Abundance and Movement of a Riparian Frog (*Rana swinhoana*) in a Subtropical Forest of Guandau Stream, Taiwan

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Yeong-Choy Kam and Te-Chih Chen (2000) Abundance and movement of a riparian frog (*Rana swinhoana*) in a subtropical forest of Guandau Stream, Taiwan. *Zoological Studies* **39**(1): 67-76. We studied a population of *Rana swinhoana* using mark-recapture methods from August 1996 to July 1998 at the Long-term Ecological Research (LTER) site at Guandau Stream, Taiwan. We established a 330-m transect at the headwaters of a tributary of Guandau Stream and censused *R. swinhoana* for 2 consecutive nights monthly. We used mark-recapture techniques to sample frogs along transects, with each individual being uniquely marked. For every animal captured, we recorded clip, sex, snout-vent length, body mass of frogs, and location along the transect. We observed 1947 but captured 1608 frogs during the 24-mo study period, including 1414 adult males and 172 adult females. Frogs were more abundant in the summer than in the winter. Monthly recapture rates varied between 30% and 81%. *R. swinhoana* moved little during the study and showed no seasonal up- or down-stream movements. The clumped distribution of frogs along the stream is probably a result of the heterogeneity of microhabitats. *R. swinhoana* sometimes made extended excursions, but returned to their usual activity ranges. The results of this study suggest that *R. swinhoana*, like many riparian anurans, is a sedentary animal with homing ability. By inhabiting riparian zones, *R. swinhoana* probably obtains sufficient ecological necessities such that long-distance movements are not required.

Key words: Anuran, Ecology, Phenology, Reproduction.

Most amphibians have permeable skins and can lose body water rapidly (Shoemaker et al. 1992); thus water availability influences distribution, activities, and movements. This can have important implications for population dynamics and life-history patterns of a species (Beshkov and Jameson 1980, Crump and Pounds 1989, Cohen and Alford 1996). For example, rapid dehydration is a major threat to the survival of land-dwelling amphibians (Malvin and Wood 1991), and they may spend time and energy moving around seeking moist micro-sites in order to maintain a proper water balance (Carpenter and Gillingham 1987, Cohen and Alford 1996). Rainfall influences the reproductive phenology of many amphibian species, particularly in tropical forests with seasonal precipitation (Inger and Greenberg 1963, Alexander et al. 1979, Bowker and Bowker 1979, Aichinger 1987, Gascon 1991, Donnelly and Guyer 1994). Dependency upon an aquatic environment for reproduction results in breeding migrations before and after spawning (Dole and Durant 1974, Beshkov and Jameson 1980, Sinsch 1991), which can cover distances of up to several kilometers (Duellman and Trueb 1986).

Reproductive phenology of stream-dwelling species may differ from that of pond-breeding species because water is more readily available in streams, and the threat of desiccation is reduced. Unfortunately, detailed information on various aspects of ecology, such as the movements, abundance, and reproduction of stream-dwelling anurans is lacking, particularly for those in tropical and subtropical regions. Some tropical and temperate stream-dwelling anurans exhibit philopatry with limited movement (Inger 1969, Daugherty and Sheldon 1982, Tessier et al. 1991). However, a riparian mem-

ber of the family Bufonidae, *Atelopus varius*, moves seasonally. Individuals are uniformly distributed along the stream during the wet season, but aggregate in areas containing waterfall spray during the dry season (Crump and Pounds 1989). In addition, many stream dwellers in the tropics reproduce in the dry season rather than in the wet season, probably because of lower water flow rates which ensure a better survivorship of larvae (Zug and Zug 1979, Petranka 1984, Jorgensen et al. 1986, Aichinger 1987).

In this study, we examined the abundance, distribution, and movement of a riparian anuran, *Rana swinhoana*, from a subtropical hardwood forest in Taiwan. *R. swinhoana* is a medium-sized frog with sexual body size dimorphism. Snout-vent lengths (SVL) are about 78 and 61 mm for female and male frogs, respectively (Kam et al. 1998). This nocturnal, riparian species is found along torrential streams, rivers, and rapids with scattered boulders of various sizes (Wang and Chan 1978, Lue 1990). Frogs retreat into crevices between boulders during the daytime, and are active at night, perching on boulders or rocks in the vicinity of rapids or riffles. *R. swinhoana* is agile during its activity, and it usually produces short, impulsive, high-pitched calls (Wang and Chan 1978) which are similar to those of many riparian species (Duellman and Trueb 1986). *R. swinhoana* breeds from November to January (Kam et al. 1998). Eggs are oviposited in small clumps (40-50 eggs) under stones or crevices in running water (Yang 1998). Eggs are whitish yellow, and diameters vary from 2.5 to 3.0 mm with a thin jelly layer that can barely be seen with the naked eye (Wang and Chan 1978). Tadpoles have cup-like oral discs and strong massive caudal musculature (Chou and Lin 1997). Metamorphosis requires approximately 2 mo depending on the thermal conditions of streams. Tadpoles are seen between November and April (Kam et al. 1998).

MATERIALS AND METHODS

Study site

This study was conducted from August 1996 to July 1998 at the Long-Term Ecological Research (LTER) site at Guandau Stream in the Huisun Experimental Forest (Lat. 24°2' to 24°6'N, Long. 120°59' to 121°59'E). This site is characterized by steep terrain with elevations ranging from 500 to 2418 m. The Huisun forest is drained by 4 main tributaries of the Peikang Stream: Hosui, Chunggu,

Tungfong, and Guandau. The steeply sloped stream channels are lined with cobblestones and boulders, which measure up to several meters in diameter.

Meteorological data were collected by an on-site weather station supported by a LTER project of the National Science Council. Weather patterns included distinct rainy (May-Aug.) and dry (Sept.-April) seasons, with the summer (July-Sept.) temperatures about 10 °C higher than those in the winter (Jan.-March) (Fig. 1). Water temperatures fluctuated less than air temperatures, being cooler in the summer and warmer in the winter. Heavy rains were mainly associated with the "plum rains" (or "Mei rains") in the spring (April-June) and the typhoon season in the summer. The "plum rain" season is characterized by continuous light rain for days with occasional heavy thunder-storms. Typhoons occur most often from June through September, and usually bring heavy rains that can cause flash floods and damage forests.

We conducted a population study on *R. swinhoana* using a mark-recapture method in a tributary (about 750 m in total length) of the Guandau Stream, which is located in a 120-ha watershed (Fig. 2). We established a 330-m transect at the headwater (elevation 1200 m) of the tributary. The stream gradient at the study site is steep (17 °). At about 300 m down-stream from the headwater, the stream flows into 4 concrete ponds: a concrete weir (length x width
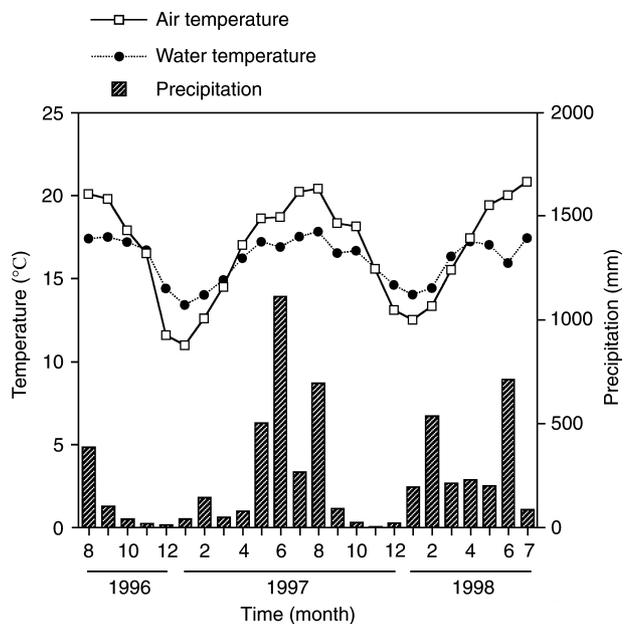
Fig. 1. Monthly mean air and water temperatures (°C) and precipitation (mm) in the study site at Guandau Stream. Numbers correspond to months.

x depth: 15 m x 5 m x 3.5 m) consisting of a triangular crest to monitor surface runoff, followed by 3 different reservoirs (referred to as C, B, and A reservoirs hereafter with dimensions of 10 m x 7 m x 2.3 m, 3.2 m x 8.5 m x 2 m, and 3.2 m x 5.6 m x 1.5 m, respectively). After reservoir A, the stream then flows under an unpaved road (15 m in width) via a culvert, encounters a steeper slope, and flows through a broadleaf forest for another 300-400 m before feeding into the Guadua Stream. We did not census frogs downstream of reservoir A due to reduced accessibility and safety concerns.

The width and depth of the stream in the study area vary considerably depending on rainfall patterns, but on average the stream is 1-3 m wide and 2-30 cm deep in the center. The stream has a permanent flow that passes through alternating riffles and pools. Stream bottoms and banks consist of sand, gravel, boulders, and bedrock. The stream is completely shaded by broadleaf trees except at the ponds. The dominant understory shrubs belong to the Rubiaceae, Myrsinaceae, and Theaceae.

Experimental protocol

Each month, 4 investigators sampled *R. swinhoana* for 2 consecutive nights (August 1996 to July 1998) along the transect with headlamps. First, we walked around each pond and searched for frogs. We then waded up the beds of the stream and searched for frogs within 1 m on each side of the stream. We painted permanent marks on the rocks at intervals of 10 m. 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 census at 1930 h and continued until all observed frogs were collected. For each frog captured, we recorded sex (male, female, or juvenile), snout-vent length (SVL), body mass, and location of capture (to the nearest m). Male frogs were identified by body size and the presence of vocal sacs while female frogs were identified by body size (Kam et al. 1998). After frogs were measured, we injected a passive integrated transponder (PIT) tag (Trovan brand) dorsally (Donnelly et al. 1994). At the same time, we clipped the inner toe of the right forelimb as a mark of capture before releasing the frog at the exact site of capture. We saw no infection caused by the PIT tags, and the wounds healed rapidly based on observations of overnight recaptured frogs. We lost only 1 tag due to malfunctioning during the 24-mo study period. For recaptured frogs, we recorded location of captures, date, SVL, and body mass. For those frogs captured on 2 consecutive nights, we

measured the daily movement patterns (directions and distance moved). Overnight recaptures were not included in the analyses of overall and monthly recapture rates. For frogs that were captured twice within a season or between years, we measured the SVL, body mass, and seasonal (or annual) movement patterns. For the analysis of seasonal movement, 1 individual may be represented by more than 1 data point, if it was caught more than 2 times within a season. January-March, April-June, July-September, and October-December were categorized as winter, spring, summer, and fall seasons, respectively. We used dip nets to collect tadpoles in the spray pools, reservoirs, and at the weir.

Statistical analyses

We performed all statistical analyses of data
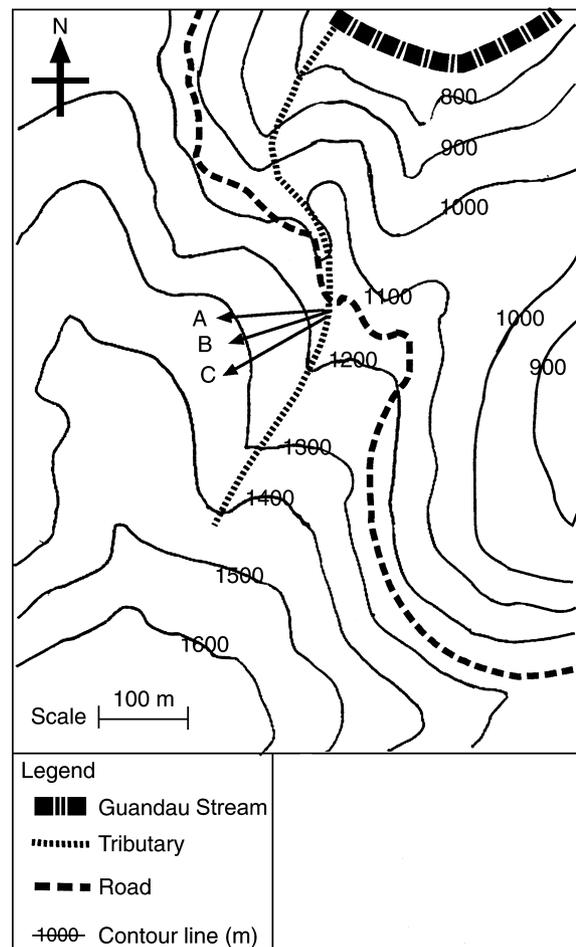
Fig. 2. Schematic drawing of the study site. A, B, and C represent the 3 reservoirs located downstream of the transect. See "Materials and Methods" for a detailed description of the transect and reservoirs.

with SAS (SAS 1988). We used Spearman's correlation coefficient to assess correlations between the number of frogs and meteorological variables. We further used a stepwise regression to determine the relative importance of each meteorological variable in predicting the number of frogs. Estimation of population size is not presented in this paper because we discuss several aspects of population dynamics of this species separately. We used X^2 test to determine movement patterns, as well as temporal and spatial distributions. Unless mentioned, the X^2 test was designated to compare the expected frequency based on equal probability of events to the observed frequency. We used t- and F-tests to compare distances moved by frogs. Movements were categorized into up-stream, down-stream, and no movements. Frogs that moved less than or equal to 2 m were defined as having "no movement". We did not compare the movement pattern between male and female frogs due to the small sample size of female frogs. The stream was divided into lower (0-100 m from the weir), middle (110-200 m), and upper portions (210-300 m). The means of all variables are reported ± SD unless otherwise noted. A value of $p <$ 0.05 is considered statistically significant.

RESULTS

Seasonal activity

We observed a total of 1947 frogs but only caught 1608 of them during the 24-mo study period. Among the captured individuals were 1414 adult males, 172 adult females, and 22 juveniles or subadults. We counted more frogs in the summer than in other seasons. We recorded the highest and lowest numbers of frogs in July 1998 and December 1996, respectively (Fig. 3). The number of frogs counted each month was significantly correlated with air temperature ($r = 0.75$, $n = 24$, $p = 0.0001$) and rainfall ($r = 0.58$, $n = 24$, $p = 0.006$). However, a forward stepwise regression analysis showed that the number of frogs was influenced significantly only by temperature (partial $r^2 = 0.34$; regression coefficient $= 0.587$, $t = 3.32$, $p = 0.003$).

We caught significantly more male than female frogs each month, but the proportion of male and female frogs fluctuated significantly across months (months vs. male or female; $X^2 = 282$, $df = 23$, $p = 0.001$). Relatively more female frogs were caught in the fall and winter than in other seasons. Female frogs comprised an average of 14.9% ± 11.9% ($n = 24$, range: 0%-37%) of total collected frogs each

month. We caught only 22 subadults or juveniles in the study period. These frogs were captured in every month of the year except for June and December (Fig. 3).

Mark-recapture

Because many individuals were captured repeatedly during the 2-yr study period, we only cumulatively marked 685 frogs even though we had 1608 frog recaptures. We marked 602 male and 83 female frogs, but only 226 and 25 were recaptured, respectively, and the recapture rate did not differ between sexes (marked males or females vs. recaptured males or females; $X^2 = 1.73$, $df = 1$, $p = 0.188$). Among the 251 recaptured frogs, 132, 44, 26, 12, 12, and 25 frogs were recaptured 1, 2, 3, 4, 5, and 6 or more times, respectively. The most frequently caught female (no. 715E51) and male (no. 977EE3) frogs were recaptured 6 times over a period of 22 mo and 10 times over a period of 18 mo, respectively. The recapture rate (mean, 55.9% ± 12.8%, $n = 23$) varied monthly between 30% (June 1998) and 81% (January 1997). More unmarked frogs appeared in the summer than in the winter, with the majority being sexually mature males or females instead of juveniles (Fig. 3). The number of unmarked frogs usually did not exceed 40 except in June and July 1998 when we caught 105 and 99 unmarked frogs, respectively (Fig. 4). The number of unmarked frogs was negatively correlated with the recapture rate
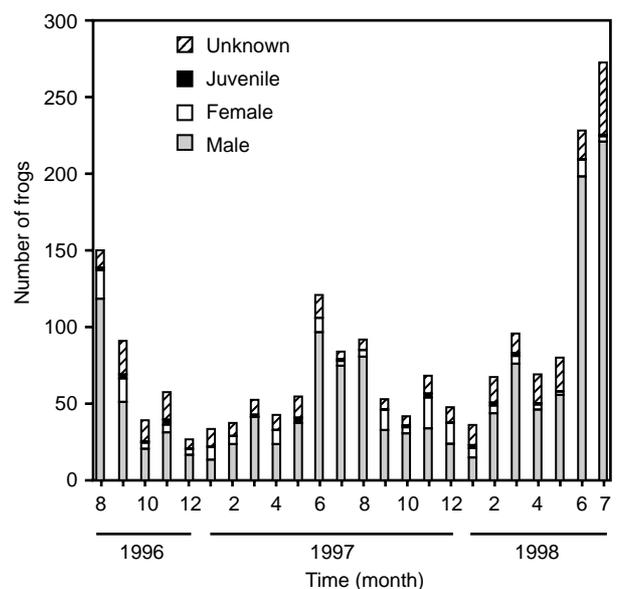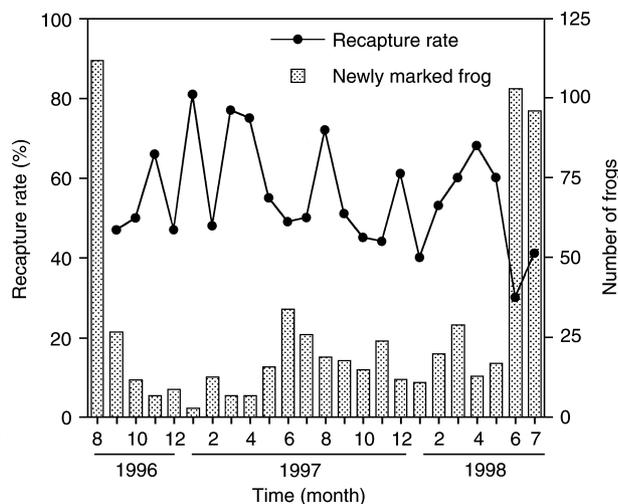

Fig. 3. Relative abundance of *Rana swinhoana* from August 1996 to July 1998.

($r = -0.584$, $n = 23$, $p < 0.05$; Fig. 4), but positively correlated with the number of total frogs ($r = 0.897$, $n = 24$, $p < 0.01$; Figs. 2, 4). We compared the SVLs of unmarked and marked male frogs for each census (in month), and we found no significant differences except in June, July, and September 1997 and May, June, and July 1998 when marked frogs had significantly longer SVLs than did unmarked male frogs ($p < 0.05$). We did not compare the SVLs between unmarked and marked female frogs due to the small sample size (Fig. 3). Male and female frogs grew by an average of 2.84 ± 2.48 mm ($n = 50$, range 0 to 8.9 mm) and 3.59 ± 2.57 mm yr^{-1} ($n = 4$, range 1.14 to 5.90 mm), respectively. Most subadults or juveniles were too small to be injected with transponders; however, we did inject a transponder into a subadult which was later identified as a male frog. This frog (no. 9782DA) grew from 51.29 to 70.18 mm in 15 mo, i.e., 15.11 mm yr^{-1} (Sept. 1996-March 1998).
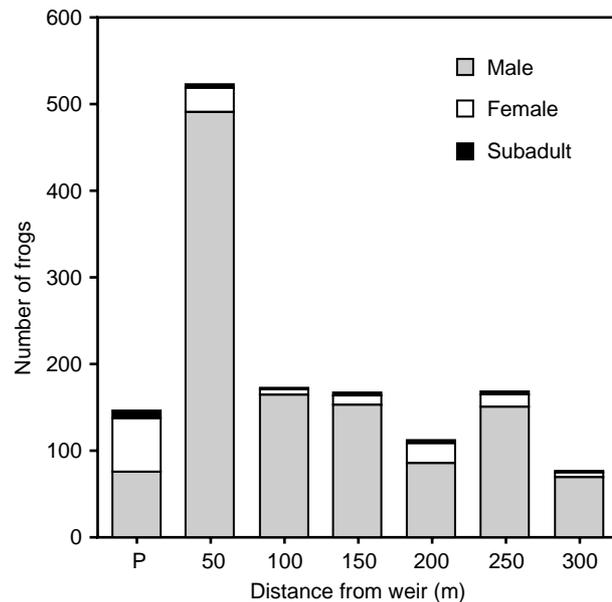
Spatial distribution

Assuming equal probabilities of distribution of frogs along the stream transect, a X^2 test of independence of the frequency of frogs along the transect gave a significant value ($X^2 = 165$, $df = 2$, $p = 0.001$; Fig. 5). Frogs were active at night, with the majority (> 85%) perched on rocks, particularly in spray zones, when we sighted them. We captured a low number of frogs in reservoirs A to C, probably because of a lack of perching substrates. By contrast, the number of frogs captured at the weir (131 frogs) was greater than the total number captured in the 3 reservoirs (A-C) combined (78 frogs) (Fig. 5). Forty-

six percent (75/163) of frogs in the ponds were female, while only 7% (97/1423) of frogs in the stream were female. The proportion of male and female frogs was strongly dependent upon location (ponds or stream vs. females or males; $X^2 = 232.3$, $df = 1$, $p = 0.001$). Body size of male frogs significantly differed among lower, middle, and upper portions of the stream ($F_{2,1063} = 7.12$, $p = 0.0009$). Multiple comparison tests show that SVLs of male frogs in the upper (64.35 ± 3.18 mm, $n = 212$) and middle (64.2 ± 3.05 mm, $n = 224$) portions of the stream did not significantly differ ($p > 0.05$), but both were significantly larger ($p < 0.05$) than SVLs of male frogs in the lower (63.5 ± 2.98 mm, $n = 630$) portion of the stream. We heard frogs calling all along the transect, particularly during the breeding season. We observed no breeding aggregations or amplectant frogs during the study period. In addition, no aggressive or territorial behaviors were observed. Tadpoles were found from November to April, but were most abundant in December and January. Newly metamorphosed froglets were found from April to June. Tadpoles were more abundant at the weir (hundreds) than in the lower 40 m section of the stream (less than a hundred). We spent many hours searching for tadpoles in other sections of the stream, but found few or no tadpoles.

Fig. 5. Spatial distribution of *Rana swinhoana* along the stream. P represents the number of frogs sighted in ponds or at the weir. Values on the *X*-axis represent distance away from the weir. For example, 50 represents those frogs which were sighted between 0 to 50 m away from the weir. See "Materials and Methods" for a detailed description of the study site.
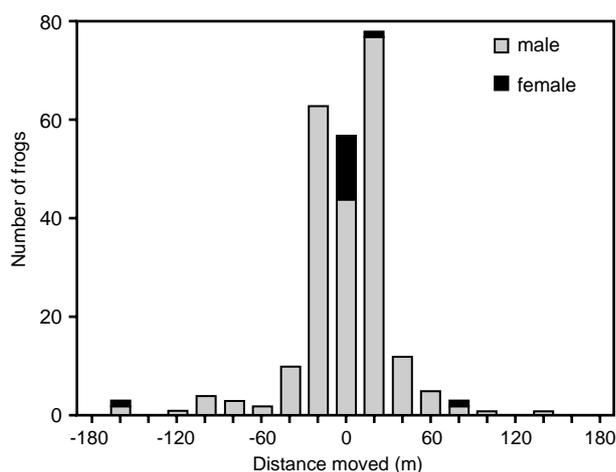

Fig. 4. Monthly fluctuations of the recapture rate and the number of newly marked frogs.

Movement

Maximal movement

The mean maximum movement by frogs during the 24-mo study period was 15.4 ± 30.0 m (n = 243, range 0-179 m), with 68.7% (167 of 243) having moved less than 10 m (Fig. 6). There were no significant differences in the number of frogs that moved up-stream (100 frogs) and down-stream (86 frogs, X^2 = 0.528, df = 1, p = 0.468) nor the distance moved (up-stream, 16.3 ± 24.5 m, n = 101; down-stream 24.4 ± 37.4 m, n = 86; X^2 = 1.76, p = 0.079). The maximal up-stream movements per recapture episode for male and female frogs were 142 and 61 m, respectively, while the maximal down-stream movements were 179 and 165 m, respectively.

Cumulative movement

Most frogs that were recaptured had remained close to the original capture site (Fig. 6). A few made extended excursions, but returned to the original capture site (Figs. 6, 7). The greatest cumulative movement of 369 m was over a 22-month period made by a female frog (no. 715E51) that was recaptured 6 times. However, this frog was last recaptured only 2 m from the initial capture site. Similarly, the greatest cumulative movement by a male frog (no. 7063FC) was 189 m over a 24-mo period. This frog was recaptured 8 times, and made 2 extended excursions, but was last recaptured only 1 m away from the site of initial capture (Fig. 7).

Daily movement

In our census of the transect for 2 consecutive nights each month, we successfully recaptured a total of 6 female and 199 male frogs. We found that 95 of these frogs had stayed at the same spots from 1 night to the next (mean, 2.07 ± 3.62 m, n = 205, range 0-30 m). There was no significant difference in the numbers of frogs that moved up-stream and down-stream (69 and 50 frogs, respectively; X^2 = 1.527, df = 1, p = 0.217). However, up-stream movements were significantly shorter than down-stream movements (2.91 ± 2.17 m, n = 72 and 5.00 ± 6.05 m, n = 43, respectively; t = 2.66, p = 0.009).

Seasonal movement

There were no demonstrable differences in movements across seasons (up-stream, down-stream, or no movement vs. spring, summer, fall, or winter; X^2 = 6.45, df = 6, p = 0.374) nor in distance moved between seasons ($F_{3,322}$ = 1.28, p = 0.281; Table 1). Within seasons, there were also no significant differences in distances moved between up-stream and down-stream movements.
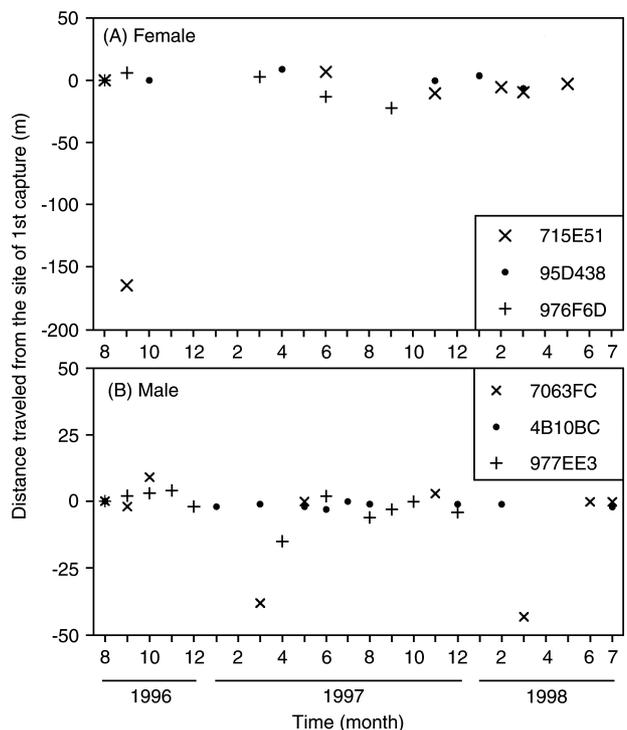

Fig. 6. Maximal movement by 251 frogs. No movement (0) was defined as frogs that moved less than or equal to 2 m. Positive and negative values represent up-stream and down-stream traveled distances, respectively. There were 434 frogs that were never recaptured during the study period; thus, we were unable to determine their distance moved.

Fig. 7. Movement patterns of the 6 most frequently caught (A) female and (B) male frogs, respectively. Positive and negative values represent up-stream and down-stream traveled distances, respectively. The transponder number for each of the frogs is labeled.

Annual movement

Thirty-nine males and 3 females were recaptured 1 yr after marking. The number of frogs recaptured up-stream (24 frogs) and down-stream (15 frogs) did not differ ($X^2 = 1.05$, $df = 1$, $p = 0.305$). There was also no difference in the distance moved up-stream (9.63 ± 16.01 m, $n = 24$) and down-stream (24.50 ± 34.18 m, $n = 15$; $t = 1.83$, $p = 0.082$).

DISCUSSION

Seasonal activity

Seasonal activity of amphibians is principally regulated by environmental temperature and moisture (Duellman and Trueb 1986), and the activity levels reflect the physiological conditions of organisms (Licht 1969, Wiest 1982, Pough et al. 1983). The result of stepwise regression reveals a significant correlation between frog abundance and air temperature, but not precipitation, suggesting that seasonal activity of *R. swinhoana* is associated more with changes in temperature than with changes in rainfall. This is probably because water is readily available in streams, and desiccation is unlikely to be a threat to *R. swinhoana* adults and larvae. By contrast, low temperatures in the winter most likely depress physiological functions, thereby, reducing activity levels. The recorded temperature difference between the coldest (11 °C from December to February) and warmest months (21 °C in July) was about 10 °C (Fig. 1), and the minimum daily temperatures dropped to 6.6, 4.6, and 8.2 °C in December, January, and February, respectively.

Kam et al. (1998) reported that *R. swinhoana* breeds during the dry season. This agrees with results of earlier studies of many tropical stream-dwelling species, such as *Hyla boans* (Aichinger 1987, Gascon 1991), *Bufo marinus* (Zug and Zug 1979, Aichinger 1987), *Bufo regularis* (Menzies 1963), and *B. melanostictus* (Jorg ensen et al. 1986). Zug and Zug (1979) hypothesized that stream breeders have been selected for dry season breeding because of low water flow rates at that time. The stream discharge at our study site varied seasonally and was closely associated with rainfall, which was exceedingly high in the summer when compared to that in the winter (Kam et al. 1998). In addition, the unpredictable occurrences of typhoon (e.g., typhoon Herb in July 1996) which usually brings high-intensity rainfall in a short time, cause flash floods making the stream unsuitable for breeding during the wet season.

Movements

Amphibian movements and dispersal are associated with shelter, predation, food, mates, and body moisture and temperature regulation (Crump and Pounds 1989, Cohen and Alford 1996). Our findings that frogs in the Guandau Stream site moved little during the 24-mo study period are probably due to their ability to obtain ecological resources in their nearby environments which obviate the need to aggregate or move long distances. Inger (1969) also reported that riparian ranids in tropical Borneo have limited linear movement. The male and female frogs captured in our study were adults with slow growth rates. This minimal movement may partially account for the high recapture rates. However, the recapture rates did not increase with time (Fig. 4), suggesting that there must have been continuous recruitment of unmarked frogs to the stream. Furthermore, the correlation between the total number of frogs and unmarked frogs suggests that the major recruitment most likely occurs in the summer when most frogs are active (Figs. 2, 3). If unmarked frogs were recruited by up-stream or down-stream movements, we would expect that the frogs moved consistently in

Table 1. Overall, up-stream, and down-stream movements by *Rana swinhoana* in different seasons

	Overall (m)[c]	Upstream (m)	Downstream (m)	t value[b]	p[b]
Winter	13.81 ± 28.38^a (38)	17.94 ± 32.58 (18)	25.25 ± 34.05 (8)	0.52	0.607
Spring	7.37 ± 19.92 (113)	7.69 ± 13.62 (46)	10.62 ± 27.97 (45)	0.64	0.526
Summer	7.59 ± 17.37 (147)	13.47 ± 25.97 (55)	6.82 ± 8.14 (55)	1.81	0.072
Fall	6.28 ± 8.56 (28)	7.54 ± 8.73 (11)	7.75 ± 9.42 (12)	0.05	0.957

[a]Values are means ± SD. Sample size is in parentheses.
[b]The t and p values are the results of comparing distance traveled by up-stream and down-stream movements.
[c]Overall movement has a larger sample size than up-stream and down-stream movements combined because it also includes data of individuals with no movement (we defined no movement as a frog moved less than or equals to 2 m).

some direction, and the distance moved away from the initial site of capture would increase in proportion to time (Beshkov and Jameson 1980). However, our data do not support this possibility because of a lack of directional movements in all seasons. Furthermore, distance moved away from the initial site of capture did not increase with time (Fig. 7). Alternatively, unmarked frogs may have been recruited by lateral movements of frogs that inhabiting adjacent wooded areas. Our study sites were physically separated from streams of other watersheds by at least 3 km of dry, precipitous mountain ridges. Thus, direct lateral movements between tributaries in different watersheds were unlikely to have occurred.

Limited movement also suggests that *R. swinhoana* individuals probably breed in their home range. The breeding peak of *R. swinhoana* is from December to January (Kam et al. 1998), but we detected no seasonal and up- or down-stream breeding migrations. This finding agrees with our earlier field observations (Kam et al. 1998). However, the number of female frogs increased disproportionally during fall and winter, which is most likely explained by lateral movements from adjacent wooded areas.

Earlier studies reported the presence of homing ability in stream-dwelling anurans, such as *A. varius* (Crump 1986), *A. truei* (Daugherty and Sheldon 1982), and *L. hochstetteri* (Tessier et al. 1991), which might be related to territoriality, food foraging, and micro-habitat conditions (Daugherty and Sheldon 1982, Crump 1986). In this study, *R. swinhoana* individuals sometimes made extended excursions and were able to return to the original site (Fig. 7), suggesting that a homing ability enables frogs to return to their ranges. The function of these excursions is not known, but earlier studies have suggested that excursions enable frogs to learn their way around in the area, thus, increasing their acquaintance with a wider area (Martof 1953, Dole 1965).

Spatial distribution

Micro-habitat heterogeneity may influence spatial distribution in *R. swinhoana*. Frogs were captured most frequently on boulders or rocks, particularly in the vicinity of rapids or riffles (Kam et al. 1998). In this study, boulders or rocks were available throughout the stream, and the presence of spray zones may have determined frog abundance. There was a large waterfall spray in the stream adjacent to the weir, and many frogs appeared to be shuttling between the spray zone and the weir. By contrast, the availability of perching substrates such as plastic pipes or floating logs in the ponds appeared to deter-

mine the frog abundance. However, we do not know if the heterogeneity of microhabitats would explain the differences in sex ratio between ponds and the stream. The proportion of male and female frogs varied in different sections of the stream (Fig. 5) which alters the operational sex ratios. It is possible that the uneven distribution of tadpoles along the transect is a result of differential mating success due to different operational sex ratios. More reproductive (e.g., courtship behavior, mating systems) and demographic (e.g., time to reach sexual maturity, survivorship to age of reproduction) parameters are needed to explain the skewed sex ratio as well as the spatial distribution of frogs.

CONCLUSIONS

Rana swinhoana is a sedentary animal, and this perhaps is a common characteristic shared by other anurans such as *L. hochstetteri* and *A. truei* which inhabit permanent streams (Inger 1969, Daugherty et al. 1981, Daugherty and Sheldon 1982, Duellman and Trueb 1986). Some frog species exhibit distinct pre- and post-breeding migrations, and they aggregate in ponds or streams to breed (Dole and Durant 1974, Beshkov and Jameson 1980, Kam et al. 1995). Our data generally support the hypothesis that *R. swinhoana* adults exhibit site fidelity, but additional movement information from juvenile populations are needed before a generalization can be reached. We captured a low number of juveniles or subadults along the transect, suggesting that they are not routinely active in stream and ponds. Thus, if any significant movement occurs among them, it is most likely to occur in terrestrial instead of aquatic habitats.

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關刀溪產斯文豪氏赤蛙族群數量及移動之研究

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我們利用標放法在臺灣中部關刀溪研究斯文豪氏赤蛙之族群生態學，時間是從 1996 年 8 月至 1998 年 7 月。我們在關刀溪一支流的水源地設 300 m 的調查線，每月連續兩個晚上調查斯文豪氏赤蛙。我們記錄個體性別、吻肛長、體重、及捕捉地點。我們共觀察 1947 隻蛙，其中 1414 及 172 隻分別為雄及雌蛙。在夏季活動的青蛙個體遠比冬季多。每月重新捕捉率大致在 30%-81% 之間。斯文豪氏赤蛙移動性低，同時也末有任何季節性的往上或下游移動的情形。沿河微棲地的異質性可能解釋何以青蛙沿溪呈塊形分布。斯文豪氏赤蛙有時也會做長距離的移動，但牠皆能回到自已的活動範圍。研究結果顯示斯文豪氏赤蛙和其他河川蛙類一樣屬移動性低的種類。因為長時間居住在河濱帶，青蛙可能已經得到生活上所需資源，所以不必做長距離的移動。

關鍵詞：兩棲動物，生態，氣候學，生殖。

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