

Diversity and Distribution of Amphibians in Ise Forest Reserve Ekiti State.

Ogunyemi O.O

*Department of Forestry, Wildlife and Fisheries Management,
Ekiti State University, Ado-Ekiti. Nigeria*

E-mail: olumideogunyemi80@yahoo.com

Abstract

The investigation of amphibian diversity and distribution in Ise Forest Reserve, Ekiti State, Nigeria, was carried out between November to July, 2014. Sampling took place in four microhabitats located in the swampy and upland areas of the reserve. 10 different species of Amphibians and belonged to order Anura and 10 families were identified. Two hundred and thirty seven (237) and one hundred and forty-nine (149) individual amphibians were counted during the wet and dry seasons respectively. This number was irregularly distributed in the four microhabitat types. The under fallen log microhabitat recorded the highest percentage (30.80%) of individual amphibians followed by stream microhabitat (29.11%), under rock habitat (20.68%) and grass vegetation microhabitat (19.41%). There were significant differences in amphibian diversity between the habitats and abundance among the species. This indicates that the amphibian species shows some level of habitat preferences. However, the under fallen log microhabitat favoured amphibian diversity and distribution most in both seasons. The results support the hypothesis that seasonal differences influence composition and abundance of some species of amphibian irrespective of habitat.

Keywords: Amphibians, Microhabitat, Anura , Diversity.

Introduction

Amphibians are an important component of many ecosystems even though their biomass is usually less than that of avian. However, amphibians occupy a diverse range of habitats and micro-habitats which ranges from the remotest deserts, oceans and mountains on earth. Although they are ubiquitous, they are certainly more numerous in some places than in others. The causes of such variations, in most cases are poorly understood.

Nigeria has some of the most beautiful amphibians in the world. The Nigerian amphibians is diverse as the environment itself because it is such a large country that stretches from the beaches and mangrove swamps of Gulf of Guinea through the remnants of the rainforest to the savannas and thorn scrub of the north. This agro-ecological diversity and

niches provides the habitats for a fascinating variety of amphibians.

Some achievements have been made in wildlife conservation over the years but it is only in recent times that the study of amphibians started gaining grounds all over the world. Amphibians are an integral part of the ecosystem; such that their study can alert us to what is going wrong in the environment, as amphibians are excellent environmental indicator. The investigations on amphibian species are receiving attention because of the roles these amphibians play as indicators of ecosystem deterioration (Wake, 1991). Behangana (2004) asserted that the general ecological importance of amphibians lies in their being predators, acting as primary and secondary carnivores on insects thereby naturally regulating their populations.

Amphibians can also be referred to as habitat quality indicators because their population declines when habitat quality is very poor especially when the environment is polluted. Moore and Church (2008) opined that the probable causes of the amphibian decline are multi-faceted and involve various complex combinations of obvious ones such as habitat destruction, habitat fragmentation or loss, pollution, over-harvesting and proliferation of invasive species.

Currently, there is expression of great concern about the extinction of amphibians globally (Reid and Zippel, 2008) as one in three amphibian species is threatened with extinction (Morris, 2007). In recent years the interest in conservation of amphibians had grown in many countries and regions emphasized the need for more studies of the ecological impact of amphibian declines and extinctions. Monney et al. (2001) asserts that amphibians in West Africa remain largely uninvestigated and that ecological research of amphibians linked to conservation activities has generally lagged behind. Thus, it is not surprising that little attention has been focused on amphibian species diversity, inventory, monitoring, distribution and abundance in Nigeria. This is despite the common roles of amphibian resources in sustaining the ecosystems but the danger is in the decimation of the ecosystems which support this large diversity of amphibians. The purpose of this study is to provide information on species diversity of the amphibian community, microhabitat preferences and distribution in Ise Forest Reserve Ekiti State, Nigeria.

Materials and Methods

Study Area

The study was carried out in the 72.52km² Ogbese Forest Reserve in Ekiti State, Nigeria and the adjoining communities. The Ogbese Forest Reserve is located between 7° 32'N and 5° 21' 43" E. The prevailing climate is tropical with an average temperature of 25°C all year

round and high relative humidity. The rainy season has an average of 240 days with mean annual rainfall of 1250 to 1400 mm. The pattern of rainfall distribution over the long rainy season between April and mid-November is bimodal with a peak in September while the dry season stretches from mid-November to the end of March.

The terrain of the reserve is flat to slightly undulating with elevation of between 12 to 110 m above sea level. Light South westerly and Northeasterly winds blow over the area throughout the year which characterized the seasons in the reserve into rainy and the dry season. The reserve is surrounded by villages and farm settlements inhabited by the largely agrarian population that engages in smallholder food and tree cash crop production systems with poor farming methods.

Surveys

The study area was classified into four different habitat types and sampled during the period of February to August 2016. A stratified random sampling was employed for the selection of four experimental sites. Site choices were based on different types of identified micro habitat that exists within the reserve and a total of two (20 x 20m) plots were formed in each of the four identified micro habitats.

The four micro habitats categories were recognized and named as stream (L1), under fallen log(L2), under rock(L3) and grassy micro habitat(L4). Visual Encounter Surveys (VES) as described by Crump and Scott (1994) was the detection technique used in all the micro habitats. Systematic searching for amphibians in the selected plots was carried out by a team of five people for about one hour in the early hours of the morning and late in the evening.

The amphibians collected were identified directly in the field to species level and their taxonomic groups properly categorized after Rodel (2007) and then released. The cumulative list of amphibians species recorded

in each of the selected micro habitats was used as a basic measure of amphibian richness. A one- way analysis of variance (ANOVA) was employed to test the significant difference at 5% level of significance in the means of population observed in selected habitats.

Diversity calculation was carried out on the identified amphibians to describe the abundance of species and individuals within the four micro habitat types.

Species diversity index (N) was determined by Shannon Wiener's index as follows.

$$H^1 = -\sum p_i \ln p_i$$

Results

A total of 386 individual anurans were recorded during the wet and dry seasons in the four micro-habitats found in Ise Forest Reserve. The species belong to ten amphibian species in the order Anurans and in eight (8) families (Table 1 and 2).

Apart from the family Hylidae which occurred under the fallen logs micro habitat the others namely: Pipidae, Rhacophoridae, Bufonidae, Pseudacrididae, Arthroleptidae, Hemisotidae and Ranidae occurred freely in the four microhabitats with the family Ranidae recording the highest encounter rate (Table 2). The highest numbers of amphibians at 70 and 49 were recorded in the under- fallen log microhabitat compared to under-rock habitat with the least number at 49 and 26 in the wet and dry seasons respectively.

where, $P_i = n_i/N$, which denotes the importance probability of each species in a population, n_i =importance value for each species,

N =total of importance value (Shannon and Weaver, 1949)

Species richness is the mean number of species per sample and determined using the formula of Margalef (1958).

$$\text{Species richness index (d)} = \frac{s-1}{\ln N}$$

where, s = number of species,

N =number of individuals of all species.

Also the under fallen log microhabitat type contained the highest species of amphibians than the other three microhabitats. The highest species of amphibians: 10 and 8 were recorded in the under fallen logs microhabitat in both the wet and dry seasons respectively. Also 9 and 7 amphibian species were obtained in the stream micro habitat, 7 and 6 species were encountered in the under-rock microhabitat while the least amphibian species, 7 and 5 were observed in the under grass microhabitat in both seasons respectively. In both seasons, 10 amphibian species were recorded with 8 species common to both seasons while 2 species were exclusive to wet season. Also one amphibian species (*Litoria aurea*) was exclusive inhabitant of the under fallen logs microhabitat while no exclusive species was recorded in the other three microhabitats (Table 3)

Table 1: Amphibian distribution based on Order, Family and Species in Ise Forest Reserve

| S/N | Order | Family | Species | Common Name |
|-----|-------|----------------|----------------------------------|-----------------------------|
| 1 | Anura | Pipidae | <i>Xenopus laevis</i> | African clawed frog |
| 2 | Anura | Rhacophoridae | <i>Rhacophorus nigropalmatus</i> | Flying frog |
| 3 | Anura | Bufonidae | <i>Atelopus zeteki</i> | Golden frog |
| 4 | Anura | Bufonidae | <i>Bufo bufo</i> | Common toad |
| 5 | Anura | Rhacophoridae | <i>Chiromantis rufescens</i> | African foam-nest tree frog |
| 6 | Anura | Arthroleptidae | <i>Cardioglossa cyaneaspila</i> | Long fingered frog |
| 7 | Anura | Hemisotidae | <i>Hemisis marmoratus</i> | Molted burrowing frog |
| 8 | Anura | Hylidae | <i>Litoria aurea</i> | Bell frog |
| 9 | Anura | Ranidae | <i>Rana temporaria</i> | Common frog |
| 10 | Anura | Ranidae | <i>Rana calamitans</i> | Green frog |

Table 2: Number of amphibian species observed during the survey

| S/N | Species | Wet Season | Dry Season | Total | Relative Abundance (%) |
|-----|----------------------------------|------------|------------|-------|------------------------|
| 1 | <i>Xenopus laevis</i> | 36 | 18 | 54 | 13.99 |
| 2 | <i>Rhacophorus nigropalmatus</i> | 6 | Nil | 6 | 1.55 |
| 3 | <i>Atelopus zeteki</i> | 6 | 2 | 8 | 2.07 |
| 4 | <i>Bufo bufo</i> | 25 | 21 | 46 | 11.92 |
| 5 | <i>Chiromantis rufescens</i> | 31 | 21 | 52 | 13.47 |
| 6 | <i>Cardioglossa cyaneospila</i> | 27 | 18 | 45 | 11.66 |
| 7 | <i>Hemisis marmoratus</i> | 37 | 25 | 62 | 16.06 |
| 8 | <i>Litoria aurea</i> | 3 | Nil | 3 | 0.77 |
| 9 | <i>Rana temporaria</i> | 36 | 25 | 61 | 15.80 |
| 10 | <i>Rana clamitans</i> | 30 | 19 | 49 | 12.69 |
| | Total | | | 386 | 100 |

Table 3: Habitat distribution of individual species

| S/N | Habitat | Wet Season | | Dry Season | |
|-----|----------------|--------------------------------------|-----|---------------------------------------|-----|
| | | Species | Qty | Species | Qty |
| 1 | Stream L1 | i) <i>Xenopus laevis</i> | 13 | i) <i>Xenopus laevis</i> | 4 |
| | | ii) <i>Rhacophorus nigropalmatus</i> | 4 | ii) <i>Bufo bufo</i> | 8 |
| | | iii) <i>Atelopus zeteki</i> | 4 | iii) <i>Cardioglossa cyaneospilla</i> | 5 |
| | | iv) <i>Bufo bufo</i> | 9 | iv) <i>Hemisis marmoratus</i> | 6 |
| | | v) <i>Chiromantis rufescens</i> | 9 | v) <i>Rana temporaria</i> | 9 |
| | | vi) <i>Cardioglossa cyaneospilla</i> | 5 | vi) <i>Rana calamitans</i> | 6 |
| | | vii) <i>Hemisis marmoratus</i> | 9 | vii) <i>Chiromantis rufescens</i> | 6 |
| | | viii) <i>Rana temporaria</i> | 11 | | |
| | | ix) <i>Rana clamitans</i> | 9 | | |
| 2 | Fallen logs L2 | i) <i>Xenopus laevis</i> | 9 | i) <i>Xenopus laevis</i> | 7 |
| | | ii) <i>Rhacophorus nigropalmatus</i> | 2 | ii) <i>Atelopuszeteki</i> | 2 |
| | | iii) <i>Atelopus zeteki</i> | | iii) <i>Bufo bufo</i> | 7 |
| | | iv) <i>Bufo bufo</i> | 1 | iv) <i>Chiromantis rufescens</i> | 9 |
| | | v) <i>Chiromantis rufescens</i> | 6 | v) <i>Cardioglossa cyaneospilla</i> | 7 |
| | | vi) <i>Cardioglossa cyaneospilla</i> | 13 | vi) <i>Hemisis marmoratus</i> | 11 |
| | | vii) <i>Hemisis marmoratus</i> | 10 | iii) <i>Rana temporaria</i> | 3 |
| | | viii) <i>Litoria aurea</i> | 16 | viii) <i>Rana calamitans</i> | 3 |
| | | ix) <i>Rana temporaria</i> | 3 | | |
| | | x) <i>Rana clamitans</i> | 5 | | |
| 3 | Under Rock L3 | i) <i>Xenopus laevis</i> | 8 | i) <i>Xenopus laevis</i> | 4 |
| | | ii) <i>Bufo bufo</i> | 6 | ii) <i>Bufo bufo</i> | 3 |
| | | iii) <i>Chiromantis rufescens</i> | 7 | iii) <i>Chiromantis rufescens</i> | 4 |
| | | iv) <i>Cardioglossa cyaneospilla</i> | 8 | iv) <i>Cardioglossa cyaneospilla</i> | 6 |
| | | v) <i>Hemisis marmoratus</i> | 12 | v) <i>Hemisis marmoratus</i> | 8 |
| | | vi) <i>Rana temporaria</i> | 4 | vi) <i>Rana calamitans</i> | 1 |
| | | vii) <i>Rana clamitans</i> | 4 | | |
| 4 | Under Grasses | i) <i>Xenopus laevis</i> | 6 | i) <i>Xenopus laevis</i> | 3 |
| | | ii) <i>Atetopus zeteki</i> | 1 | ii) <i>Bufo bufo</i> | 3 |
| | | iii) <i>Bufo bufo</i> | 4 | iii) <i>Chiromantis rufescens</i> | 2 |
| | | iv) <i>Chiromantis rufescens</i> | 2 | iv) <i>Rana temporaria</i> | 13 |
| | | v) <i>Cardioglossa cyaneospil</i> | 4 | v) <i>Rana calamitans</i> | 9 |
| | | vi) <i>Rana temporaria</i> | 16 | | |
| | | vii) <i>Rana clamitans</i> | 12 | | |

Table 4: Habitat Distribution of Amphibians

| S/N | Habitat | Wet Season | Relative Abundance | Dry Season | Relative Abundance | Total |
|-----|------------------|------------|--------------------|------------|--------------------|-------|
| 1 | Stream | 73 | 30.80 | 44 | 29.53 | 117 |
| 2 | Under fallen log | 70 | 29.11 | 49 | 32.89 | 119 |
| 3 | Under Rock | 48 | 20.68 | 26 | 17.45 | 74 |
| 4 | Grass | 46 | 19.41 | 30 | 20.13 | 76 |
| | Total | 237 | | 149 | | 386 |

Thus, amphibians are more fairly distributed in the under fallen logs microhabitat than other microhabitat types (Table 4). *Hemisus marmoratus* recorded the highest abundance value of 62 in both seasons of study though *Rana temporaria*, *Xenopus laevis*, *Bufo bufo*, *Chiromantis rufescens*, *Rana clamitans* and *Cardioglossa cyaneospilla* also occurred in fairly high abundance and the other species occurring at low abundance in the study area, the least of 3.0 being *Litoria aurea*.

The means of amphibian population that occurred in all the four microhabitat types in both seasons differed significantly ($p > 0.05$)

(Table 6). Furthermore, homogeneity test indicated that the difference between the species richness of amphibians in all the four microhabitat types was not significant (Table 8). The highest species diversity during the wet and dry seasons were observed in the stream and under fallen logs microhabitats (0.92) and (0.85) respectively while the lowest diversity (0.74) and (0.59) were recorded in the under grass microhabitat in both the wet and dry seasons respectively (Table 5). A significant difference was found in the diversity between the microhabitat types in both wet and dry seasons of the study ($p > 0.05$) (Table 7).

Table 5: Species Richness and Shannon Wiener Index For the Four Locations

| Locations | | L1 | L2 | L3 | L4 |
|------------|---|------|------|------|------|
| Species | W | 4.30 | 5.00 | 3.53 | 4.11 |
| Richness D | D | 3.66 | 4.12 | 3.57 | 2.67 |
| Shannon | W | 0.92 | 0.89 | 0.82 | 0.74 |
| Weiner | D | 0.83 | 0.85 | 0.72 | 0.59 |
| Index | | | | | |

Table 6: Mean seasonal amphibian occurrence in both seasons

| Mean | Treatment |
|-------------------|-----------|
| 23.7 ^a | Wet |
| 14.9 ^b | Dry |

Mean with the same superscript in the columns are not significantly different ($P < 0.05$).

Table 7: Mean diversity of Amphibian species in selected locations

| Variables | L1 | | L2 | | L3 | | L4 | |
|-----------|------|--------------|------|-----------------|------|--------------|------|--------------|
| | Wet | Dry | Wet | Dry | Wet | Dry | Wet | Dry |
| Shannon | 0.88 | $\pm 0.10^a$ | 0.87 | $\pm 0.10^{ab}$ | 0.77 | $\pm 0.10^b$ | 0.67 | $\pm 0.10^c$ |

Mean with the same superscript in the columns are not significantly different ($P < 0.05$).

Discussion

Natural fauna inventories provide basis for the selection of priority sites and assist in the identification of priority species (Daily et al, 2003, Pineda and Halfpeter, 2004) and the role played has been more important to conservation of endangered wildlife species (Santos-Barrera et al, 2008). Amphibians occupy a distinct position in forest and aquatic food webs ecology and thereby serve as key

species for nutrient portion of vertebrate biomass (Hutchen and De Perno, 2009). The present study reveals that Ise Forest Reserve microhabitats support ten (10) amphibian-species which differ in composition and abundance for the four microhabitat types and seasons. The species composition and abundance of amphibians differ between the two seasons ($p > 0.05$), in line with the hypothesis that seasonal differences influence

amphibians species composition and abundance. This may be due to the fact that variation in weather parameters impact significantly on amphibians and so would not have evolved features for efficient adjustment to the local conditions, especially the fluctuation between the seasons. Marracci and Ragghianti (2008) asserted that a great degree of general morpho-anatomical and functional differentiation occurs on certain amphibian species as a result of different susceptibility to environmental factors. Another explanation may be that the seasonal conditions were extreme enough to bring about significant changes in both species composition and abundance. Barandun and Reyer (1997) reported that amphibian species have several adaptations to breeding such as short larval periods, high phenotypic plasticity and that multiple breeding is synchronized with rainfall. The findings of this study agree with Donnelly and Crump 1998, Carey and Alexander, 2003) that global climate change threatens amphibians during the dry season period. The amphibians were distributed within the four identified microhabitat types with the under fallen logs microhabitat most favourable to amphibians. A test of significant difference in the species richness among the microhabitats was not significant ($p > 0.05$) with the slight variation probably due to habitat preferences. Dey (2004) reported that the fresh water and thick tropical vegetation ecosystems offer excellent habitat for anurans. Also variation in amphibians' species abundance in the microhabitat types of the reserve may be due to vulnerability of amphibian species to predations especially during the dry season period. This is consistent with the observation of Moyle (1973); Hayes and Jennings (1986); Lawler et al, (1999), Adams (2009), Knapp and Matthews (2000) and Gillespie (2001) that amphibians are more vulnerable to predation during the dry season period. The variation in amphibian abundance cannot but be linked

with the variation in food and cover availability as a result of climatic variation which is consistent with the results obtained by Afolayan and Ajayi (1980) and Crowel et al, (1981) that the distribution of animals is largely dependent on the availability of food, water and cover. The study further revealed that almost all the amphibian species identified were residential while only two species *Rhacophorus nigropalmatus* and *Litoria aurea* were completely absent during the dry season. The residential nature of the majority of amphibians in the reserve may be due to full adaptation to the prevailing conditions of the reserve. Gaston et al, (2003) reported that over the years, the amphibians developed adaptive features towards mitigating the challenges in the environment.

Conclusion

Amphibians are critically important in the ecosystem as they act as bio-monitors, alerting people about what is happening in an ecosystem. Therefore, it is necessary to have a data base for the diversity and distribution of amphibian species present in Ise Forest Reserve. The result of this study revealed the diversity and abundance of different species of amphibians, their most preferred micro habitat and the season of their abundance. The number of species is relatively low and lends credence to the fear that there is a global decline in amphibian diversity. The amphibians found were all in only two classes i.e. the classes of frog and toad. Other classes of amphibian which include newts and salamander, caecilians were not encountered during the research. The fact that the other classes of amphibians were not encountered does not indicate that they were totally absent in the reserve but it is an indication that the other classes were very rare in the forest reserve and express the urgent need to map out effective strategy for the conservation of amphibians in Ise Forest Reserve, Ekiti state.

References

- Adams, M.J. (2000). Pond permanence and the effects of exotic vertebrates on anurans. *Ecological Applications* 10:559:568.
- Afolayan, T.A. and Ajayi, S.S. (1980). The influence of seasonality on the distribution of large mammals in Yankari Game Reserve, Nigeria. *African Journal of Ecology* Vol. (18) No. 1, pp. 87-93.
- Barandwn, J., and H. U. Reyer (1997). Reproductive ecology of *Bombina* variegata: characterization of spawning ponds. *Amphib. Reptilia* 18:143-154.
- Behangana, M. Arusi, J. (2004). The distribution and diversity, of amphibian fauna of Lake Nabugabo and surrounding areas. *Afri. J. Ecol.*, 42 (suppl. 1) 6-13.
- Carey, G., and M.A. Alexander (2003). Climate change and amphibian declines: is there a link? *Diversity and Distributions* 9:111-121.
- Crowel, C.M., J.C., Schiff and A.A. Gubb (1981). Effect of rainfall variation, fire vegetation and habitat physiognomy on Northern Animal community. *South African Wildlife resources* Vol. 11, pp. 87-104.
- Crump, M.C., Scott Jn NJ (1994). Visual Encounter-Surveys, In Heyer WR
- Donnelly M.A. Mc Diarmid R.M Hayek, L.C., Foster, M.S. (Eds) *Measuring and monitoring Biological Diversity, Standard Methods for Amphibians*.
- Smithsonian Institution, Washington DC, USA. Pp. 84-92.
- Daily G.C., Ceballos G, Pacheco J. Suzan G., Sanchez – Azofeifa A. (2003). *Countryside Biogeography of Neotropical Mammals: Conservation Opportunities in Agricultural landscape of Costa Rica*. *Conserve. Biol.*, 17:1-11.
- Dey, M. (2004). Decline of *Rana taipehensis* population in Southern Assam, Frog leg, Newsletter of the DAPTH South Asia, August, 09.
- Donnelly, M.A., and M.L. Crump (1998). Potential effects of climate change on two neotropical amphibian assemblages. *Climate change* 39:541-561.
- Gaston, K.J. (2003). *The structure and dynamics of geographic ranges*. Oxford: Oxford University Press.
- Gillespie, G.R. (2001). The role of introduced trout in the decline of the spotted tree frog (*Litoria Spenceri*) in South eastern Australia. *Biological conservation* 100:187-198.
- Hayes, P.M. and R.M. Jennings (1986). Decline of ranid-frog species in Western North America are bullfrogs (*Rana catesbiana*) responsible? *Journal of Herpetology*. 20:490-509.
- Hutchens, S. Deperno C. (2009). Measuring species diversity to determine land-use effects on reptile and amphibian assemblages. *Amphibian – Reptilia* 30:81-85.
- Knapp. R.A., and K.R. Mathews, (2000). Non nature fish introductions and the decline of mountain yellow-legged frog from within protected areas. *Conservation Biology* 14:1-12.
- Lawler, S.P., D. Drite, T. Strange and M. Holyoak. (1998). Effects of mosquito fish and bullfrogs on the threatened California red-legged frog. *Conservation Biology* 13: 613-622.

- Margalef, R. (1958). Information theory in ecology. *General Systematics* 3:36-71.
- Money, K.A., M.L. Darkey and K.B., Dakwa (2011). Diversity and distribution of amphibians in the Kakum National park and its surroundings. *International journal of Biodiversity and conservation* Vol. 3 (8), pp. 358-366.
- Moore, R.D. Church D.R. (2008). Implementing the amphibian conservation action plan. *International zoo yearbook*, 42:15-23.
- Moyle, P.B. (1973). Effects of introduced bullfrogs. (Rana on the nature frogs of the San Joaquin valley, California-*Copeia* 1973:18-22.
- Norris S. (2007). Ghosts in the midst coming to terms with amphibian extinctions. *Bio Science*, 57:311-316.
- Pineda E., Halffter G. (2004). Species diversity and habitat fragmentation: frogs in a tropical montane-landscape in Mexico. *Biol. Conservi*; 117:499-508.
- Reid, G.M, Zippel, K.C. (2008). Can zoos and aquariums ensure the survival of amphibians in the 21st century? *International zoo yearbook*, 42:1-6.
- Rodel, M.O. (2007). Herpetofauna of West Africa Savanna. Frankfurt an Main (Edition Chimaria).
- Santos – Barrera G; Pacheco J, Mendoza – Quijano F., Bolanos F., Chaves G., Daily G. C., Errlich P.R., Ceballos G. (2008). Diversity, natural history and conservation of amphibians and reptiles from the san Tropi., 56(2), 755-778.
- Shannon, C. E. and Weaver, W. (1949). *The Mathematics theory of communication*, University of Illinois Press, Urbana.
- Wake, D.B. (1991). Declining amphibian populations: a global phenomenon? *Science* 253:860.