777 pp.
- WILBUR, H. M. 1980. Complex life cycles. *Annual Review of Ecology and Systematics* 11:67–93.
- WILLIAMS, S. W. & HERO, J.-M. 1998. Rainforest frogs of the Australian wet tropics: guild classification and the ecological similarity of declining species. *Proceedings of the Royal Society of London, Series B* 265:597–602.
- ZIMMER, K. D., HANSON, M. A. & BUTLER, M. G. 2000. Factors influencing invertebrate communities in prairie wetlands: a multivariate approach. *Canadian Journal of Fisheries and Aquatic Sciences* 57:76–85.

APPENDIX 1

Catalogue numbers of specimens lodged at the Museum Zoologicum Bogorinse, Indonesia.

Bufo celebensis (Guenther 1859) MZB7034, 7035; *Pejervaria cancrivora* (Gravenhorst 1829) MZB7037; *Limnonectes* cf. *grunniens* (Daudin 1801) MZB7012–7018, 7028, 7029; *Limnonectes* cf. *modestus* (Boulenger 1982) MZB6995–7001; *Polypedates leucomystax* (Gravenhorst 1829) MZB7091–7021; *Rana celebensis* (Peters 1872) MZB7007–7009; *Rana chalconota* (Schlegel 1837) MZB7032, 7033; *Rheophorus* cf. *monticola* (Boulenger 1896) MZB7002–7006.