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Population Decline of the Jambato Toad *Atelopus ignescens* (Anura: Bufonidae) in the Andes of Ecuador

SANTIAGO R. RON,[1,2] WILLIAM E. DUELLMAN,[3,4] LUIS A. COLOMA,[1] AND
MARTÍN R. BUSTAMANTE[1]

[1]*Museo de Zoología, Centro de Biodiversidad y Ambiente, Departamento de Ciencias Biológicas,*
Pontificia Universidad Católica del Ecuador, Apartado Postal 17-01-2184, Quito, Ecuador
[3]*Natural History Museum and Biodiversity Research Center, and Department of Ecology and Evolutionary Biology,*
University of Kansas, Lawrence, Kansas 66045-7561, USA; E-mail: duellman@ku.edu

ABSTRACT.—**The Jambato Toad, *Atelopus ignescens*, is endemic to montane forests, inter-Andean valleys, and paramos in Ecuador. Although formerly abundant and widely distributed, the species has not been recorded in nature since 1988. To determine its population status, data from intensive surveys in 1999–2001 are compared with those from 1967 and 1981. Presence-absence data from several localities also are reported. Temperature and precipitation between 1891 and 1999 were analyzed to determine whether these correlate with population trends. *Atelopus ignescens* was abundant in 1967 at Paramo de Guamaní (47 individuals recorded in 120 pers/min) and in 1981 at Paramo del Antisana (up to 0.75 individuals/m^2). In the 1999–2001 surveys, *A. ignescens* was absent despite considerably higher survey efforts. The presence-absence data at several localities also indicate a dramatic decline. Before 1988, *A. ignescens* was present during 64% of the visits to sites throughout its range. After 1988, *A. ignescens* was absent at all sites. The results strongly suggest that *A. ignescens* is extinct. Climatic data show that 1987, the year previous to the last record of *A. ignescens*, was particularly warm and dry. The reasons for the decline in pristine areas remain unclear, although the available information suggests that a combination of factors such as pathogens and unusual weather conditions may have played an important role.**

RESUMEN.—**El sapo jambato, *Atelopus ignescens* es endémico de bosques montanos, valles interandinos, y páramos del Ecuador. A pesar de que anteriormente era abundante y ampliamente distribuido, *A. ignescens* no ha sido registrado en la naturaleza desde 1988. Para establecer su estado poblacional, monitoreos intensivos llevados a cabo entre 1999–2001 fueron comparados con muestreos efectuados en 1967 y 1981. Datos de presencia-ausencia en varias localidades también fueron considerados. La temperatura y precipitación entre 1891–1999 fue analizada para encontrar correlaciones con tendencias poblacionales. *Atelopus ignescens* era abundante en 1967 en Páramo de Guamaní (47 individuos registrados en 120 pers/min) y en 1981 en Páramo del Antisana (hasta 0.75 individuos/m^2). En los monitoreos 1999–2001 *A. ignescens* estuvo completamente ausente a pesar de que hubo un esfuerzo de muestreo considerablemente mayor. Los datos de presencia-ausencia en varias localidades también sugieren una declinación dramática. Antes de 1988, *A. ignescens* estuvo presente en el 64% de las visitas a localidades a lo largo de su rango. Luego de 1988, estuvo ausente en todos los sitios. La información combinada sugiere que *A. ignescens* está extinto. Los datos climáticos muestran que 1987, el año previo al último registro de *A. ignescens*, fue inusualmente cálido y seco. Las razones para la declinación en áreas no disturbadas no están claras. Sin embargo la evidencia disponible sugiere que factores como la acción de patógenos y condiciones climáticas inusuales pueden haber jugado un rol importante.**

During the last two decades, several declines and extinctions of populations and species of amphibians have been reported worldwide (Barinaga, 1990; Blaustein and Wake, 1990; Wyman, 1990; Tyler, 1991; Wake, 1991; Vial and Saylor, 1993; Drost and Fellers, 1996; Lips, 1999; Young et al., 2001). As in other groups of organisms, some of these extinctions have been the consequence of habitat destruction. However, a unique feature of this global amphibian diversity crisis is that it also has affected species that lived in apparently undisturbed natural areas. Research on causes for amphibian declines suggests that there are several factors acting around the world. Some of these are (1) epidemic diseases (e.g., Blaustein et al., 1994b; Berger et al., 1998; Lips, 1998); (2) unusual weather patterns (e.g., Pounds and Crump, 1994; Pounds et al., 1999); (3) introduced species (e.g., Drost and Fellers, 1996; Knapp and Matthews, 2000); and (4) ultraviolet radiation (e.g., Blaustein et al., 1994a; Broomhall, et al., 2000).

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[2] Present address: Texas Memorial Museum and Department of Integrative Biology, University of Texas, Austin, Texas 78712, USA.

[4] Corresponding Author.

Changes in climate can influence population dynamics of amphibians (e.g., Heyer et al., 1988; Beebee, 1995; Blaustein et al., 2001). Extended periods of unusual low precipitation and high temperatures may increase mortality rates and reduce recruitment (Stewart, 1995). Water availability is influenced by temperature because heat generates evaporative water loss through the skin. Many authors have investigated relationships between amphibian declines and extreme weather or climate (e.g., Corn and Fogelman, 1984; Heyer et al., 1988; Osborne, 1989; Pounds and Crump, 1994; Beebee, 1995; Donnelly and Crump, 1998; Pounds et al., 1999; Blaustein et al., 2001). However, the cause-and-effect linkage between weather changes and amphibian declines have not been explored.

Population declines in amphibians in Ecuador have been reported since the early 1990s (Vial and Sailor, 1993; Coloma, 1995, 1996, 2002; Stebbins and Cohen, 1995; Lötters, 1996; Coloma et al., 2000). These reports have been based on unsuccessful efforts to find species in their natural range by several biologists since the mid-1980s. Unfortunately, these observations have not been based on standardized survey techniques, and for some species and regions, the information is scant and inconclusive. Such deficiencies in the data are the most significant obstacle that conservationists face in their attempts to delineate programs to protect endangered species of amphibians in Ecuador.

Existing evidence suggests that populations of at least 25 species of frogs may have declined in Ecuador (Ron et al., 2000). The greatest number of species affected belong to the genus *Atelopus* (Ron et al., 2000); of 18 species of *Atelopus* known from Ecuador (Coloma and Quiguango, 2000; Coloma, 2002), 11 apparently have declined during the last 15 years (Ron et al., 2000).

The terrestrial, diurnal toads of the genus *Atelopus* commonly are associated with streams, where females deposit eggs and tadpoles develop (Reproductive Mode II, as defined by Duellman and Trueb, 1994). Habitats of these toads range from lowland tropical rain forests to paramos at elevations as high as 4500 m (Lötters, 1996). *Atelopus* probably is the most specious genus of toads (family Bufonidae) in the Neotropical region (Lötters, 1996). The genus is primarily montane; only 21 of the nearly 70 species (Frost, 2000) have populations below 1000 m. Species have restricted areas of distribution with high regional endemism (Lötters, 1996).

Until the 1980s, one of the most conspicuous anurans in the highlands of Ecuador was *Atelopus ignescens*, a diurnal species easily observed moving slowly on the ground. This species is endemic to Ecuador and inhabits inter-Andean valleys and montane forests and paramos between 2800 and 4200 m (Coloma et al., 2000). Its latitudinal range (Fig. 1) encompasses Provincia de Imbabura in the north to Provincias del Chimborazo and Bolívar in the south (Coloma, 1997; Coloma et al., 2000). Anecdotal information suggests that *A. ignescens* was abundant throughout most of its range (see Discussion). Despite its former abundance and extensive geographic range, no records (published or unpublished) or collected specimens of the species exist after 1988 (Ron et al., 2000). The absence of records is puzzling in areas without evident signs of habitat degradation.

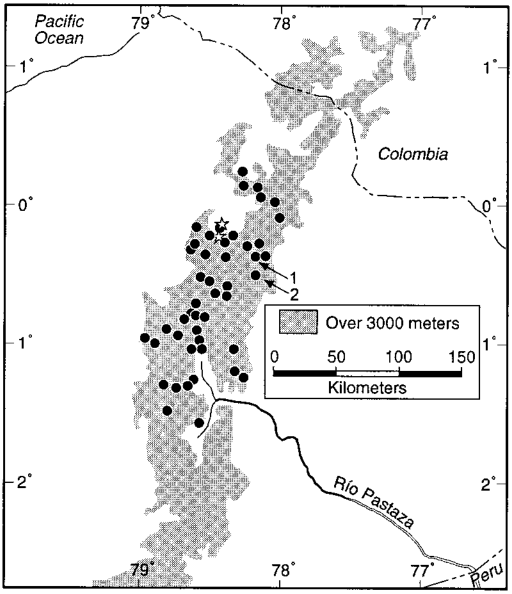

FIG. 1. Andean region of Ecuador showing distribution of *Atelopus ignescens* based on locality data for specimens deposited in Field Museum of Natural History, Museo de Zoología Pontificia Universidad Católica del Ecuador, Museo de Historia Natural Gustavo Orcés, Museum of Comparative Zoology Harvard University, Museum of Zoology University of Michigan, Museum of Vertebrate Zoology University of California, Natural History Museum University of Kansas, and Natural History Museum of Los Angeles County. Because of the close proximity of many sites, the number of dots does not represent all of the localities. The stars are the locations of the weather stations that provided information for climate analyses. Arrows show localities for population surveys: (1) Paramo de Guamaní, and (2) Paramo del Antisana (see text for details).

Herein, we summarize and analyze data from the literature, records in natural history museums, herpetologists' field notes, and population surveys, to assess the magnitude of population declines of *A. ignescens* in the Andes of Ecuador. Additionally, we analyze weather information within the distribution range of *A. ignescens* to

TABLE 1. Abundance of *Atelopus ignescens* during diurnal visual encounter surveys made at Paramo de Guamaní (1967–2001) and Ingaloma (*1968*). Relative abundance is expressed as individuals registered per person per minute of search (ind/pers/min).

Date	Locality	Season	Surveyed area (m)	Surveyed time (pers/min)	Absolute abundance (number of individuals recorded)	Relative abundance (ind/pers/min)	Relative abundance (ind/m^2)
26 March 1967	Guamaní	wet	?	120	47	0.38	?
16 August 1968	Ingaloma	wet	?	240	194	0.81	?
13 March 2000	Guamaní	wet	500 × 2	60	0	0	0
13 March 2000	Guamaní	wet	500 × 2	120	0	0	0
15 April 2000	Guamaní	wet	500 × 2	60	0	0	0
15 April 2000	Guamaní	wet	500 × 2	60	0	0	0
15 April 2000	Guamaní	wet	500 × 2	60	0	0	0
15 April 2000	Guamaní	wet	500 × 2	60	0	0	0
15 April 2000	Guamaní	wet	500 × 2	60	0	0	0
18 April 2000	Guamaní	wet	500 × 2	60	0	0	0
18 April 2000	Guamaní	wet	500 × 2	60	0	0	0
18 April 2000	Guamaní	wet	500 × 2	60	0	0	0
18 April 2000	Guamaní	wet	500 × 2	60	0	0	0
1 May 2000	Guamaní	wet	500 × 2	60	0	0	0
1 May 2000	Guamaní	wet	500 × 2	60	0	0	0
26 Nov. 2000	Guamaní	dry	500 × 2	75	0	0	0
26 Nov. 2000	Guamaní	dry	500 × 2	75	0	0	0
26 Nov. 2000	Guamaní	dry	500 × 2	75	0	0	0
26 Nov. 2000	Guamaní	dry	500 × 2	75	0	0	0

identify correlates between population declines and changes in weather patterns.

MATERIALS AND METHODS

Population Surveys.—Changes in relative abundance of *A. ignescens* were examined at La Virgen at Paramo de Guamaní (78°12′10.5″W, 0°19′52.3″S, 4020 m, Reserva Ecológica Cayambe-Coca) and Río Antisana at Paramo del Antisana (78°12′8″W, 0°29′41.6″S, 4202 m, Reserva Ecológica Antisana). Localities were chosen because they were sampled several years before population declines were evident. Both localities are in Provincia del Napo in the Cordillera Oriental. The vegetation at both localities is Herbaceous Paramo, dominated by grasses *Calamagrostis* spp. and *Festuca* spp. (Valencia et al., 1999).

At Paramo de Guamaní, a diurnal visual encounter survey (VES) was done in March 1967 by W. E. Duellman and L. Trueb. Relative abundance from that survey was compared with relative abundance from 17 diurnal VES carried out between March and November 2000 by M. Bustamante, P. Espinosa, L. López, A. Merino, and S. Ron. At Paramo del Antisana, four 100 × 2 m diurnal transect surveys were done in June 1981 by J. Black (Black, 1982). Two of the four transects were along a stream and two along a trail. Relative abundance from those surveys was compared with 24 diurnal transect surveys carried out between July 1999 and January 2001 at Paramo del Antisana by M. Bustamante, L. Coloma, J. Guayasamín, A. Merino, and S. Ron. The transects in 1999–2001 were set up along a stream and were carried out by one person. Transect sizes are shown in Tables 1 and 2.

Atelopus ignescens was last recorded in nature in 1988 (Coloma et al., 2000; Ron et al., 2000). To test whether the presence or absence of *A. ignescens* at six localities (Laguna de Mojanda, Oyacachi, Papallacta, Paramo de Guamaní, Paramo del Antisana, and Volcán Cotopaxi) is independent from collection time (before 1988/after 1988), Fisher's exact test for independence was applied ($\alpha = 0.05$). Presence/absence data were obtained from herpetologists' field notes.

Climatic Analyses.—Extreme dry and/or warm conditions can produce hydric stress that can affect amphibians at the individual, population, and community levels (Donnelly and Crump, 1998). To identify the occurrence of warm and dry periods, we analyzed climate information from two weather stations within the range of *A. ignescens*: (1) Izobamba, Provincia de Pichincha, (78°33′11″W, 0°21′45″S, 3058 m) and (2) Astronomical Observatory of Quito, Provincia de Pichincha, (78°29′59.9″W, 0°12′59.9″S, 2800 m). Airline distance between the two stations is 17 km (Fig. 1).

Climatic data from Quito include 90 years of annual precipitation and mean annual temperatures from 1891 and 1984. There was a signif-

TABLE 2. Abundance of *Atelopus ignescens* during transect surveys made at Paramo del Antisana. 1864 data from Jiménez de la Espada (1875); 1981 data from Black (1982).

Date	Season	Surveyed area (m)	Absolute abundance (number of individuals recorded)	Relative abundance (ind/m^2)
Dec. 1864	dry	?	"thousands"	?
3 June 1981	wet	100 × 2	5	0.025
3 June 1981	wet	100 × 2	84	0.42
9 June 1981	wet	100 × 2	84	0.42
9 June 1981	wet	100 × 2	150	0.75
3 July 1999	dry	200 × 2	0	0
3 July 1999	dry	200 × 2	0	0
3 July 1999	dry	200 × 2	0	0
3 July 1999	dry	200 × 2	0	0
3 July 1999	dry	100 × 2	0	0
3 July 1999	dry	100 × 2	0	0
3 July 1999	dry	100 × 2	0	0
3 July 1999	dry	100 × 2	0	0
29 April 2000	wet	500 × 2	0	0
29 April 2000	wet	500 × 2	0	0
29 April 2000	wet	500 × 2	0	0
29 April 2000	wet	500 × 2	0	0
29 April 2000	wet	500 × 2	0	0
24 June 2000	wet	500 × 2	0	0
8 Aug. 2000	dry	250 × 2	0	0
8 Aug. 2000	dry	250 × 2	0	0
8 Aug. 2000	dry	250 × 2	0	0
8 Aug. 2000	dry	250 × 2	0	0
8 Aug. 2000	dry	250 × 2	0	0
8 Aug. 2000	dry	250 × 2	0	0
8 Aug. 2000	dry	250 × 2	0	0
8 Aug. 2000	dry	250 × 2	0	0
25 Nov. 2000	wet	500 × 2	0	0
27 Jan. 2001	dry	500 × 2	0	0

icant linear relationship in annual precipitation between Quito and Izobamba ($F = 31.04$, $P < 0.0001$). The relationship also was significant for mean annual temperature ($F = 65.67$, $P < 0.0001$). The equations of both linear regressions were used to predict annual precipitation and mean annual temperature in Quito from 1985 to 1999 (data for this period were not available). Standardized values for annual precipitation and for mean annual temperature were obtained to determine what years had the greatest difference, expressed in standard deviation units, between temperature and precipitation (i.e., the years that were simultaneously warmest and driest).

Climate information from Izobamba includes a shorter period (1962–1999) but is more detailed. The variables considered at Izobamba are (1) annual precipitation, (2) mean annual temperature, (3) number of dry days (precipitation = 0) per year, (4) monthly precipitation, and (5) mean monthly temperature. Mean annual and monthly temperatures are the average of daily temperatures. Daily temperatures are the average between maximum and minimum daily temperatures.

RESULTS

Population Surveys.—Relative abundance of *A. ignescens* decreased drastically at Paramo de Guamaní and Paramo del Antisana. At Paramo de Guamaní in 1967, relative abundance was 0.38 ind/pers/min (individuals registered per person per minute of search) during one VES. In 2000, relative abundance was 0 ind/pers/min in 17 VES (Table 1). In 1967, 120 pers/min, yielded 47 individuals, whereas in 2000, *A. ignescens* was completely absent despite a search effort 9.5 times higher (1140 pers/min).

In surveys at Paramo del Antisana in 1981, *Atelopus ignescens* relative abundance was mean (± SE) = 0.34 ind/m^2 (0.025–0.75, $N = 4$). In 1999–2001 relative abundance was 0 ($N = 24$, Table 2). In 1981, 323 individuals were recorded during four transect surveys. In 1999–2001, *A. ignescens* was absent during 24 transect surveys (1465 pers/min; Table 2). No tadpoles or egg masses of *A. ignescens* were observed during the 1999–2001 surveys. At both localities during the 1999–2001 surveys, a total search effort of 2665 pers/min yielded no *A. ignescens*.

Presence or absence was not independent of time of visit (before 1988/after 1988) to five localities (Fisher's exact test $P < 0.0001$). Between 1967 and 1987, *A. ignescens* was present in nine of 14 visits; between 1988 and 2001, *A. ignescens* was present in one (1988) out of 30 visits (Table 3). Presence or absence was not independent of time of visit to Paramo de Guamaní (Fisher's exact test $P = 0.002$). From 1967 to 1987, *A. ignescens* was present in five of eight visits, whereas from 1988 to 2001, it was absent in all 15 visits.

Climatic Analyses.—Annual precipitation and mean annual temperatures at Izobamba and Quito are shown in Figures 2 and 3. Mean annual precipitation at Izobamba was 1422.03 mm (SD = 239.95, $N = 38$); at Quito it was 1230.1 mm (SD = 214.7, $N = 105$). At Izobamba, the years with the least precipitation were 1985 (983.6 mm), 1987 (994.6 mm), and 1992 (1027 mm). At Quito, the years with the least precipitation were 1926 (692.2 mm), 1985 (882.3 mm), and 1987 (890.4 mm).

Mean annual temperature at Izobamba was 11.33 °C SD = 0.62, $N = 38$); at Quito it was 13.4°C (SD = 0.7, $N = 105$). At Izobamba, the warmest years were 1998 ($\bar{x}$ temperature = 12.56°C), 1987 ($\bar{x}$ temperature = 12.48°C), and 1997 ($\bar{x}$ temperature = 12.26°C). At Quito, the warmest years were 1998 ($\bar{x}$ temperature =

TABLE 3. Presence/absence of *Atelopus ignescens* at six localities in Andean Ecuador.

Date	Locality	Occurrence
26 March 1967	Guamaní	present
1 Dec. 1983	Volcán Cotopaxi	absent
1 March 1984	Volcán Cotopaxi	absent
1 June 1984	Volcán Cotopaxi	present
20 Oct. 1984	Guamaní	present
1 May 1985	Papallacta	present
1 Dec. 1985	Papallacta	present
1 May 1986	Guamaní	present
8 July 1986	Guamaní	present
1 Oct. 1986	Guamaní	absent
1 June 1987	Guamaní	present
5 Dec. 1987	Guamaní	absent
1 Dec. 1987	Laguna de Mojanda	present
13 Dec. 1987	Guamaní	absent
30 March 1988	Oyacachi	present (**last record**)
14 April 1988	Papallacta	absent
1 May 1988	Guamaní	absent
1 June 1988	Guamaní	absent
26 June 1988	Guamaní	absent
21 June 1989	Guamaní	absent
5 July 1989	Cotopaxi	absent
12 July 1991	Cotopaxi	absent
17 Aug. 1991	Papallacta	absent
1 Oct. 1991	Cotopaxi	absent
18 May 1993	Guamaní	absent
25 Nov. 1993	Papallacta	absent
1 Sept. 1994	Guamaní	absent
30 Jan. 1999	Guamaní	absent
21 April 1999	Cotopaxi	absent
3 July 1999	Antisana	absent
2 Oct. 1999	Laguna de Mojanda	absent
11 Nov. 1999	Cotopaxi	absent
13 March 2000	Guamaní	absent
16 March 2000	Guamaní	absent
15 April 2000	Guamaní	absent
18 April 2000	Guamaní	absent
29 April 2000	Antisana	absent
1 May 2000	Guamaní	absent
24 July 2000	Antisana	absent
1 Oct. 2000	Guamaní	absent
26 Nov. 2000	Guamaní	absent
27 Jan. 2001	Antisana	absent
7 Dec. 2001	Papallacta	absent
7 Dec. 2001	Guamaní	absent

15.4°C), 1987 ($\bar{x}$ temperature = 15.3±C), and 1997 ($\bar{x}$ temperature = 15.1°C).

At Quito, between 1891 and 1999, the warmest decades were 1991–1999 ($\bar{x}$ annual temperature = 14.81°C, SD = 0.39, $N = 9$) and 1981–1989 ($\bar{x}$ annual temperature = 14.47d°, SD = 0.49, $N = 10$). The 1981–1990 decade was significantly warmer than all previous decades (all P-values for t-tests < 0.001). The 1990–1999 period also was significantly warmer than all previous decades (all P-values for t-tests < 0.001) except 1981–1990 ($t = -1.66$, $P = 0.115$).

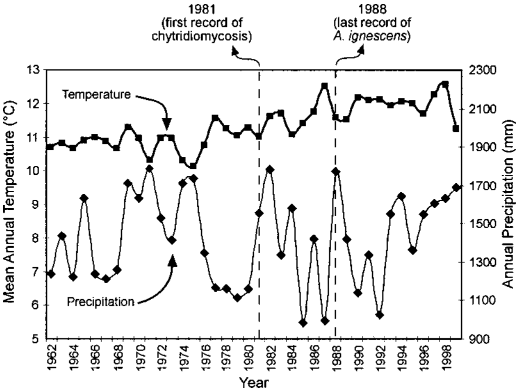

FIG. 2. Mean annual temperature and annual precipitation at Izobamba, Provincia del Pichincha, Ecuador. Note that the year before 1988, when *Atelopus ignescens* was recorded in the field for the last time, weather was unusually warm and dry.

There is a significant positive correlation between year and temperature in Quito (Spearman's Rho = 7.98, $P < 0.0001$). The increase in mean annual temperature is also evident in Figures 2 and 3. Mean annual temperatures after 1985 are significantly higher from those between 1891 and 1907 ($t = -13.118$, one tail $P < 0.0001$). Between 1891 and 1907, $\bar{x}$ mean annual temperature = 12.764 (SD = 0.418). Between 1986 and 1999, $\bar{x}$ mean annual temperature = 14.771 (SD = 0.391).

At Quito, between 1891 and 1999, the driest decades were 1951–1960 (mean annual precipitation = 1095.4 mm, SD = 117.9, $N = 10$) and 1931–1940 (mean annual precipitation = 1162.3 mm, SD = 117.9, $N = 10$). At Quito, the years

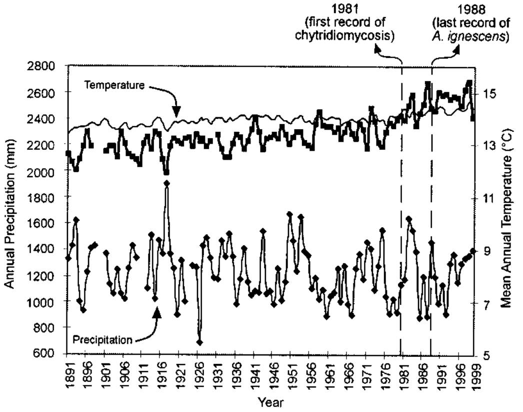

FIG. 3. Mean annual temperature (squares) and annual precipitation (diamonds) at Quito, Provincia del Pichincha, Ecuador. The smooth line shows world mean annual temperature (from Goddard Institute for Space Studies, 2002). Note that the year before 1988, when *Atelopus ignescens* was recorded in the field for the last time, weather was unusually warm and dry.

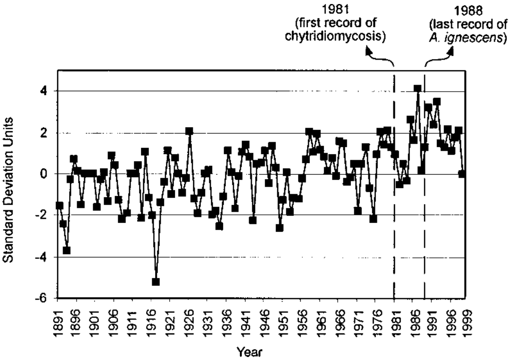

FIG. 4. Difference between standardized values of temperature and precipitation at Quito. High values represent climate conditions simultaneously warm and dry. Note that of 90 years of climate records, 1987 shows the highest value.

with the highest difference between the standardized values of mean annual temperature and annual precipitation were 1987 (4.125 SD units) and 1994 (3.466 SD units; Fig. 4).

At Izobamba, average monthly precipitation from 1962 to 1999 was significantly different from monthly precipitation in 1987 and 1988 (Table 4). Average monthly temperatures from 1962 to 1999 were significantly different from those in 1981, 1982, 1983, 1986, and 1987 (Table 4). The combined weather information shows that 1987 (the year before *A. ignescens* was recorded for the last time) was unusually warm and dry (Figs. 2–3, Table 4). Monthly precipitation and mean temperature for 1987 are shown in Figure 5.

The mean number of dry days per year at Izobamba was 149.51 (SD = 24.42, $N = 35$; Fig. 6). The years with the most dry days were 1985 (192 days) and 1967 (181 days). Years with low number of dry days are associated with El Niño events (e.g., 1982, 1988, 1998). There are not evident abnormalities in the number of dry days/year between 1962 and 1999 (Fig. 6).

TABLE 4. Wilcoxon signed rank test values for the comparison between average monthly precipitation and average monthly temperature between 1962 and 1999 with monthly precipitation and monthly temperature for the years 1981–1988; weather data from Izobamba, Provincia del Pichincha, Ecuador. Bold characters show significant differences.

	Monthly precipitation		Monthly temperature	
	Z	*P*	*Z*	*P*
1981	−1.02	0.308	−3.06	**0.002**
1982	−0.86	0.388	−2.27	**0.023**
1983	−0.23	0.814	−2.59	**0.009**
1984	−0.47	0.638	−1.72	0.086
1985	−1.88	0.06	−0.71	0.48
1986	−0.16	0.875	−2.35	**0.019**
1987	−2.35	**0.019**	−3.06	**0.002**
1988	−1.96	**0.05**	−1.73	0.084

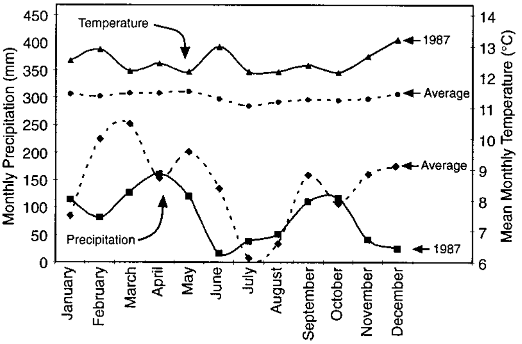

FIG. 5. Mean monthly temperature and precipitation for 1987 compared with mean values for 1962–1999 at Izobamba, Provincia del Pichincha, Ecuador.

DISCUSSION

There is strong evidence of a drastic population decline of *A. ignescens*. This can be inferred from (1) the population data presented, (2) anecdotal information indicating that before 1988 *A. ignescens* was an abundant species (see below), and (3) the absence of records after 1988.

It is unlikely that the complete absence of records during the 1999–2000 population surveys is an artifact of unfavorable environmental conditions. The surveys in 1999–2001 encompassed a longer period and a wider set of environmental conditions than those in 1967 and 1981. In spite of the high search effort (2665 pers/min), the absence of *A. ignescens* is a clear indication of a severe population decline at the surveyed localities.

Anecdotal information shows that *A. ignescens* formerly was abundant. In December 1864, the Spanish naturalist M. Jiménez de la Espada observed at Paramo del Antisana (Laguna de la Mica) the occurrence of "thousands of individuals in the herbaceous and humid prairies close

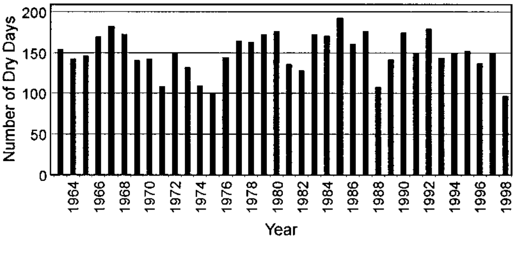

FIG. 6. Number of dry days (precipitation = 0) at Izobamba, Provincia del Pichincha, Ecuador. Sixty days of data are missing from 1996.

to streams, pools, and lakes'' (Jiménez de la Espada, 1875:146). Field parties from the University of Kansas documented high densities of *A. ignescens* in the 1960s and 1970s (e.g., 194 individuals (0.81 ind/pers/min) at Ingaloma, Provincia de Pichincha, 3780 m on 16 August 1968). At Paramo del Antisana, densities were as high as 50 individuals/m^2 in 1981 (Black, 1982). Also, there are reports of mass migrations that resulted in large numbers of individuals smashed across 1–8 km of highways in Provincia del Tungurahua and Provincia de Bolívar in 1958 and 1959 (Peters, 1973). *Atelopus ignescens* has been recorded in human disturbed areas, such as backyards in Quito in 1959 and 1983 and in Latacunga in 1979 (J. A. Peters, L. A. Coloma, field notes).

Population data are not available for the period 1982–1988, and therefore it is difficult to determine the timing and rate of the decline. However, evidence suggests that *A. ignescens* was still abundant at some localities between 1984 and 1986. In October 1984, 19 *A. ignescens* were collected at Paramo de Guamaní (Museo de Zoología, Pontificia Universidad Católica del Ecuador 264–270; Muséum d'Histoire Naturelle Geneva 2273.48, 2273.81–82, 2273.84, 2273.86, 2273.88–93, 2273.96). On 15 May 1985, a mass migration at Paramo del Chimborazo (border between Provincia de Bolívar and Provincia de Tungurahua) left thousands of smashed toads along 1 km of the Guaranda-Ambato highway (L. A. Coloma, field notes). On 8 March 1986, 29 *A. ignescens* were collected at Papallacta (Provincia de Pichincha, Museo de Historia Natural Gustavo Orcés 3261–3289). In August 1986, 64 *A. ignescens* were collected in Zumbahua (Provincia de Cotopaxi, Muséum d'Histoire Naturelle Geneva 2385.001–010, 2384.047–100).

The complete absence of records after 1988 indicates that population declines of *A. ignescens* have occurred throughout its geographic range. The absence of records does not seem to be an artifact of low search effort. A considerable portion of the range of *A. ignescens* is easily accessible and repeatedly visited by herpetologists.

The available evidence suggests that *A. ignescens* is extinct. However, the possibility of its presence in areas of difficult access cannot be ruled out.

The decline of *A. ignescens* seems to be part of a generalized process that has affected several species of the genus. *Atelopus* declines have been reported from Costa Rica (Lips, 1998), Panama (Lips, 1999), Venezuela (La Marca and Lötters, 1997), Ecuador (Ron et al., 2002), and Peru (Vial and Saylor, 1993). *Atelopus* is the amphibian genus with the most declines reported from South America. Declines from Andean Venezuela, Ecuador, and Peru include a total of 43 species, of which 21 are *Atelopus* (48.8%; Ron et al., 2002). Possible causes for the population declines of *A. ignescens* are discussed below.

Habitat Degradation.—During the last two decades, significant portions of the geographic range of *A. ignescens* have been modified by human activities. By 1996, 27.1% of the paramo and 33.3% of Andean forests had been cleared in Ecuador (Sierra, 1999). Brandbyge and Holm-Nielsen (1991) estimated that only 3.5% of native forest remained in the inter-Andean region. Habitat degradation in some parts of its range may be a factor for population declines in *A. ignescens*. However, *A. ignescens* can withstand some degree of habitat degradation, as seen by its presence in cities such as Quito and Latacunga.

The most puzzling declines are those that have occurred in places such as Paramo del Antisana and Paramo de Guamaní, where human-mediated habitat destruction has been minor. Both localities are located within protected areas. Although more detailed habitat analyses may reveal subtle forms of degradation (e.g., chemical contamination), at present it seems unlikely that habitat destruction is the cause for the disappearance of A. ignescens in apparently undisturbed regions.

Introduced Species.—Presence of introduced predatory fishes have been identified as a possible factor linked with declines of several amphibian species in many regions (e.g., La Marca and Reinthaler, 1991; Brönmark and Edenhamn, 1994; Drost and Fellers, 1996; Adams, 1999; Knapp and Matthews, 2000). Two exotic species of salmonids (*Onchorhynchus mykiss* and *Salmo trutta*) are present in streams and lakes in the highlands of Ecuador. *Onchorhynchus mykiss* is present in Paramo del Antisana (Laguna de la Mica) and Paramo de Guamaní. However, it was never observed in the streams where the intensive surveys took place.

Although there are no studies on the impact of salmonid predation on the tadpoles or eggs of *Atelopus*, it is reasonable to assume that introduced fishes may have contributed to population declines at least in some parts of the distribution range. However, it is unlikely that salmonid predation is the driving cause for the decline of *A. ignescens* throughout its entire range. Salmonids have been established in aquatic ecosystems of Ecuador since the 1950s (R. Barriga, pers. com.), decades before *A. ignescens* declines were evident.

Pathogen Outbreak.—Chytridiomycosis is a deadly fungus disease that attacks amphibians. Its presence has been linked to declines in several species in Australia (Berger et al., 1998), Central America (Berger et al., 1998; Lips ,1999; Young et al., 2001), and Europe (Bosch et al., 2000), and its has been found in frogs in zoos in North America (Nichols et al., 1998; Pessier et al., 1999). The first report of the disease in South America is from five Ecuadorian species (Berger et al., 1999; Ron and Merino Viteri, 2000). The species positive for chytridiomycosis are *Atelopus bomolochos, Atelopus* sp. (from Provincia del Carchi, Ecuador), *Gastrotheca pseustes, Hyla psarolaima*, and *Telmatobius niger* (Ron and Merino Viteri, 2000). The last records in the field of *A. bomolochos* and *Atelopus* sp. were in 1994 and 1993, respectively. The first record of chytridiomycosis in Ecuador is from an *A. bomolochos* collected in Provincia del Cañar in 1980. This indicates that chytridiomycosis was present in Ecuador several years before the disappearance of highland *Atelopus*. So far, 89 museum specimens of *A. ignescens* have been examined for chytridiomycosis. All specimens have tested negative (Merino Viteri, 2001). Of the 89 specimens, 53 were collected after the first record of the disease: one in 1983, seven in 1984, three in 1985, 29 in 1986, 11 in 1987, and two in 1988 (Merino Viteri, 2001). However, extensive analyses may reveal the presence of chytridiomycosis in *A. ignescens*. This is a likely scenario because chytridiomycosis has low host specificity (Speare and Berger, 2000) and is present in *A. bomolochos* and *Atelopus* sp. Both species are parapatric to *A. ignescens* (Ron and Merino Viteri, 2000).

Five *A. bomolochos* infected with chytridiomycosis were collected in January 1991. The specimens (Museo de Zoología, Pontificia Universidad Católica del Ecuador 2911, 2913, 2923, 2939, 2949) were examined because when found in the field they were either dead or evidently unhealthy and died within a few hours after collection. Similar observations are available for *A. ignescens*. In November 1987, three females were found dead 20 km SE of Latacunga (Provincia del Cotopaxi) by G. Onore and LAC (Coloma et al., 2000). The three specimens tested negative for chytridiomycosis (Merino Viteri, 2001).

A pathogen outbreak during the late 1980s could have been mediated by favorable environmental conditions (e.g., dry and/or warm climate; see below). Additional pathological diagnoses of preserved specimens are needed to understand the geographic and temporal distribution of chytridiomycosis and other pathogens within the range of *A. ignescens*.

Changes in Climate and UV Radiation.—A sharp increase in mean annual temperature during the last 15 years is evident within the distribution range of *A. ignescens*. Of 90 years of climatic data analyzed in this study, 1987 has the most extreme combination of dry and warm conditions (Fig. 4). Concomitantly, in the period 1987–1989 six species of *Atelopus* were recorded for the last time in the Ecuadorian Andes (Ron et al., 2003). Climate may have affected the toads directly (by increasing adult mortality and/or reducing reproductive success) and/or indirectly (e.g., by weakening the immune system facilitating pathogen outbreaks). Unusually dry and warm conditions during 1987 also may have played a roll in the decline of several species of frogs in Monteverde, Costa Rica (Pounds and Crump, 1994; Pounds et al., 1999).

There are an increasing number of reports of changes in population sizes (including extinctions), reproductive cycles, and distribution ranges of vertebrates as a consequence of global warming (e.g., Pounds et al., 1999; Sæther et al., 2000; Sillett et al., 2000; Wuethrich, 2000). Global warming has increased worldwide temperatures an average of 0.5 °C (Hasselmann, 1997). Our data show that the temperature increase in the equatorial Andes is four times higher than the global average increase (approximately 2°C during the last century; Fig. 3). Accordingly, changes in population sizes in the equatorial Andes are expected to be more drastic than in other regions. Extinctions also are predicted to be more numerous, and the disappearance of several species of amphibians from the Andes of Ecuador may be a manifestation of this climatic trend.

An additional factor on the decline *A. ignescens* may be UV radiation. A number of studies have demonstrated that UV radiation can affect amphibian survival, specially during early development (e.g., Blaustein et al. 1994a, 1995, 1999; Anzalone et al., 1998; Lizana and Pedraza, 1998). Satellite measurements show that annually averaged UV-B radiation has increased significantly in South America since 1979 (Middleton et al., 2001). According to Middleton et al. (2001), of 20 sites in Central and South America where annual UV-B levels were measured between 1979 and 1998, the site with the highest values was the one with the highest altitude (Cordillera de Mérida at 4000 m in Venezuela). This site also shows the highest rate of increase in UV-B when compared to other South American localities (Middleton, 2001). In Cordillera de Mérida, *Atelopus oxyrhynchus, Atelopus carbonerensis, Atelopus mucubajiensis*, and *Atelopus sorianoi* have declined (La Marca and Lötters, 1997).

Ultraviolet radiation levels are considerably higher in highlands than at sea level (Blumthaler et al., 1997). *Atelopus ignescens* is a highland species that must have been exposed to high levels of UV-B radiation. Increased UV-B radiation may have exceeded the limits of tolerance of some highland species; further increases would be expected to result in more adverse effects on populations.

Conclusions.—There has been a severe population decline and extinction of the formerly abundant toad *A. ignescens*. The causal factors of the decline need further research, although possible causes are (1) a pathogen outbreak, (2) unusual climate patterns including increased levels of UV-B radiation, (3) habitat modification, (4) the presence of exotic predatory salmonid fishes, and/or (5) synergistic interactions among factors.

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Intra- and Interspecific Competition among the Water Snakes *Nerodia sipedon* and *Nerodia rhombifer*

JOHN G. HIMES[1]

Department of Biological Sciences, Box 5018, University of Southern Mississippi,
Hattiesburg, Mississippi 39406-5018, USA

ABSTRACT.—I investigated the potential role of intra- and interspecific competition for food in Midland Watersnakes (*Nerodia sipedon pleuralis*) and Diamond-Backed Watersnakes (*Nerodia rhombifer rhombifer*) during the summers of 1999 and 2000. Snakes offered prey (juvenile spotted bass, *Micropterus punctulatus*) at low densities (five fish/enclosure/week) had significantly lower proportional changes in mass than snakes offered prey at high densities (10 fish/enclosure/week). However, differences in mass changes of *N. sipedon* were not significant at constant relative densities of prey to snakes. *Nerodia sipedon* and *N. rhombifer* that were offered 10 fish per week and tested individually had significantly higher mass changes than snakes tested in intraspecific pairs. For snakes maintained in interspecific pairs and offered 10 fish per week, *N. sipedon* had higher mass changes than *N. rhombifer*, although the difference was not significant. I lab-tested the potential for exploitation as a mechanism of competition between *N. sipedon* and *N. rhombifer* by comparing rates of gastric breakdown after feeding snakes a goldfish (*Carassius auratus*), forcing regurgitation at six, 12, and 18 h after ingestion, and comparing ash-free dry masses (AFDMs) of the digested fish. Relatively higher AFDMs of digested fish were obtained from *N. sipedon* than from *N. rhombifer* at six and 12 hours after ingestion. Thus, the former species exhibited a faster rate of gastric breakdown than the latter. These differences in competitive abilities may potentially contribute to the higher abundance of *N. sipedon* than *N. rhombifer* in the upper Pascagoula River system of southeastern Mississippi.

Relative to most organisms that inhabit freshwater communities, the ecological role of snakes has been little-studied, and few studies conducted on aquatic snakes have focused on the comparative ecology of coexisting species. Moreover, I am not aware of any studies in which the primary objective was to determine the role of snakes as potential intra- and interspecific competitors in freshwater communities. Nonetheless, some community-level ecological studies on activity patterns, dietary preferences, habitat selection, and abundances of aquatic snakes have been conducted, particularly in the southeastern and south-central United States

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[1] Present address: Nevada Division of Wildlife, Southern Region Headquarters, 4747 Vegas Drive, Las Vegas, Nevada 89108-2135; E-mail: jhimes@ndow.state.nv.us

(Clark, 1949; Diener, 1957; Preston, 1970; Kofron, 1977, 1978; Mushinsky and Hebrard, 1977; Hebrard and Mushinsky, 1978; Mushinsky et al., 1980). The baseline data provided by these studies indicate that freshwater assemblages of snakes often consist of several species and that snakes frequently are abundant top predators in freshwater communities. Thus, snakes may significantly influence the structure of freshwater communities, because of their roles as top predators and as potential intra- and interspecific competitors.

Two of the most abundant species of snakes in freshwater communities of the southeastern United States are the Midland Watersnake (*Nerodia sipedon pleuralis*) and Diamond-Backed Watersnake (*Nerodia rhombifer rhombifer*). These species have broadly overlapping distributions (Conant and Collins, 1998); their diets consist primarily of fishes (Diener, 1957; Laughlin, 1959); they are primarily nocturnal during the summer and diurnal during the spring and fall (Diener, 1957; Mushinsky et al., 1980); and they frequently occur in syntopy (pers. obs.). Because these species are upper-level predators that have similar habits and may occupy the same areas, their coexistence and relative abundances are potentially influenced by intra- or interspecific competition for the same vital resources.

Both *N. sipedon* and *N. rhombifer* have peripheral distributions in southeastern Mississippi (Conant and Collins, 1998), where they frequently occur in sympatry (pers. obs.). However, along the upper Pascagoula River system of southeastern Mississippi, *N. sipedon* is approximately five times more abundant than is *N. rhombifer* (pers. obs.). The far greater abundance of *N. sipedon* in this area may imply that it has a competitive advantage over *N. rhombifer* in peripheral areas. Moreover, *N. rhombifer* is most often associated with larger water bodies (Preston, 1970; Kofron, 1978) and is not as inclined to wander overland as is *N. sipedon* (Preston, 1970; Tiebout and Cary, 1987). Therefore, *N. rhombifer* may not be as capable of colonizing areas at the periphery of its distribution or of sustaining populations in nonpermanent water-bodies as is *N. sipedon*.

According to the principles of competition theory, when putative competitors occur at high densities and food is therefore limited, intraspecific food competition should be more intense than when the organisms occur at low densities. Also, when prey occurs at high densities (per capita) and is not limited, intraspecific food competition should be less intense than when prey occurs at low densities. However, before concluding that competition is potentially a major factor, one must first determine whether the organisms share vital resources that are limited. If competition (either intra- or interspecific) occurs, then one may proceed in an attempt to determine the mechanism (exploitation vs. interference) by which it occurs.

To test the potential for competition as a factor influencing community relationships among and between *N. sipedon* and *N. rhombifer* in the upper Pascagoula River system, I studied these species in the field and in the laboratory. I tested for intraspecific food competition: (1) in *N. sipedon* at constant relative densities of prey to snakes; (2) in *N. sipedon* at low prey densities; and (3) among *N. sipedon* and *N. rhombifer* at high snake densities. In addition, I tested for interspecific food competition between *N. sipedon* and *N. rhombifer* at constant relative densities of prey to species of snake and tested for food exploitation as a mechanism of such competition.

MATERIALS AND METHODS

For all experiments, I used adult male snakes collected from tributaries of the Bouie River and adjacent portions of the Leaf River in Jones and Forrest Counties, Mississippi. All snakes were within 5 cm (snout–vent length; range = 51–56 cm) and 20 g (range = 136–156 g) of each other to minimize difference in rates of mass change or gastric breakdown attributable to body size. Field experiments were conducted on privately owned land in Jones County, Mississippi, where snakes were tested in enclosures (1.22 × 1.22 × 0.91 m) constructed of a wooden frame and removable lid and fiberglass screen walls. Enclosures were placed half on land and half in water at the edges of a series of ponds, to simulate the natural riparian habitat of *Nerodia*. Enclosures were arranged according to a randomized block design (each pond represented a block), and snakes were randomly placed in enclosures.

For all field experiments, I recorded snout–vent length (cm), total length (cm), and mass (g) of each snake the day before (31 May; Mass #1) and after (1 September; Mass #2) testing to determine changes in body condition. I considered body condition to be a correlate of fitness, which enabled me to determine whether intra- and/or interspecific competition may have taken place. The testing variable was proportional change in mass: (Mass #1 to Mass #2)/(Mass #1) of snakes from 31 May to 1 September. For treatments involving two individuals of the same species, I sketched the unique ventral pattern of dark markings of each snake to identify individuals.

To test the potential for intraspecific food competition among individuals of *N. sipedon*, I calculated proportional changes in mass of similarly sized snakes through experimental manipulation of snake and prey densities. I collected 35 snakes during May 2000. For 14 weeks (June to August 2000), I tested snakes in the enclosures under three treatments: (1) one snake per enclosure and five juvenile spotted bass (*Micropterus punctulatus*) added as prey (total length = 2–3 cm); (2) two snakes per enclosure and five juvenile *M. punctulatus*; and (3) two snakes per enclosure and 10 juvenile *M. punctulatus*. For each treatment, fish were added into the water section of each enclosure once a week. The first and third treatments were replicated five times each; the second treatment was replicated 10 times; and different snakes were used for each replicate. Data were analyzed (with α set at 0.05) with a one-way ANOVA and a Tukey's HSD test (posthoc to ANOVA).

To test the potential for interspecific food competition between *N. sipedon* and *N. rhombifer*, I collected 12 individuals of each species of snake during May 1999. For 14 weeks (June to August 1999), I tested snakes in the enclosures and had five treatments: (1) one *N. sipedon* per enclosure; (2) one *N. rhombifer*; (3) one *N. sipedon* and one *N. rhombifer* together; (4) two *N. sipedon* together; and (5) two *N. rhombifer* together. Ten juvenile *M. punctulatus* were added as prey into the water section of each enclosure once a week. Each treatment was replicated $N = 3$ times for a total of 15 tests and different snakes were used for each replicate. Data were analyzed (with α set at 0.05) with a 2 × 3 ANOVA (species × treatment): species = *N. sipedon, N. rhombifer*; treatment = 1 snake per enclosure, 2 snakes (heterospecifics) per enclosure, 2 snakes (conspecifics) per enclosure.

To determine whether *N. sipedon* and *N. rhombifer* may compete by exploitation, I measured differential rates of gastric breakdown in snakes in the laboratory. I collected snakes during September 1998. During October 1998, I maintained five *N. sipedon* and five *N. rhombifer* alone in plastic containers (59.1 × 43.2 × 15.2 cm). Snakes were maintained at 25 C ± 2 C (cloacal temperatures of active individuals of *N. sipedon* and *N. rhombifer* in the summer generally range from 23–27°C; pers. obs.), provided with fresh water daily, and fed ad libitum on goldfish (*Carassius auratus*; total length = 4.2–5.2 cm, wet mass = 0.65–0.85 g) prior to testing. Snakes were not fed within two days of testing to ensure that their stomachs did not contain any remains of a prior meal.

To begin testing for exploitation, each snake was fed a goldfish (range of total lengths and wet masses of fish were 4.5–5.0 cm and 0.70–0.80 cm, respectively, thereby minimizing variability in surface area to volume ratio) and examined three times (one time per test): six, 12, and 18 h after ingestion, when snakes were palpated to obtain the goldfish regurgitant (with a 48-h recovery period between feedings/tests), resulting in five replicates per species of snake for each hour and a total of 30 tests (3 treatments [= hours after feeding] × 5 replicates × 2 species). The regurgitants were dried (to remove moisture content) and ashed (to remove organic matter; Paine, 1971) to determine their ash-free dry mass (AFDM).

The net mass of 20 goldfish not used in the feeding trials was determined. These fish were then dried and ashed to determine their AFDM. I produced a regression of the resulting AFDMs and WMs; the slope of the regression line (AFDM = $-0.004018 + 0.154$ WM; $r^2 = 0.6406$; $P < 0.001$) enabled me to calculate the initial AFDM (= mass before digestion) of the experimental goldfish. By subtracting the $\mathrm{AFDM}_{\mathrm{regurgitant}}$ (= mass after digestion) from the $\mathrm{AFDM}_{\mathrm{initial}}$, I calculated the amount of AFDM that had been digested, which was used as an indicator of the rate of gastric breakdown. Data were analyzed (with α set at 0.05) with a two-factor repeated-measures ANOVA (time [six, 12, 18 h] × species [*N. sipedon, N. rhombifer*]).

RESULTS

All snakes gained mass from the time of first measurement (on day preceding study) to the time of second measurement (on day following study), and thus all proportional changes in mass were positive. The experiment on intraspecific competition in *N. sipedon* indicated that proportional changes in mass of snakes were significantly different between the three treatments ($F_{2,17} = 12.56$, $P < 0.001$; Fig. 1). Mass changes did not significantly differ between snakes that were maintained at low densities (one snake per enclosure) and offered five fish per week and snakes that were maintained at high densities (two snakes per enclosure) and offered 10 fish per week ($q_{1,8} = 3.26$, $P = 0.69$; Fig. 1). However, mass changes were significantly higher in snakes that were maintained at high densities and offered 10 fish per week than in snakes that were maintained at high densities and offered five fish per week ($q_{1,13} = 3.06$, $P = 0.007$; Fig. 1).

Again, all snakes gained mass from the time of first measurement to the time of second measurement, and thus all proportional changes in mass were positive. The experiment on interspecific competition between *N. sipedon* and *N. rhombifer* indicated that snakes of both species tested individually had significantly higher proportional changes in mass than snakes tested in intraspecific pairs ($F_{2,18} = 9.73$, $P = 0.002$; Fig. 2). For snakes maintained in interspecific pairs, *N. sipedon* had higher mass changes than *N. rhombifer*, although the difference was not significant ($F_{1,18} = 0.01$, $P = 0.94$; Fig. 2). In addition, the species × treatment interaction effect

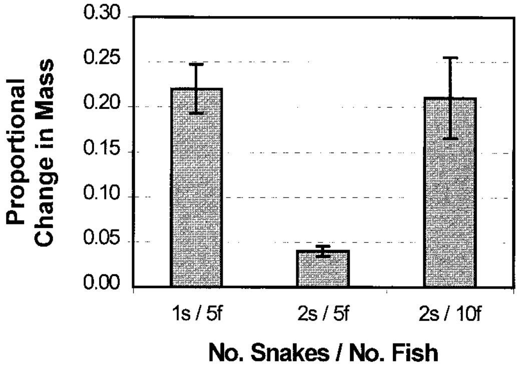

FIG. 1. Proportional change in mass (± 1 SE) in *Nerodia sipedon* maintained at low (one snake/enclosure) and high (two snakes/enclosure) densities and offered prey at low (five juvenile *Micropterus punctulatus*/enclosure/week) and high (10 juvenile *Micropterus punctulatus*/enclosure/week) densities. The first (one snake and five fish) and third treatments (two snakes and 10 fish) were replicated five times each and the second treatment (two snakes and five fish) was replicated 10 times for a total *N* of 20 tests. Different snakes were used for each replicate for total *N* of 35 snakes. All snakes gained mass, and thus all mass changes were positive. Proportional change in mass = (snake mass [g] before testing − snake mass [g] after testing)/(snake mass [g] before testing); f = fish; s = snake.

was not significant ($F_{2,18} = 1.63$, $P = 0.23$; Fig. 2).

The experiment on interspecific food exploitation indicated that, for snakes of both species, the mass of the goldfish that had been digested through gastric breakdown was significantly higher at 18 h than at 12 h after ingestion, and was significantly higher at 12 h than at six hours (time $F_{2,7} = 135.36$, $P < 0.001$; Fig. 3). *Nerodia sipedon* had relatively faster gastric breakdown rates at six and 12 h after ingestion than *N. rhombifer* ($F_{1,8} = 8.51$, $P = 0.19$; Fig. 3). Moreover, the time × species interaction was significant ($F_{2,7} = 7.00$, $P = 0.02$; Fig. 3).

DISCUSSION

The results of these experiments indicate that (1) food competition does not occur in *N. sipedon* at constant relative densities of prey to snakes; (2) intraspecific food competition in *N. sipedon* at low prey densities may occur; (3) intraspecific food competition among *N. sipedon* and *N. rhombifer* at high snake densities may occur; (4) *N. sipedon* may be a superior food competitor to *N. rhombifer* at constant relative densities of prey to species of snake; and (5) *N. sipedon* may be a superior exploitative food competitor to *N. rhombifer*.

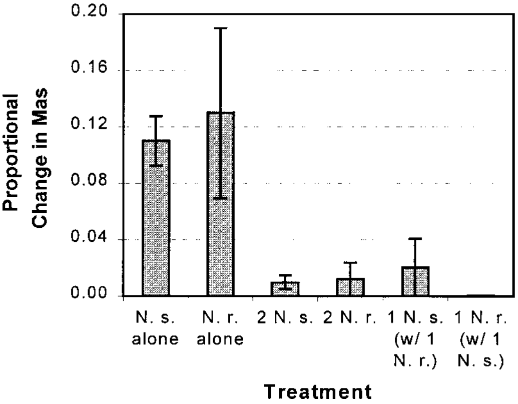

FIG. 2. Proportional change in mass (± 1 SE) in *Nerodia sipedon* (N. s.) and *Nerodia rhombifer* (N. r.) maintained at low densities (one snake/enclosure) and high intra- and interspecific densities (two snakes/enclosure). For all tests, 10 juvenile *Micropterus punctulatus*/enclosure/week were added as prey. Each treatment was replicated three times for a total *N* of 15 tests. Different snakes were used for each replicate for a total *N* of 12 *N. sipedon* and 12 *N. rhombifer*. All snakes gained mass, and thus all mass changes were positive. See Figure 1 for calculation of proportional change in mass.

The results indicating that intra- and interspecific food competition may occur, respectively, among and between *N. sipedon* and *N. rhombifer* may seem untenable in freshwater communities that are typified by a generally high diversity and abundance of potential prey species to the snakes. However, water levels of the Pascagoula River system became very low during the period when snakes were collected for this study (summers of 1998–1999). Because ofthis multiyear drought, the water became restricted to a series of small pools (usually < 1 m in depth). During nights when snakes were

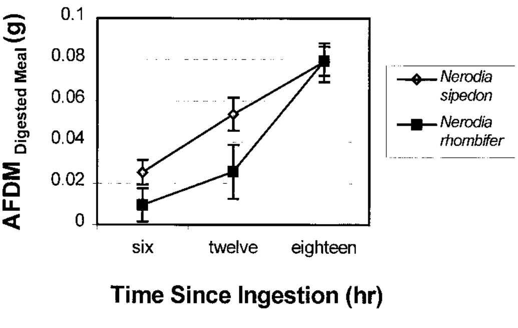

FIG. 3. Ash-free dry mass (AFDM; mean [± 1 SE]) of the digested meal of five *Nerodia sipedon* and five *Nerodia rhombifer* at six, 12, and 18 h after ingestion of a goldfish by each snake. Each individual snake was tested once under each treatment, resulting in five replicates per species of snake for each hour and a total *N* of 30 tests. For procedures used in the removal of moisture and organic matter, see Paine (1971).

collected, up to 10 individuals of *N. sipedon* and *N. rhombifer* combined were observed actively foraging in the same pools for fishes and frogs. Moreover, on several occasions, multiple individuals of snakes were observed attacking the same fish or frog. Although the snakes were ''free'' to move overland to search for food after they had exhausted the supply of fishes and frogs in the pools, neither *N. sipedon* nor *N. rhombifer* are inclined to do so except during periods of heavy rain (Preston, 1970; Meyer 1992). Thus, it does appear that the snakes are competing for a limited/limiting food source, at least during low water periods.

The faster digestion rate in *N. sipedon* may allow it to resume feeding more rapidly, leading to the consumption of more prey per unit time relative to *N. rhombifer* during periods of food limitation. This may translate into higher growth rates and greater reproductive potential in *N. sipedon*, ultimately resulting in the greater overall abundance of this species. Nonetheless, it is unknown whether *N. sipedon* actually spends more time foraging than does *N. rhombifer*. Moreover, a comparison of foraging success by both species is needed to determine whether the hunting skills of *N. sipedon* enable it to capture and consume more prey. The abundances and types of prey present (Mushinsky and Hebrard, 1977; Kofron, 1978; Miller and Mushinsky, 1990), habitat complexity (Mullin and Mushinsky, 1995, 1997), and climatic conditions (Mushinsky et al., 1980) may dictate in part the foraging success of *Nerodia* spp. Thus, the ability of *N. sipedon* to capture more prey than can *N. rhombifer* is probably subject to geographical and temporal variation.

The competitive relationships of *N. sipedon* and *N. rhombifer* should be further tested to determine whether interference competition may potentially occur as well. Exploitation and interference are frequently coexisting in the same community (e.g., Fellers, 1987; MacIsaac and Gilbert, 1991; Deslippe and Savolainen, 1995) and thus, although the results indicate that exploitation may be occurring, interference may also potentially occur between snakes. Moreover, although the results also indicate that interspecific competition may potentially occur for food, snakes may compete for other vital resources, regardless of the mechanism(s) involved. For example, in the upper Pascagoula River system, *N. sipedon* and *N. rhombifer* appear to have a strong preference for basking only on objects overhanging or partially submerged in the water (pers. obs.). Thus, the availability of suitable basking sites, especially for gravid females, may be a limited resource for which snakes may potentially compete.

To further substantiate the finding that *N. sipedon* and *N. rhombifer* may potentially compete for food, the diets of snakes should be determined and assessed for the degree of similarity. Moreover, the foraging habits of free-ranging snakes should be carefully observed and compared. For example, *N. sipedon* and *N. rhombifer* may forage in different microhabitats or during different times of the night, although I have found these two species repeatedly within the same area and foraging at the same time. Regarding foraging tactics, I have observed *N. sipedon* to attack live fishes only from the water's edge, whereas *N. rhombifer* attacks live fishes from the water (Savitsky, 1989). If these observations are accurate descriptors of these species normal foraging tactics, then the two species may encounter and consume different species or size classes of fishes, with *N. sipedon* taking more fishes that inhabit the land-water interface than does *N. rhombifer*.

The potential importance of *N. sipedon* and *N. rhombifer* as competitors in freshwater communities may be underestimated if adults are studied to the exclusion of neonates and juveniles. The smaller head and body size of young *N. rhombifer* limits the range of food sources available to them by inhibiting the consumption of large fishes, which are preferred by the adults (Mushinsky et al., 1982). These differences in diet between size classes may therefore lessen food competition between young and adult snakes. However, *N. sipedon pleuralis* and *N. rhombifer rhombifer* give birth annually to an average of 21 and 37 offspring, respectively (Tennant and Bartlett, 2000). Thus, until or unless the neonates disperse from their parturition site or their numbers are lowered by predation or other factors, the high density and more stenophagous diet (relative to adults) of young snakes may lead to increased food competition by individuals within this size class.

Assuming that competition is a major factor in communities that include *N. sipedon* and *N. rhombifer*, competition may be strongest not between species of snakes, but between snakes and other predators, such as piscivorous fishes. Although a snake-fish competitive interaction has not been documented to my knowledge, competition between taxonomically disparate species may be more prevalent than is commonly assumed, perhaps because most researchers do not test for competition between species that they assume a priori not to be likely competitors. For example, Resetarits (1991, 1995) found that the demography of a stream-inhabiting population of spring salamanders (*Gyrinophilus porphyriticus*) was strongly influenced by competitively asymmetrical interactions with brook trout (*Salvelinus fontinalis*).

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