

## Predictive Distribution of Hynobiid Salamanders in Taiwan

Pei-Fen Lee<sup>1</sup>, Kuang-Yang Lue<sup>2</sup>, and Shan-Huah Wu<sup>1,\*</sup>

<sup>1</sup>Institute of Ecology and Evolutionary Biology, and Department of Life Science,  
National Taiwan University, Taipei, Taiwan 106, R.O.C.

<sup>2</sup>Department of Life Science, National Taiwan Normal University, Taipei, Taiwan 106, R.O.C.

(Accepted November 15, 2005)

**Pei-Fen Lee, Kuang-Yang Lue, and Shan-Huah Wu (2006)** Predictive distribution of hynobiid salamanders in Taiwan. *Zoological Studies* 45(2): 244-254. The distribution patterns of hynobiid salamanders in Taiwan, based on species and species complex, i.e., *Hynobius arisanensis*, the *H. formosanus-sonani* complex, and *Hynobius* sp. 1 (an undescribed species), were studied using a wildlife distribution database and an environmental factor database with univariate statistics and discriminant function analysis (DFA). The distribution maps suggested that these salamanders are restricted to certain regions and show distribution patterns distinct from each other. The *H. arisanensis* population has the largest range of distribution, while the *H. formosanus-sonani* complex was only found in the southwestern corner of Taroko National Park (in the Hehuanshan area) and in the center of Yushan National Park. Distributions of *H. arisanensis* and the *H. formosanus-sonani* complex overlapped in the center of Yushan National Park. Additionally, *Hynobius* sp. 1 was only found in the northern part of the range of the *H. formosanus-sonani* complex, mostly localized in the Shei-pa and Taroko National Park regions. Although both *H. arisanensis* and *Hynobius* sp. 1 are found in Shei-pa National Park, they show differences in microhabitat use with each other. The only overlapping site of these 2 species is located in the Hehuanshan region. The predictive DFA model has 82% classification accuracy with 5 predictive variables, including total precipitation in the dry period (Oct.-Mar.), and proximity to major roads, the coastline, rivers, and areas above 3000 m. We applied the classification rules to predict the potential distributions of salamanders in Taiwan and discussed the viability of the salamanders with respect to their population distributions and conservation. <http://zoolstud.sinica.edu.tw/Journals/45.2/244.pdf>

**Key words:** *Hynobius*, Conservation, GIS, Discriminant function analysis.

Taiwan is the southernmost region of distribution of hynobiid salamanders in the world (Seto and Utsunomiya 1987, Zhao and Hu 1988). The Taiwanese species, all belonging to the genus *Hynobius*, are endemic to the island, and their population sizes are extremely small (Lue et al. 1989). These salamanders reside in mountain meadows, woodlands, and broadleaf and coniferous forests, ranging from 2000 to 3650 m in elevation (Chen 1984, Lue et al. 1989 1990). They spend most of their lives under rocks and logs near standing water and small creeks in local habitats. Eggs are laid in clusters with egg sacs (Lue and Chuang 1992). The breeding seasons of these species generally range from Nov. to Jan.,

and the clutch size is usually less than 25 (Yeh 1991, Lue and Chuang 1992). Adult salamanders usually search for food actively at night under debris on the forest floor (Chen 1984, Yeh 1991), and prey mainly on sow bugs, earthworms, and other terrestrial invertebrates (Du and Lue 1982). Their natural enemies are snakes and other predators (Yeh et al. 1988).

The taxonomic status of the Taiwanese salamanders has long been debated (Lue et al. 1989, Yeh 1991, Matsui and Ota 1995, Lue and Lai 1997), mainly due to the loss of pertinent type specimens during World War II (Lue and Lai 1997) and insufficient diagnoses in the original descriptions of relevant species. From Taiwan, Maki

\*To whom correspondence and reprint requests should be addressed. Tel: 886-2-23623501. Fax: 886-2-23686750.  
E-mail: shwu2@ntu.edu.tw

(1922) recognized 3 species, *Hynobius sonani* Maki, *H. formosanus* Maki, and *H. arisanensis* Maki, on the basis of external characters and the vomerine tooth arrangements. However, Dunn (1923) only recognized *H. sonani* as a valid species, whereas Sato (1941, 1943) recognized *H. sonani* and *H. formosanus*, with synonymization of *H. arisanensis* with the latter. Recently, Chen (1984) and Lue et al. (1989) argued that the *Hynobius* populations in Taiwan are morphologically more diversified than previously considered. Chen (1984), however, hesitated to utilize the ordinary Linnean classification to express such diversity of the Taiwanese salamanders and instead divided them into 3 phenotypes (i.e., Alishan, Nengao, and Nanhu phenotypes) on the basis of color patterns. Chen and Lue (1986) suspected that there was only 1 species (*H. formosanus*) in Taiwan.

Because classification of members of the genus *Hynobius* at the species level solely on the basis of morphological characteristics sometimes involves great difficulties (Matsui et al. 1992), in recent years, molecular techniques have often been applied to obtain more-convincing data. Initial comparative genetic work by (Iizuka and Kakegawa 1989) and (Kakegawa et al. 1989) using small samples from only a few localities yielded results that supported the validity of all 3 nominal species from Taiwan (i.e., *H. sonani*, *H. arisanensis*, and *H. formosanus*; see above). With a greater geographic extent but small-sized samples from Taiwan, (Lue and Lai 1997) applied an electrophoretic method to quantify genetic differentiations. The results, while supporting (Iizuka and Kakegawa 1989)'s view, further demonstrated the presence of a previously unknown species at Guanwu (in the northwestern corner of Shei-Pa National Park) and also confirmed the independent specific status of the Nanhu phenotype of (Chen 1984). Thus, it is now obvious that the Alishan phenotype of (Chen 1984) corresponds to *H. arisanensis*. The Nengao phenotype should include 2 species, most likely *H. sonani* and *H. formosanus* (Iizuka and Kakegawa 1989, Lue and Lai 1997), but since this phenotype cannot be further divided morphologically, it is henceforth referred to as the *H. formosanus-sonani* complex. From the results of allozyme analyses by (Lue and Lai 1997), the Nanhu and Guanwu phenotypes obviously represent 2 undescribed species, and thus are henceforth referred to as *Hynobius* sp. 1 and sp. 2, respectively.

In Taiwan, 2 salamanders (*H. sonani* and *H.*

*formosanus*) were first protected under the *Cultural Heritage Preservation Law* in 1986 as precious and rare species, and later by the *Wildlife Conservation Law* which was promulgated in 1989. This designation was based on the work by (Maki 1923) and subsequent inventory studies. However, those species are not listed in the *IUCN Red Data List* (Anonymous 1996) despite their rarity. One of the possible reasons is a deficiency of data regarding their geographic distributions and the size of each local population.

Many studies have also shown that landscape features can potentially be used as predictors of overall species distribution with the help of statistics (e.g., Beebe 1985 1996, Pavignano et al. 1990). Romero and Real (1996) demonstrated that macroenvironmental factors are the ultimate determinants of species distribution for some amphibians. Therefore, we studied the current distribution patterns of Taiwanese salamanders using a database of macroenvironmental factors to discern possible correlations between the distributions and environmental factors. We, furthermore, performed distribution predictions using the correlated environmental factors for the future conservation and management of these precious and rare species.

## MATERIALS AND METHODS

Based on the amphibian database of (Lue and Chuang 1990), we compared the distribution patterns of the 3 Taiwanese salamander species and 1 species complex: *H. arisanensis* (referred to as the Alishan phenotype in the database), the *H. formosanus-sonani* complex (the Nengao phenotype), and *Hynobius* sp. 1 (the Nanhu phenotype; see above). Since *Hynobius* sp. 2 (the Guanwu phenotype; see above) was not identified in the database, this species was not included in the present study. Environmental factors which affect the distribution patterns were estimated using environmental factor databases (Lee et al. 1997). Discriminant function analysis (DFA) was conducted to predict the distributions of these taxa. Moreover, the viability of these Taiwanese salamanders with respect to the population distributions and their conservation were analyzed for future studies.

### Observation data

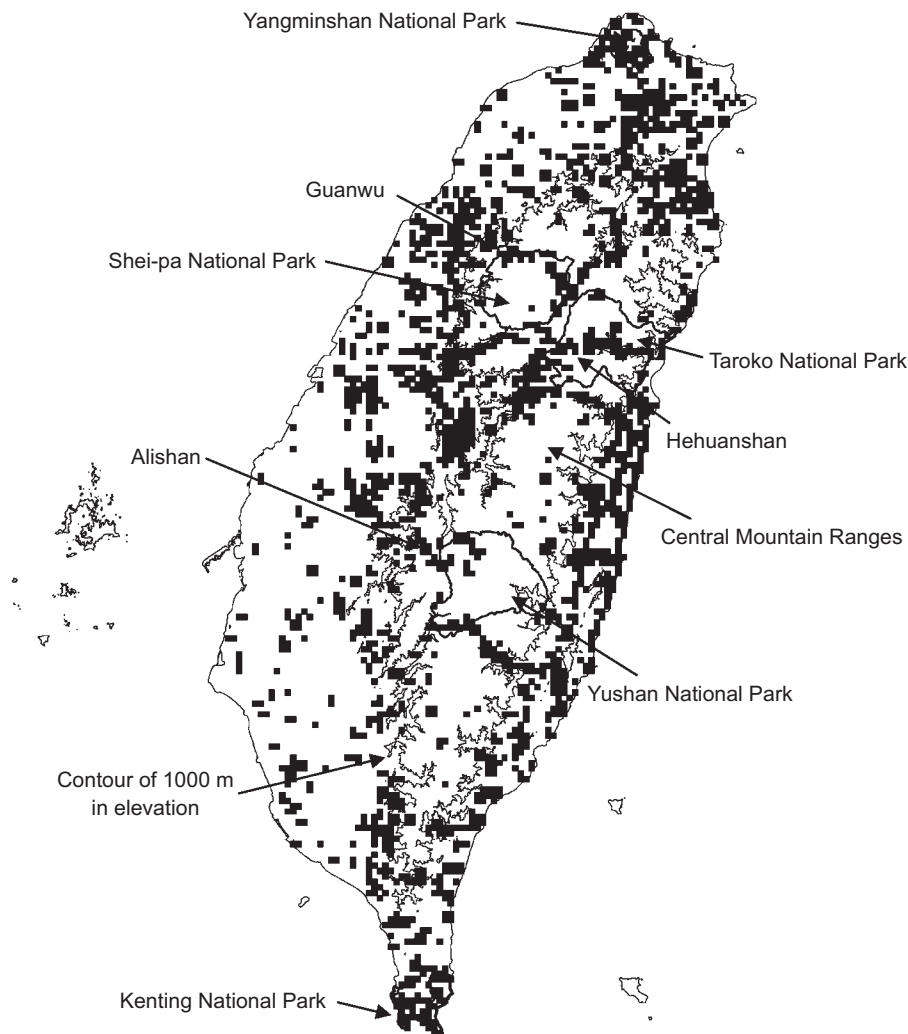
The sighting/collection data were obtained

from the Taiwan Amphibian Database (Lee et al. 1998), which was derived from field studies conducted from 1981 to 1994 covering all representative spots in Taiwan (Fig. 1) with over 15,000 sighting records. A record was defined as a sighting of an animal at a location about 200 m away from other locations. For each collection, we recorded the species or species complex and approximated the locality in coordinates of the Transverse Mercator projection based on 1: 25,000 topographic maps. In total, 162 records of individual salamanders were sorted for this study. Of these data, 87 were for *H. arisanensis*, 60 for the *H. formosanus-sonani* complex, and 15 for *Hynobius* sp. 1. Since some of the early records were not mapped precisely enough for us to apply an ecological and

environmental-factor database in a 2 x 2 km grid system, we converted these sighting data into the grid system using a geographic information system, i.e., ArcGIS. In total, 51 grids were generated for this study of salamanders, in which *H. arisanensis* occurred in 28 grids, the *H. formosanus-sonani* complex in 13 grids, and *Hynobius* sp. 1 in 10 grids. Although the elevations were between 1900 and 3650 m for all sighting records (Lue and Chuang 1992), the vertical distribution ranged from 1361 to 3429 m after applying the grid system.

### Environmental factor database

An ecological and environmental GIS database of Taiwan (Lee et al. 1997) was used to esti-



**Fig. 1.** Location of the amphibian survey squares (2 x 2 km) and 5 national park boundaries in Taiwan. The contour line indicates 1000 m in elevation. Areas above this elevation correspond to the Central Mountain Range.

mate the environmental characteristics of the hynobiid distribution. We selected 19 environmental variables from the database, including temperature, precipitation, level of human development, and topographic factors (Table 1). We also used a GIS to generate the following distance measurements: the distances to regions above 3000 m in elevation, rivers, major roads, major cities, and the coastline (explained below) for further comparisons and analyses. Most of the original map sources were at resolutions of 1:25,000 or 1:100,000. These maps were digitized and rasterized into 2 x 2 km grid cells.

Climatic variables were obtained and digitized for further analyses. A warmth index was derived by adding up each monthly mean temperature minus 5 (Liu and Su 1983). Dry season precipitation was the sum of monthly precipitation levels

from Oct. to Mar., and was used to represent the rainfall of the dry period in Taiwan (Central Weather Bureau 1990). The ratio of the dry period precipitation and the annual total precipitation was calculated. The water supply of each month was determined by comparing the monthly mean precipitations with the critical amount of rainfall, i.e., multiplying the monthly mean temperature by 2. Negative values indicated a water shortage (coded as 1), while positive values meant an abundance (coded as 0). Furthermore, the total number of months under water stress was estimated.

Elevation contours were digitized in 100 m intervals using 1:50,000 topographic maps. The layers for the shortest distances (in km) to areas above 3000 m in elevation, rivers, major roads (railways, highways, and freeways), the coastline, and major cities were derived from a raster-based

**Table 1.** Environmental and landscape variables used in the analysis. Values are derived from data shown which are representative values in a 2 x 2 km grid. Significant levels for *F*-test: NS for not significant, \**p* < 0.05, \*\**p* < 0.01, \*\*\**p* < 0.001

Environmental variable	Taiwan			Areas where other amphibians were found			Areas where salamanders were found			<i>p</i> (difference between other amphibians and salamanders)
	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	
Temperature										
Annual mean temperature (°C)	19.5	6.7	25.2	20.0	8.8	25.0	11.3	7.0	16.0	***
Jan. mean (°C)	12.9	1.0	21.0	13.5	3.0	21.0	5.6	1.0	11.0	***
July mean (°C)	24.4	11.0	31.0	25.3	13.0	31.0	15.5	11.0	20.0	***
Warmth index (°C)	173.7	32	242	180.2	49	240	77.4	32	137	***
Precipitation										
Annual precipitation (mm)	2393	1182	5650	2536	1204	5562	3032	2098	4006	***
Total precipitation in the dry period (Oct.-Mar.) (mm)	427	93	2800	549	93	2800	571	189	912	NS
Ratio of dry-period to annual precipitation	0.17	0.03	0.55	0.20	0.04	0.54	0.20	0.06	0.30	NS
Number of months short of precipitation	1.6	0	7	1.8	0	7	0.1	0	1	***
Human development and topographic factors										
Proximity to areas above 3000 m (km)	43.8	0.0	145.1	48.8	0.0	145.1	13.4	0.0	69.7	***
Proximity to rivers (km)	2.0	0.0	10.1	1.9	0.0	9.5	2.2	0.0	6.5	NS
Proximity to roads (km)	4.3	0.0	23.3	2.9	0.0	20.5	5.3	0.0	18.7	***
Proximity to the coastline (km)	24.7	0.0	66.9	22.5	1.0	66.5	39.6	23.4	66.4	***
Proximity to major cities (km)	20.5	0.0	88.3	19.0	0.0	83.3	34.1	20.9	49.5	***
Urban development index	45.9	13.0	99.0	53.4	13.0	99.0	29.6	13.0	50.0	***
Elevation (m)	696	50	3429	505	50	3058	2461	1361	3429	***
Maximum elevation (m) in the grid	957	50	3950	752	50	3350	2908	2150	3950	***
Minimum elevation (m) in the grid	472	50	3050	327	50	2750	1946	850	3050	***
Population density in 1994 (number/ha)	58	0	27516	828	5	27516	12	5	40	**
Naturalness index	6.1	0	10	5.6	1	10	9.3	4	10	***

GIS package, IDRISI (IDRISI 1997). An urban development index, calculated based on the proportion of people participating in different types of industry in a township, was used to represent the development degree of a particular area. A naturalness index was generated from a vegetation map by assigning wilderness conditions to each forest type on a 0 (developed and highly disturbed)-to-10 (undisturbed and highly natural) scale (Lee et al. 1997). Human populations in 1994 within townships were sorted from population census datasets and converted to densities (per square kilometer). Most of the data were first digitized in ArcGIS and rasterized or calculated using SAS or IDRISI.

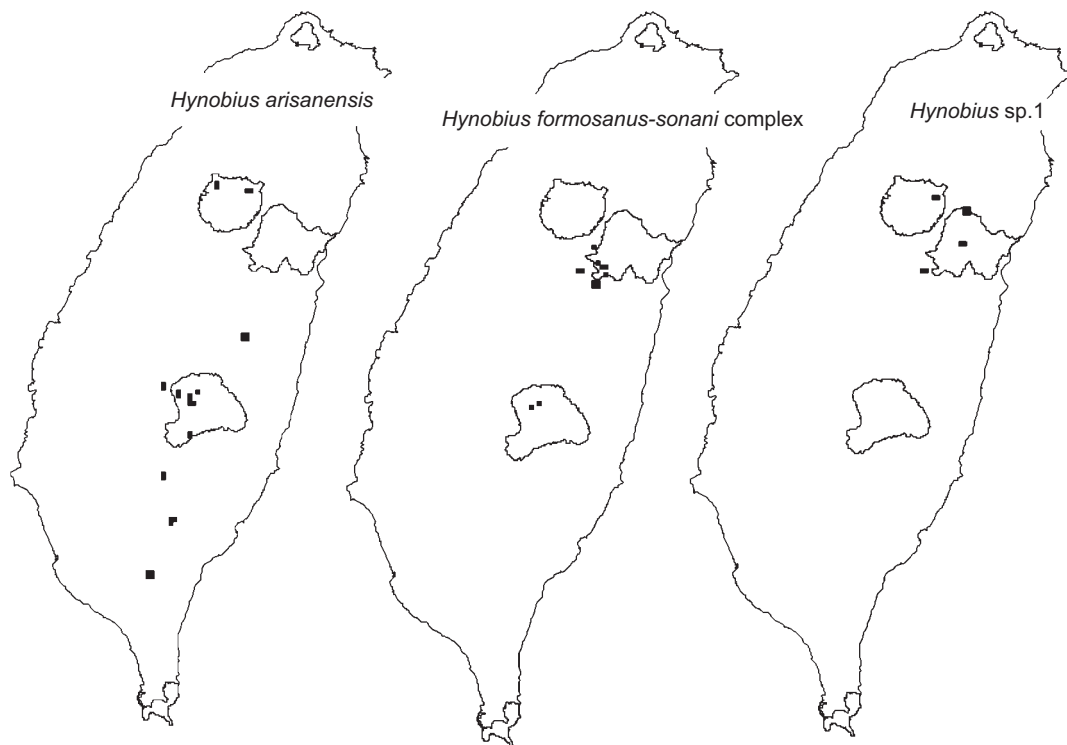
### Statistical analysis

Differences between the habitats of salamanders and other amphibians, and among the 3 salamanders species/species complex were analyzed by ANOVA based on deviations of the transformed variables from a normal distribution. Furthermore, Duncan's new multiple range test was applied to determine significant differences among means of

the variables.

DFA was used to estimate the distribution characteristics of these species. We first produced a complete model using all of the variables which showed significant contributions in order to distinguish the habitats of these species based on the previous ANOVAs. Moreover, we performed a stepwise DFA to generate the most important variables for a final model. We selected the final model for the analysis based on close agreement of the initial and jackknifed classification matrices and Wilks' $\lambda$  (Afifi and Clark 1996). Canonical DFA was performed to evaluate the contributions of the predictor variables.

The DFA classification rules were applied to classify areas above 1300 m in elevation to approach the potential distributions for these species. Our calculations were performed in SAS and SYSTAT. The protection status of these salamanders was investigated by overlaying the boundaries of 5 national parks in Taiwan with the observed records and predicted suitable habitat. The total potential areas for each species and species complex in the national parks were estimated for comparisons.



**Fig. 2.** Currently known distributions of *Hynobius arisanensis*, the *H. formosanus-sonani* complex, and *Hynobius* sp. 1 in Taiwan, and the locations of the 5 national parks.

## RESULTS

### Distribution

The distribution maps (Fig. 2) show that the salamanders are restricted to small patches of habitat, and the 3 species and species complex exhibit distinct distribution patterns. Most of the *Hynobius* populations are small in size and isolated. *Hynobius arisanensis*, which shows a north-south pattern along the Central Mountain Range, is relatively widely distributed. Distribution of the *H. formosanus-sonani* complex is restricted to the southwestern corner of Taroko National Park (in the Hehuanshan area) and in the center of Yushan National Park. *Hynobius* sp. 1 can be found in the northern part of the *H. formosanus-sonani* complex's distribution area; however, it is only represented in the Shei-pa and Taroko National Park regions. The geographic range, characterized by the latitudinal distance, for *H. arisanensis* is 210 km, which is larger than those of the *H. formosanus-sonani* complex (84 km) and *Hynobius* sp. 1 (30 km). The habitats of *H. arisanensis* and the *H. formosanus-sonani* complex overlap at the center of Yushan National Park. One overlapping area for *H. arisanensis* and *Hynobius* sp. 1 is found at the northeastern corner of Shei-pa National Park. The site where the habitats of the *H. formosanus-sonani* complex and *Hynobius* sp. 1 found is in the Hehuanshan area, outside the southwestern corner of Taroko National Park.

Compared to other amphibian species (frogs

and toads), the hynobiid salamanders in Taiwan tend to occur in high-elevation montane areas, with low temperatures, high annual precipitation, little disturbance, and high humidity (Table 1). The mean annual precipitation is 3031 mm (SD = 484). Most of the sightings occurred near small, slow-moving bodies of water. The average temperature in Jan. (the minimum mean) was 5.6°C and in July was 15.5°C (the maximum mean). Vegetative cover types include conifer forests (of fir *Abies kawakamii*, spruce *Picea morrisonicola*, hemlock *Tsuga chinensis*, and red cypress *Chamaecyparis formosensis*), broadleaf forests, mixed forests, and high-mountain grassland.

### Predictive distribution

Seven landscape attributes, i.e., annual precipitation, total precipitation in the dry period (Oct.-Mar.), ratio of precipitation in the dry period to the annual amount, and distances to areas above 3000 m in elevation, rivers, major roads, and the coastline, differed for the habitats of these species (Table 2). No significant differences were found for temperatures (Jan., July, and annual average), the warmth index, elevation, proximity to major cities, naturalness index, or human population density.

The discriminant function analysis based on the prediction variables showed that a 5 variable model (Wilks'λ = 0.22,  $F = 9.94$ ,  $df = 10, 88$ ,  $p < 0.001$ ), in the order of the stepwise sequence, total precipitation in the dry period, and distances to major roads, the coastline, rivers, and areas above

**Table 2.** Mean and standard deviation (SD) of the environmental variables that significantly differed ( $p < 0.05$ ) among locations of the 3 *Hynobius* species and species complex of salamanders. Means with different letters in a row indicate a significant difference based on Duncan's new multiple-range test

Variable	<i>H. arisanensis</i> ( $n = 28$ )		<i>H. formosanus-sonani</i> complex ( $n = 13$ )		<i>Hynobius</i> sp. 1 ( $n = 10$ )	
	Mean	SD	Mean	SD	Mean	SD
Annual total precipitation (mm)	3056.7 <sup>a</sup>	452.9	3266.4 <sup>a</sup>	424.8	2655.5 <sup>b</sup>	453.5
Total precipitation in the dry period (Oct.-Mar. (mm))	471.1 <sup>a</sup>	174.5	775.6 <sup>b</sup>	120.9	635.8 <sup>c</sup>	90.5
Ratio of dry-period to annual precipitation	0.16 <sup>a</sup>	0.07	0.24 <sup>b</sup>	0.03	0.24 <sup>b</sup>	0.03
Proximity to areas above 3000 m in elevation (km)	20.4 <sup>a</sup>	23.0	4.7 <sup>b</sup>	3.9	5.0 <sup>b</sup>	6.0
Proximity to rivers (km)	2.9 <sup>a</sup>	1.5	1.8 <sup>b</sup>	0.9	0.9 <sup>b</sup>	0.7
Proximity to major roads (km)	7.0 <sup>a</sup>	6.4	1.5 <sup>b</sup>	1.7	5.4 <sup>a</sup>	3.3
Proximity to the coastline (km)	42.2	13.1	37.9	7.6	34.5	8.6

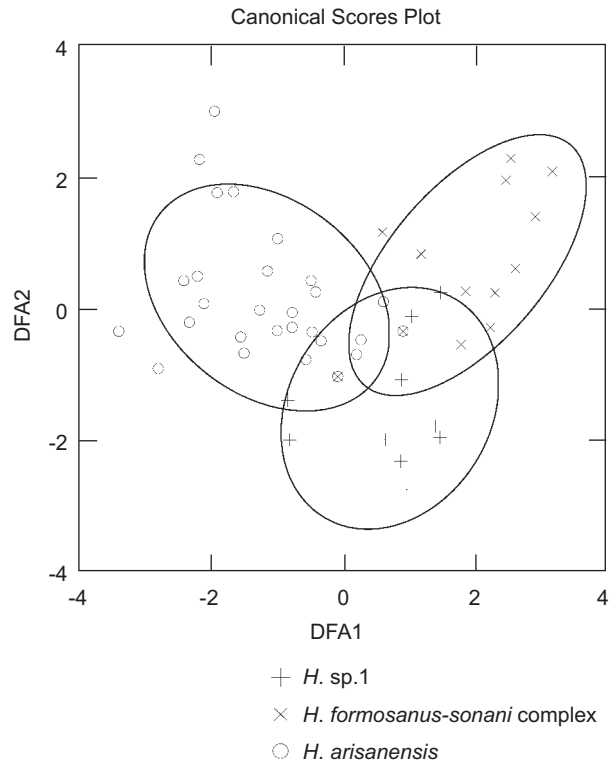
3000 m, was the “best” model to discriminate the occurrence of these species. The classification accuracy was 82% with Cohen’s kappa of 0.72 (Table 3). Predictability of the presence varied from 80% for *Hynobius* sp. 1 to 84.6% for the *H. formosanus-sonani* complex. The canonical score plot (Fig. 3) shows that there are some overlapping areas for each pair of species and possible overlapping areas for all of the species and the species complex. The potential area of overlap between the *H. formosanus-sonani* complex and *Hynobius* sp. 1 was higher than those of the other combinations, while the area of overlap between the *H. formosanus-sonani* complex and *H. arisanensis* was the smallest. The areas occupied by *H. arisanensis* were more heterogeneous than those of the others.

The 1st DFA axis explained 75% of the total variation, while the 2nd axis represented 25%. The 1st axis reflected the combination of the total precipitation in the dry period, and distances to major roads and the coastline, whereas the proximity to areas above 3000 m in elevation, total precipitation in the dry period, and proximity to the coastline dominated the 2nd axis (Table 4). *Hynobius arisanensis* had larger variations for both axes, whereas *Hynobius* sp. 1 and the *H. formosanus-sonani* complex showed relatively smaller variations for the 1st axis than for the 2nd axis. Based on the standardized canonical discriminant function coefficients (Table 4), total precipitation in the dry period, and the proximity to major roads and the coastline contributed more than the other variables.

### Protection status

Most of the potential habitats (Fig. 4) generat-

ed from the DFA classification rules are outside the boundaries of the national parks (Table 5). *Hynobius arisanensis* had larger potential areas of habitat than the other types (60% for *H. arisanensis*; 21% for the *H. formosanus-sonani* complex;



**Fig. 3.** Discriminant function analysis of the distributions of *Hynobius arisanensis*, the *H. formosanus-sonani* complex, and *Hynobius* sp. 1 in Taiwan. Canonical scores of the 3 groups with the 95% confidence interval of the means are plotted. Canonical scores of group means for the Alishan type are -1.13 for DFA1 and 0.20 for DFA2, for Nengao are 1.89 for DFA1 and 0.70 for DFA2, and for Nanhu are 0.72 for DFA1 and -1.48 for DFA2.

**Table 3.** Classification efficiency (%) for the discriminant function model based on total precipitation in the dry period, and proximities to major roads, the coastline, rivers, and areas above 3000 m. The overall correct classification efficiency was 82% with Cohen’s kappa equal to 0.72. Numbers of grid cells are shown in parentheses

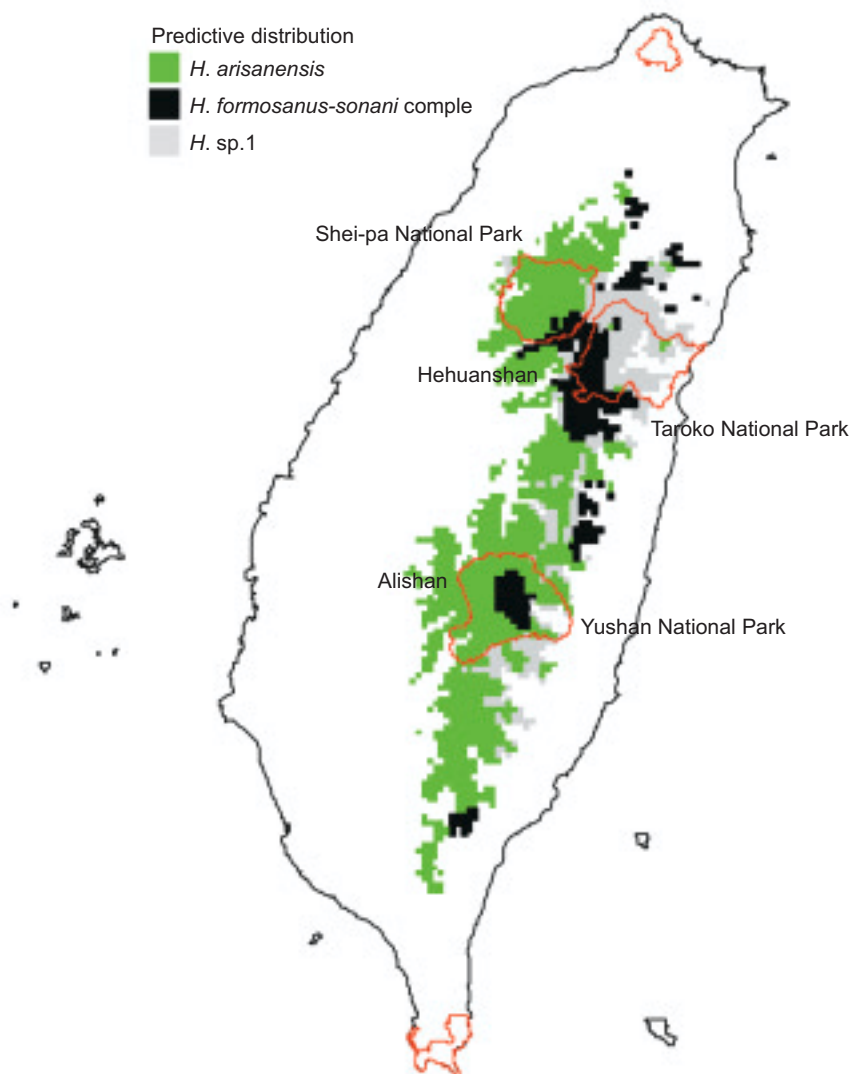
Observed	Predicted			Total
	<i>Hynobius arisanensis</i>	<i>H. formosanus-sonani</i> complex	<i>Hynobius</i> sp. 1	
<i>H. arisanensis</i>	82.1 (23)	3.6 (1)	14.3 (4)	(28)
<i>H. formosanus-sonani</i> complex	0.0 (0)	84.6 (11)	15.4 (2)	(13)
<i>Hynobius</i> sp. 1	0.0 (0)	20.0 (2)	80.0 (8)	(10)

and 19% for *Hynobius* sp. 1). *Hynobius arisanensis* had large and non-fragmented habitats inside Yushan and Shei-pa National Parks. The *H. formosanus-sonani* complex was characterized by many smaller patches occurring along the Central Mountain Range with major distribution centers located in areas between Shei-pa and Taroko National Parks, and in Taroko National Park. Despite its relatively few known records, the prediction model shows that *Hynobius* sp. 1 potentially occurs mainly on the eastern side of the Central Mountain Range and inside Taroko National Park, with some smaller potential habitat areas occurring between Taroko and Yushan National Parks but outside their boundaries.

## DISCUSSION

Differences in the geographic distributions of *Hynobius* species and other amphibian species (frogs and toads in Taiwan) are probably reflections of their varied life history traits and population structures (Beebee 1996). Our results confirmed that the habitats of the salamanders substantially differ from those of other amphibian species. These salamanders occur in higher-elevation habitats with lower temperatures and higher precipitation (Table 1).

Five landscape factors that showed the best correlations to the distributions possibly indicate the great importance of precipitation to salamanders. Since factors contributing to an adequate



**Fig. 4.** Predictive classification results of discriminant function analysis of *Hynobius* spp. for areas above 1300 m in elevation.

habitat description for many amphibians are complex and diverse (Beebee 1985, 1996), multivariate approaches at various spatial scales may generate valuable insights and a better understanding of the spatial distribution of salamanders in Taiwan. It has been hypothesized that the total precipitation in the dry period is important for maintenance of the life history of salamanders and thus plays an important role in delimiting the distributions of *Hynobius* species in Taiwan (Chen 1984). Our results also suggest that precipitation variables have greater contributions to the discrimination of their distributions than do temperature and elevation variables. Dry-period precipitation is largely influenced by the northeast monsoon winds during the winter (Nov.-Feb., Su 1984a b) and shows considerable variations in high-elevation alpine areas.

Results of the DFA prediction (Fig. 4) indicated that *H. arisanensis* may have adapted to broader environmental conditions and may have colonized relatively heterogeneous habitats. In con-

trast, the *H. formosanus-sonani* complex and *Hynobius* sp. 1 have relatively specific ecological requirements. The known distribution records and the DFA prediction indicate that the northern parts of the distribution range, especially the Hehuanshan area, are potential areas of overlap for these salamanders. Lue et al. (1989) found diverse color patterns of salamanders in this region and suggested that these areas might have played an important role in terms of the zoogeographical distributions and evolution of salamanders in Taiwan.

Our study supports the idea that the Alishan and Hehuanshan areas are possible important habitats for salamanders in Taiwan (Chen and Lue 1986, Lue et al. 1989). It has been shown that 3 national parks located in the Alishan and Hehuanshan regions harbor large undisturbed areas suitable for salamanders, and these salamanders are mainly located inside or close to these national parks. These areas, therefore, may be considered potential reserves for these sala-

**Table 4.** Discriminant function and canonical discriminant functions (standardized by within variances) for these species and species complex of salamanders (*Hynobius* spp.)

	Classification function coefficients			Standardized canonical discriminant function coefficients	
	<i>H. arisanensis</i>	<i>H. formosanus-sonani</i> complex	<i>Hynobius</i> sp. 1	DFA 1	DFA 2
Constant	-73.38	-82.18	-58.03	-	-
Total precipitation in the cold season (Oct.-Mar.)	0.10	0.13	0.10	0.934	1.184
Proximity to areas above 3000 m	9.36	10.11	8.33	0.273	1.619
Proximity to rivers	2.92	2.45	1.69	-0.287	0.584
Proximity to major roads	0.28	-0.23	0.06	-0.805	-0.238
Proximity to the coastline	1.22	1.17	1.01	-0.526	0.811

**Table 5.** Comparison of the total potential habitats (%) for *Hynobius arisanensis*, the *H. formosanus-sonani* complex, and *Hynobius* sp. 1 within and outside the national parks in Taiwan

Species	Within national parks						Outside national parks		Total area (ha)
	Yushan		Taroko		Shei-pa		No. of patches	Area (ha)	
	No. of patches	Area (ha)	No. of patches	Area (ha)	No. of patches	Area (ha)			
<i>H. arisanensis</i>	4	62,057 (13)	1	1195 (0)	5	54,491 (11)	43	375,443 (76)	493,186 (60)
<i>H. formosanus-sonani</i> complex	2	21,679 (12)	2	28,316 (16)	2	12,196 (7)	28	114,610 (65)	176,800 (21)
<i>Hynobius</i> sp. 1	16	11,354 (7)	5	45,198 (28)	5	5899 (4)	43	963,52 (61)	158,803 (19)

mander species. However, these sites include a number of famous scenic areas that attract numerous visitors, and the salamander habitats may be threatened by potential frequent human disturbances. Long-term monitoring programs of population dynamics and distributions of salamanders are highly recommended for conservation purposes.

The predicted distributions presented in our study may provide insights into potential locations of populations of salamanders in Taiwan. Although the distribution records obtained from this study show that salamanders have restricted home ranges, the habitat predictions seem to be more optimistic concerning the presence of these species. Hence, we suggest an assessment of the current field status based on our predictions to estimate the distributions of these salamander species. Such an investigation will contribute to verifying the current rarity of these salamander species. Furthermore, the accuracy of our prediction model may also be evaluated.

To better understand salamanders in Taiwan, the following tasks should be considered: taxonomic clarification, distribution assessment, life history approaches, basic ecological studies, demographic estimations, and monitoring of population dynamics. These efforts may generate a better understanding for the management and conservation of salamander species.

**Acknowledgments:** We thank S. N. Chan, S. L. Garman, and 2 anonymous reviewers for valuable comments and suggestions on this manuscript; S. H. Chen, M. C. Yeh, and K. C. Yeh for conducting the field survey; Y. C. Lee, Y. H. Pan, W. H. Fu, and J. C. Hsieh for GIS work on environmental factor databases and wildlife distributions; and T. S. Ding and C. Y. Liao for help with the literature. Collection of the salamander database was partially funded by the National Park Administration, the Council of Agriculture, and the National Science Council, Taiwan. Preparation of this paper was supported by the Ministry of Education, Taiwan.

## REFERENCES

- Affi AA, V Clark. 1996. Computer-aided multivariate analysis. 3rd edn. London: Chapman and Hall.
- Anonymous. 1996. The 1996 IUCN red list of threatened animals. Cambridge, UK: The World Conservation Union.
- Beebee TJC. 1985. Discriminant analysis of amphibian habitat determinants in south-east England. *Amphibia-Reptilia* **6**: 35-43.
- Beebee TJC. 1996. Ecology and conservation of amphibians. London: Chapman and Hall.
- Central Weather Bureau. 1990. Climatic atlas of Taiwan, the Republic of China. Taipei, Taiwan: Central Weather Bureau, Ministry of Communications. (in Chinese)
- Chen SH. 1984. The biology of salamanders in Taiwan. Master's thesis, National Taiwan Normal Univ., Taipei, Taiwan. (in Chinese)
- Chen SH, KY Lue. 1986. Studies on Taiwanese hynobiids: preliminary studies on history, distribution and morphology. In YS Lin, KH Chang, eds. Proceeding for the Symposium on Wildlife Conservation (I): Wildlife in National Parks and Natural Reserves. Taipei: SWAN, pp. 79-104.
- Du MJ, KY Lue. 1982. Comparative stomach content analysis on the eleven species of amphibian in Taiwan, including endemic *Hynobius formosanus*. *Annual Taiwan Mus.* **25**: 225-234. (in Chinese)
- Dunn ER. 1923. The salamanders of the family Hynobiidae. *Proc. Am. Acad. Arts Sci.* **58**: 445-523.
- IDRISI. 1997. IDRISI for Windows, version 2.0. Worcester: Clark Univ.
- Iizuka K, M Kakegawa. 1989. Comparative karyology in five rare species of hynobiid salamanders from Taiwan and Japan. In M Matsui, T Hikida, RC Goris, eds. Current herpetology in East Asia. Kyoto, Japan: Herpetological Society of Japan, pp. 95-105.
- Kakegawa M, K Iizuka, S Kuzumi. 1989. Morphology of egg sacs and larvae just after hatching in *Hynobius sonani* and *H. formosanus* from Taiwan, with an analysis of skeletal muscle protein compositions. In M Matsui, T Hikida, RC Goris, eds. Current herpetology in East Asia. Kyoto, Japan: Herpetological Society of Japan, pp. 147-155.
- Lee PF, CY Liao, YC Lee, YH Pan, WH Fu, HW Chen. 1997. An ecological and environmental GIS database for Taiwan. Taipei, Taiwan: Council of Agriculture. (in Chinese with English abstract)
- Lee PF, KY Lue, CC Hsieh, YC Lee, YH Pan, HW Chen, TC Pan, YS Ding. 1998. A wildlife distribution database in Taiwan. Taipei, Taiwan: Council of Agriculture. (in Chinese with English abstract)
- Liu TR, HJ Su. 1983. Forest ecology. Taipei, Taiwan: Sangwu Publisher. (in Chinese)
- Lue KY, KS Chuang. 1992. The discovery of metamorphosed juveniles of Formosan salamander (*Hynobius formosanus*) in Yushan National Park. *Bull. Inst. Zool. Acad. Sinica* **31**: 312-316.
- Lue KY, KS Chuang, CY Lin. 1989. The survey on salamanders in the great Hohuan Shan area of Taroko National Park. Hualien: Taroko National Park. (in Chinese with English abstract)
- Lue KY, JS Lai. 1997. How many species of hynobiid salamanders in Taiwan? In KY Lue, TH Chen, eds. The Symposium on the Phylogeny, Biogeography and Conservation of Fauna and Flora of East Asian Region. Taipei, Taiwan: Department of Biology, National Taiwan Normal Univ., pp. 87-98.
- Lue KY, CY Lin, KS Chuang. 1990. Wildlife database in Taiwan: amphibians (II). Taipei, Taiwan: Council of Agriculture. (in Chinese)
- Maki M. 1922. Notes on the salamanders found in the island of Formosa. *Zool. Mag. Tokyo* **34**: 635-639.
- Matsui M, H Iwasawa, H Takahashi, T Hayashi, M Kumakura. 1992. Invalid specific status of *Hynobius sadoensis* Sato:

- electrophoretic evidence (Amphibia: Caudata). J. Herpetol. **26**: 308-315.
- Matsui M, H Ota. 1995. On Chinese herpetology. Herpetologica **51**: 234-250.
- Pavignano I, C Giacoma, S Castellano. 1990. A multivariate analysis of amphibian habitat determinants in north western Italy. Amphibia-Reptilia **11**: 311-324.
- Romero J, R Real. 1996. Macroenvironmental factors as ultimate determinants of distribution of common toad and natterjack toad in the south of Spain. Ecography **19**: 305-312.
- Sato I. 1941. The salamanders of Formosa. Trans. Nat. Hist. Soc. Formosa **31**: 114-124. (in Japanese)
- Sato I. 1943. A monograph of the tailed Batrachians of Japan. Osaka, Japan: Nippon Shuppan-sha. (in Japanese)
- Seto T, T Utsunomiya. 1987. Chromosome analysis of *Hynobius arisanensis* Maki, a salamander endemic to Taiwan. Herpetologica **43**: 117-119.
- Su HJ. 1984a. Studies on the climate and vegetation types of the natural forests in Taiwan (I): analysis of the variations in climatic factors. Q. J. Chin. For. **17**: 1-14.
- Su HJ. 1984b. Studies on the climate and vegetation types of the natural forests in Taiwan (II): altitudinal vegetation zones in relation to temperature gradient. Q. J. Chin. For. **17**: 53-73.
- Yeh KC, KS Chuang, KY Lue, SH Chen. 1988. The study of antipredator behaviors of Formosan salamanders (*Hynobius formosanus*). Bull. Inst. Zool. Acad. Sinica **27**: 37-48.
- Yeh MC. 1991. Habitat and population dynamics of *Hynobius formosanus*. Master's thesis, National Taiwan Normal Univ., Taipei, Taiwan. (in Chinese)
- Zhao EM, Q Hu. 1988. Studies of Chinese tailed amphibians. Oxford, OH: Society for the Study of Amphibians and Reptiles.