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Population Patterns of a Riparian Frog (*Rana swinhoana)* Before and After an Earthquake in Subtropical Taiwan

Yung-Chih Lai

Department of Biology, National Changhua University of Education, Changhua, Taiwan

Bao-Sen Shieh

Department of Biomedical Science and Environmental Biology, Kaohsiung Medical University, Kaohsiung 807, Taiwan

and

Yeong-Choy Kam[1]

Department of Life Science, Tunghai University, Taichung 407, Taiwan

ABSTRACT

We compared the population dynamics of a riparian ranid frog, *Rana swinhoana,* before (1996–1999) and after (1999–2001) a strong earthquake. This earthquake caused little disturbance to the vegetation and landscape of the study site but the stream and ponds dried up within a week. Nearly all frogs marked (1002 of 1004) before the earthquake had disappeared after the earthquake. Smaller, unmarked frogs began to appear in stream habitats about 9 mo after the earthquake, and the frog population was much smaller than it was before the earthquake. Population dynamics and temporal and spatial distribution of frogs before and after the earthquake correlated closely with the hydrology of the stream and ponds. The movement patterns of frogs before and after the earthquake were similar, suggesting frog behavior did not change in response to drastic changes in hydrology, and frogs continued to exhibit strong site-fidelity. Following the earthquake, stream water volume was much lower, especially in the summer, which allowed the normally winter-breeding frogs to breed year-round. Results demonstrate that a population of *R. swinhoana* can disappear suddenly as the result of a natural disturbance. We propose that anuran species that exhibit strong site-fidelity are particularly susceptible to extirpation of local populations because frogs may lack the behavioral plasticity to respond to sudden water depletion.

Key words: anuran; disturbance; ecology; population dynamics.

A LARGE DISTURBANCE, EVEN IF IT OCCURS INFREQUENTLY and is of relatively short duration, can have profound effects on biological components at all levels, from individuals to ecosystems (Attiwill 1994, Wood *et al.* 1998). Disturbances may alter temporal and spatial distributions (Reagan 1991; Waide 1991a, b; Wunderle *et al.* 2004), reduce body size and survivorship (Woolbright 1991, Swilling *et al.* 1998), alter breeding behavior and breeding success (Wojnowski 2000, Jones *et al.* 2001), reduce population size (Askins 1991, Lynch 1991), and even extirpate entire populations (Willig & Camilo 1991, Woolbright 1997). Disturbances likely affect different species differently (Waide 1991a, Woolbright 1991, Hughes 1994, Greenberg 2001), which can change community structure and function (Lynch 1991, Will 1991).

Few studies have been carried out on the effects of disturbances on populations and communities. One reason for this is that disturbances occur unpredictably in time and space, so it is difficult for researchers to set up experiments prior to disturbance. As a result, studies of the effect of disturbance have concentrated on short-term changes in population dynamics or community structure after the disturbances (Askins 1991, Willig & Camilo 1991). Unfortunately, these studies may overlook factors that are masked by natural fluctuations but could be detected by long-term studies.

On 21 September 1999, central Taiwan was hit by a strong earthquake (7.3 on the Richter scale) that lasted *ca* 40 sec. Two strong aftershocks (6.8 on the Richter scale) and nearly a thousand minor aftershocks occurred during the next several months. The earthquakes caused displacement along 80 km of a fault line and caused massive landslides that destroyed vegetation in many areas. Although earthquakes are common in Taiwan, they are rarely as severe as the 21 September quake, which was the largest earthquake recorded in Taiwan in 100 yr. The Huisun Experimental Forest (HEF) in central Taiwan was one of the areas hardest hit by the earthquake. Although massive landslides occurred in many parts of HEF, the vegetation and landscape at a site where we have been monitoring a population of a riparian ranid frog (*Rana swinhoana*) since 1996 was nearly undisturbed. However, the stream in the study site dried up completely within a week. Apparently, the earthquake damaged the geological structure of underlying strata, and most of the water infiltrated underground. Later, when the stream contained some aboveground water, the water volume was much lower than pre-earthquake levels. During the wet season, the stream is comprised of spatially disjunct sections of flowing water that appear from and then disappear into the ground. During the dry season, the stream dries up completely.

Rana swinhoana is a nocturnal riparian frog that lives along torrential streams, rivers, and rapids under undisturbed forest (Wang & Chan 1978) and exhibits a strong site-fidelity with limited movement (Kam & Chen 2000). Due to recent deforestation and loss

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[1] Corresponding author; e-mail: biyckam@thu.edu.tw

of habitat, populations of this species have been fragmented and can only be found in undisturbed forests in low-to-mid elevations. With 3 yr of pre-earthquake data, we had a unique opportunity to monitor the responses of *R. swinhoana* to changes in stream hydrology resulting from an earthquake. The purpose of this study was to compare the temporal and spatial distribution, population dynamics, and reproduction of *R. swinhoana* before and after the earthquake and to elucidate the possible casual relationship between population dynamics of frogs and hydrological fluctuations.

METHODS

STUDY ANIMALS.—*Rana swinhoana* is a medium-sized frog, sexually dimorphic in body size, which can live 6–11 yr (Lai *et al.* 2005). The natural history and morphology of the species has been reported previously (Kam *et al.* 1998, Kam & Chen 2000). It is an agile and good jumper, and a pad-like structure on each toe enables frogs to cling to and climb on rocks and boulders easily. It breeds from November through January, and the larval period is *ca* 2 mo.

STUDY SITE.—The study was conducted from August 1996 to September 2001 at the Long-Term Ecological Research (LTER) site at Guandaushi in the HEF (24°2′–24°6′ N, 120°59′–121° 59′ E). This site is characterized by a steep terrain and is drained by four main tributaries of Peikang Stream (Kam & Chen 2000). There are distinct wet (May–August) and dry (September–April) seasons. Heavy rain falls during the spring (April–June) 'mei rains' and during summer typhoons.

We studied a population of *R. swinhoana* in a tributary of Guandau stream using a mark–recapture protocol described previously (Kam & Chen 2000). Briefly, we established a transect line running 330 m downstream from the headwaters of the tributary. About 300 m downstream from the headwater, the stream flows into three man-made ponds (hereafter referred to as ponds 1, 2, and 3). Beyond pond 3, the stream flows under an unpaved road (4 m in width) via a culvert, encounters a steeper slope, and flows through a broadleaf forest for another 300–400 m before feeding into Guandau Stream.

Due to inaccessibility and safety concerns, we were not able to reach our study site until 27 November 1999, 2 mo after the earthquake. We found that the vegetation and landscape at the study site were largely undisturbed. However, the stream and ponds 1 and 2 contained no water. Pond 3 contained a pool of water *ca* 10 cm in depth and 3 m in diameter. We did not see adult frogs in pond 3, but there were tadpoles. We were told by a worker who was trapped at HEF that the stream had dried up 2 d after the earthquake. The streambed looked the same as before the earthquake. Apparently, the impermeable layer that kept ground water near the surface was broken by the earthquake, allowing surface water to leak underground.

From the earthquake through to December 1999, only pond 3 contained water. In January 2000, the other two ponds began to fill with water from underground. All three ponds were full of water by May 2000, and they contained water until the end of this study, even though the water levels varied between wet and dry seasons. The stream was dry from September 1999 to April 2000. In May 2000, water started flowing in a short section (*ca* 10 m) of the stream (*i.e.*, 200 m upstream from pond 1) on the transect line. From May 2000 to December 2000, the stream was comprised of spatially disjunct sections of flowing water that appear from and then disappeared into the ground. The stream dried up again from January to March 2001 in the dry season, but water reappeared in April 2001 until the end of this study.

SAMPLING PROTOCOL.—Before the earthquake (August 1996–August 1999), we (a team of three to four investigators) sampled *R. swinhoana* monthly for two consecutive nights along the transect using headlamps. From November 1999 through October 2000, we conducted frog surveys only one night per month due to safety concerns. From November 2000 through July 2001, we surveyed frogs two nights per month. We did not survey frogs in October 1999, and February 2000, because landslides made the study site inaccessible.

For each survey, we first walked around each pond and searched for frogs. Then, we waded up the streambed and searched for frogs within 1 m on each side of the stream. We painted permanent marks on the rocks at 10-m intervals. Frogs were easy to spot at night because they usually perched on boulders or rocks, particularly in the vicinity of rapids or riffles. We began each survey at 1930 h and tried to catch all the frogs that were observed. We recorded the sex (male, female, or juvenile), snout-vent length (SVL), body mass, and capture location (to the nearest meter) of each captured frog.

Adult male frogs called year-round and were identified by the presence of vocal sacs and/or nuptial pads (Kam *et al.* 1998). Frogs showed sexual dimorphism in body size; the SVL of adult female frogs was seldom less than 60 mm (Kam *et al.* 1998). Thus, frogs with SVL greater than 60 mm and lacking a vocal sac were classified as adult females, whereas frogs with SVL less than 60 mm and lacking a vocal sac were classified as subadults or juveniles. After frogs were measured, we injected a passive integrated transponder (PIT) tag (Trovan^{TM}) dorsally (Donnelly *et al.* 1994). At the same time, we clipped the first digit of the forth toe of the right forelimb as a mark of capture before releasing the frog at the exact capture site. No infections were associated with the PIT tags and the wounds healed rapidly, based on frogs recaptured the following night. During the 5-yr study period, we lost only one tag due to malfunction. For recaptured frogs, we recorded the capture location, date, SVL, and body mass.

POPULATION ESTIMATION.—We used the Jolly–Seber full model (Pollock *et al.* 1990) of POPAN-5 (Arnason *et al.* 1998) to estimate the population size, survival (or retention) rate, and recruitment of frogs. Population parameters were estimated from combined data for each 6-mo period. Since we did not collect data in October and February 2000, estimates for October 1999 to March 2000 were calculated based on data from four surveys instead of six. Frog catchability was examined with the Leslie test (Leslie *et al.* 1953).

ABUNDANCE, RECAPTURE, AND SEX RATIO.—The frog abundance index was the number of frogs observed during each survey. Because many field surveys were conducted on two nights per month, we averaged the number of frogs observed. The recapture rate is the number of marked frogs divided by the total number of frogs captured. The sex ratio is the number of male frogs divided by the number of female frogs. Individuals that escaped were not included in the calculations.

MEASUREMENTS OF ENVIRONMENTAL VARIABLES.—We monitored stream hydrology during the study period. The stream was divided into 30, 10-m long sections. Each month, we recorded the stream sections that contained surface water. The cumulative stream sections (in meters) that contained surface water were used as an index of the hydrological status of the stream. For example, if all sections of the stream contained surface water, the sum would be 300, but if the stream was completely dry, then the sum would be zero. In addition, for each month, we recorded whether each section of stream contained surface water, and the cumulative duration (in months) that a stream section contained surface water was used as an index of its hydrological status. For example, we found that stream section 2 contained surface water in 18 of 24 mo surveyed after the earthquake, thus the hydrological status of stream at section 2 would be 18 mo.

STATISTICAL ANALYSES.—We performed all statistical analyses of the data with SAS (SAS 1996). Movement was categorized as upstream, downstream, or none. Frogs that moved 2 m or less were considered to have had no movement. Variable means ± SD are reported, unless noted otherwise. A value of $P < 0.05$ was considered statistically significant.

RESULTS

TEMPORAL DISTRIBUTION OF FROGS.—Prior to the earthquake, we recorded 2952 *R. swinhoana* frogs in surveys on 76 nights (8/1996–9/1999); after the earthquake we observed only 274 frogs in surveys on 33 nights (11/1999–9/2001). We marked 866 males and 138 females before the earthquake, of which 243 males and 39 females were recaptured. After the earthquake, we marked 106 males and 29 females, of which 15 males and 2 females were recaptured. Before and after the earthquake, we counted more frogs in summer (June–August) than in other seasons ($\chi^2 = 180.2$, df = 11, $P = 0.001$; Fig. 1). After the earthquake, the proportion of frogs observed in summer (64.1%) was much greater than the proportion observed in summer before the earthquake (48.4%). The proportion of frogs observed in winter decreased from 14.6 percent to 2.0 percent

Before the earthquake, the lowest frog count was 14 per night in February 1999, but after the earthquake, we observed fewer than 10 frogs per night in 14 of 24 surveys. After the earthquake, the stream was fragmented. Surface water flowed for short stretches in many sections of the stream, appearing from, and then disappearing into, the "leaky" streambed. Ponds 1 and 2 dried up for 7 mo. During this period, zero to five frogs were observed during surveys. The number of frogs observed each month was significantly correlated with the total length of the stream with surface water ($r_s = 0.72$, $P < 0.0001$).

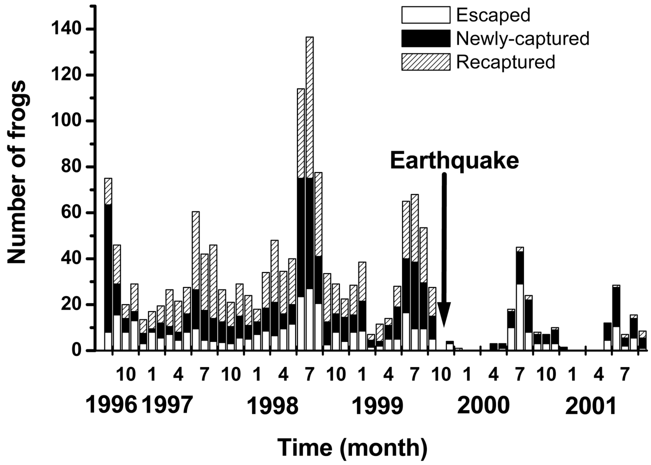

FIGURE 1. Relative abundance of *R. swinhoana* from August 1996 to September 2001. The earthquake occurred on 21 September 1999.

SPATIAL DISTRIBUTION OF FROGS.—Before the earthquake, we found more frogs in the stream (86.2% of total frogs) than in the ponds (13.8%). After the earthquake, about the same proportion of frogs were found in the ponds (50.9%) and stream (49.1%). After the earthquake, certain sections of the fragmented stream, such as the stream section 20 (*i.e.*, 200 m upstream from pond 1), held water longer than other sections. The number of frogs observed along a stream section was correlated significantly with the cumulative time (in months) the stream section contained surface water ($r_s = 0.54$, $P = 0.007$).

The mean maximum movement of recaptured frogs before (16.4 ± 29.3 m, $N = 343$) and after the earthquake (25.1 ± 45.70 m, $N = 9$) was not significantly different (Wilcoxon test: $Z = 0.427$, $P = 0.335$). Before the earthquake, 141 frogs moved upstream and 144 frogs moved downstream. After the earthquake, three moved upstream and two frogs moved downstream. Most frogs (65%) before and after (78%) the earthquake moved < 10 m. The numbers of frogs that moved up and downstream before ($\chi^2 = 0.0002$, df = 1, $P = 0.99$) and after (Fisher's Exact Test, $P = 1.00$) the earthquake were not significantly different.

MARK–RECAPTURE.—Many frogs were captured repeatedly during this study. Before the earthquake, we marked 1004 individual frogs and recaptured 382. After the earthquake, we marked 135 frogs and recaptured only 17. Among the 382 frogs recaptured before the earthquake, 200, 65, 43, 22, 14, 15, 7, and 16 were recaptured one, two, three, four, five, six, seven, and eight or more times, respectively. Of the 17 frogs marked after the earthquake, 14 and 3 frogs were recaptured one and two times, respectively.

Of the 1004 frogs marked before the earthquake, only two male frogs were observed after the earthquake. One was marked in June 1999, recaptured *ca* 70 m upstream in June 2000, and recaptured at the same location in July 2000. The other was marked in August 1999, and recaptured in July 2000, *ca* 200 m downstream at pond 1. The new population of *R. swinhoana* that established in

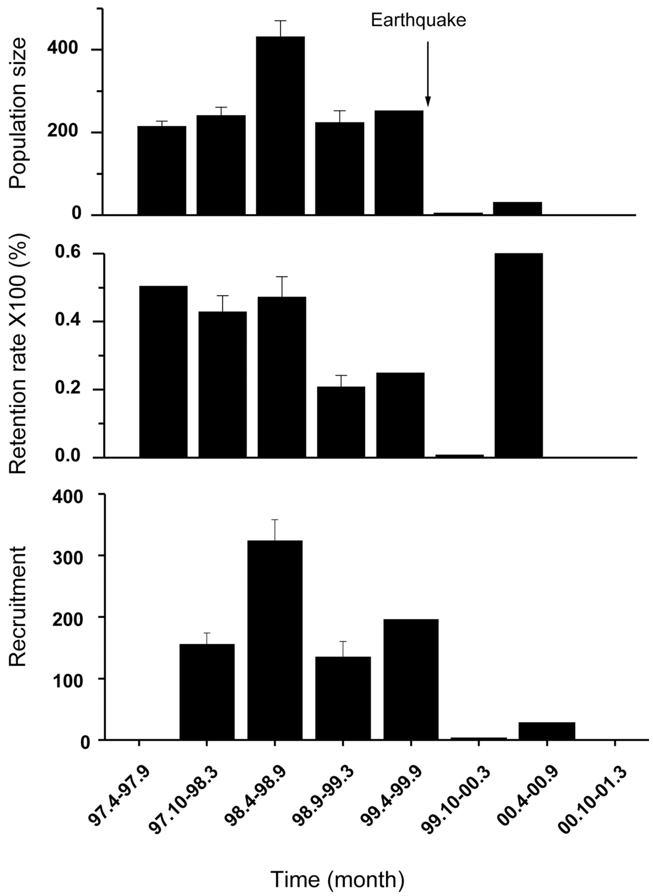

FIGURE 2. Estimated population size, retention rate, and recruitment of *R. swinhoana* before and after earthquake using the Jolly–Seber full model. Population parameters were estimated by using the combined data for each 6-mo period.

the stream after the earthquake was comprised mostly of unmarked frogs.

Before the earthquake, the mean monthly recapture rate (59 ± 14%, $N = 38$, range: 17–83%) was significantly greater than the recapture rate (20 ± 24%, $N = 15$, range: 0–100%) after the earthquake (Wilcoxon test: $Z = 5.375$, $P = 0.0001$).

POPULATION DYNAMICS.—A Leslie test indicated that the probability of capture did not differ significantly among sampling periods ($\chi^2 = 38.62$, df = 37, $P = 0.40$). Estimated population size, retention rate, and recruitment were much lower after the earthquake (Fig. 2)

Estimated population size correlated significantly with the proportion of the stream containing surface water ($r_s = 0.85$, $P = 0.008$). It was not significantly correlated with air temperature ($r_s = 0.48$, $P = 0.22$) or precipitation ($r_s = 0.29$, $P = 0.49$). After the earthquake, the number of frogs observed each month was significantly correlated with the cumulative stream sections (meter) that contained surface water ($r_s = 0.72$, $P < 0.0001$).

BODY SIZE AND MASS DISTRIBUTION.—The SVL of male (63.7 ± 3.6 mm; $N = 866$) and female frogs (77.5 ± 4.7 mm; $N = 138$) captured before the earthquake was significantly greater than the SVL of male (59.6 ± 4.2 mm; $N = 106$, $t = 10.67$, $P < 0.0001$) and female frogs (72.4 ± 2.79 mm; $N = 29$, $t = 9.08$, $P < 0.0001$) captured after the earthquake.

The body mass of male (23.7 ± 3.8 g) and female frogs (43.2 ± 7.5 g) before the earthquake was significantly greater than the body mass of male (20.9 ± 3.7 g; $t = 7.98$, $P < 0.0001$) and female frogs (38.2 ± 7.3 g; $t = 3.65$, $P = 0.0003$) after the earthquake, respectively.

REPRODUCTIVE PHENOLOGY AND SEX RATIOS.—Before the earthquake, we found gravid females from November to January, and tadpoles from November to April in all ponds and stream. Tadpoles were most abundant in December and January. After the earthquake, we found tadpoles year-round but the number was *ca* 100 times lower. During the wet season, tadpoles could be seen in ponds and the stream, but during the dry season, were only found in the ponds. The mean monthly sex ratio (male:female) of captured frogs, which probably reflects the operational sex ratio, before the earthquake (14.4 ± 25.8; $N = 37$) was significantly greater than the sex ratio after the earthquake (3.6 ± 2.7, $N = 14$; Wilcoxon test: $Z = 2.221$, $P = 0.013$). Before the earthquake, reproduction of *R. swinhoana* was concentrated between November and April, and the monthly sex ratios of captured frogs during the breeding (November–April: 8.2 ± 10.0; $N = 19$) and nonbreeding seasons (May–October: 20.3 ± 28.0; $N = 18$) were significantly different ($Z = 2.326$, $P = 0.010$).

The sex ratio of frogs after the earthquake was not significantly different from the sex ratio of frogs during the breeding season prior to the earthquake (Wilcoxon test: $Z = 1.103$, $N = 19$, $N = 14$, $P = 0.135$). However, the sex ratio of frogs after the earthquake was significantly lower than the sex ratio of frogs during the nonbreeding season prior to earthquake (Wilcoxon test: $Z = 2.819$, $N = 18$, $N = 14$, $P = 0.002$).

DISCUSSION

Disappearance of the *R. swinhoana* population shortly after the earthquake demonstrated that a short-lived, natural disturbance can have serious immediate consequences on a frog population. In contrast, many other natural disturbances reduce the size of animal populations at much slower rates (Waide 1991b, Woolbright 1996). Earthquakes may either cause frogs to behave abnormally (Sharygin 1995, Yosef 1997), leading them to emigrate from the stream area or affect frog populations indirectly by decreasing the availability or quality of shelters, food, and/or water (Tweddle & Crossley 1991, Waide 1991b, Pounds & Crump 1994, Stewart 1995, Woolbright 1996). At our study site, the most dramatic effect of the earthquake was the complete disappearance of the stream water. Terrestrial habitats were essentially undisturbed and intact, but *R. swinhoana* disappeared within 2 mo. We contend that the disappearance of *R.*

swinhoana was most likely caused by loss of water from the stream after the earthquake, followed by the subsequent winter dry season.

After the earthquake, stream habitats were occupied by a much smaller frog population that consisted of unmarked, smaller frogs. Our initial prediction was that there would be a dramatic decrease in the size of the frog population immediately after the earthquake, but that later a subset of the original population would return to stream habitats. If this was true, then we should have detected at least some marked individuals in the population that recolonized the area, especially since marked frogs represented a high proportion of the original population. However, we did not detect any marked individuals in the post-earthquake population. The causal mechanism for this finding is not clear at this point. Colonizing frogs may immigrate from tributaries in different watersheds, although it seems unlikely because our study site was physically separated from streams in other watersheds by at least 3 km of dry, precipitous mountain ridges. On the other hand, differential mortality of adults and subadults could have occurred due to their different habitat requirements and the changes in stream hydrology. During the 6-yr study period, most frogs caught in stream surveys were adults (3178 adults vs. 41 juveniles or subadults). We occasionally surveyed the stream bank and found many more juveniles in wooded habitats than in the stream (Kam, pers. obs.). Adults and subadults often utilize different habitats, which is probably the result of intraspecific competition for space (Martof 1953, Colley *et al.* 1989, Camp & Lee 1996). Thus, as the stream dried up after the earthquake, adult frogs, which depend more on the stream ecologically or physiologically, may have suffered higher mortality than the juveniles or subadults. When water returned to the stream, it could have been recolonized by smaller, unmarked frogs that had survived in wooded habitats.

Rana swinhoana did not actively respond to habitat drying by seeking water up- or downstream after the earthquake, suggesting that the frog behavior does not change in response to drastic changes in the hydrology of its home habitat, and they continued to exhibit high site-fidelity. Our results suggest that *R. swinhoana* inhabiting an environment with constantly available water lacks the behavioral plasticity to respond to sudden water depletion, as in the case of a rare disturbance such as an earthquake. As a result, frogs may suffer high mortality due to dehydration in an unexpectedly long dry season.

Changes in the reproductive activity of *R. swinhoana* following the earthquake probably occurred in response to changes in stream hydrology. A similar finding was reported in an earlier study in which the reproductive phenology of *Rana boylii* was synchronized with stream hydrology, and frogs bred earlier in drier years when water flow decreased much earlier than usual (Kupferberg 1996). Before the earthquake, *R. swinhoana* at the study site bred in the dry season, from November to April (Kam *et al.* 1998). Stream discharge varied seasonally and was strongly correlated with rainfall, which was exceedingly high in the summer and much lower in the winter (Kam *et al.* 1998). *Rana swinhoana*, like other stream breeders, breeds in the dry season because water flow is lower and less variable (Menzies 1963, Zug & Zug 1979, Jorgensen *et al.* 1986, Aichinger 1987). After the earthquake, stream water volume was much lower, even during the summer, allowing frogs to breed year-round.

The marked population of *R. swinhoana* almost completely disappeared following the earthquake. Thus, an earthquake, though very short in duration, can have devastating effects on a frog population. Our results suggest that this single unusual event, an earthquake that caused the sudden loss of water from a stream and ponds during the dry season, could explain the disappearance of the *R. swinhoana* adult population. We propose that anuran species that exhibit strong site-fidelity are particularly susceptible to extirpation of local populations because adult frogs probably lack the behavioral plasticity to respond to sudden water depletion and the adult population could collapse in only 1 or 2 mo. Our results also suggest that a frog population could resist an apparent catastrophe through recolonization by juveniles as suitable habitats become available.

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