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**Daily Behavior and Microhabitat Use of
the Waterfall Frog, *Litoria nannotis* in
Tully Gorge, Eastern Australia**

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The daily activities of amphibians are influenced by their need to obtain food, mates, and shelter; avoid predators; and maintain adequate physiological conditions (Dole, 1965; Beshkov and Jameson, 1980; Woolbright, 1985; Zug, 1993; Cohen and Alford, 1996; De Oliveira, 1996). Most amphibians share certain behavioral similarities. Because of the permeability of their skin, they are highly susceptible to dehydration from evaporative water loss. Therefore, most amphibians are typically nocturnal and tend to shelter in moist refuges during the day and become active only at night (Duellman and Trueb, 1986).

Compared to other small-bodied tetrapods, amphibians are relatively sedentary animals, most displaying movements in the order of only tens to hundreds of meters (Sinsch, 1990; Zug, 1993; Blaustein et al., 1994). The orientation of amphibian movements depends on the shape of their local habitat (Duellman and Trueb, 1986). Although many stream-breeding amphibians migrate to terrestrial habitats during non-breeding periods, stream-dwelling species usually reside permanently at the breeding site. In stream-dwelling species, movements upstream and downstream tend to be more substantial than any lateral movement away from the stream (Ashton, 1975; Holomuzki, 1982; Beshkov and Jameson, 1980; Duellman and Trueb, 1986). Nevertheless, stream-dwelling frogs have been known to forage away from the stream at night, particularly following rains, when the risks of dehydration are substantially reduced (Martof, 1953; Daugherty and Sheldon, 1982).

The waterfall frog, *Litoria nannotis* is among seven species of frogs which have mysteriously declined from pristine upland regions of North Queensland in recent years (Richards et al., 1993; Trenerry et al., 1994; Hero et al., 1998). Knowledge of their behavior and general ecology may be important in the search for potential causal factors for the declines. *Litoria nannotis* is considered to be a true stream-dwelling anuran, unlikely to venture far from the stream (Liem, 1974); however individuals have sometimes been found in stream-side vegetation (Hero and Fickling, 1994). The extent to which they utilize the forest as an



FIG. 2. Waterfall frog, *Litoria nannotis*, with transmitter attached.

alternative habitat is unknown. Similarly, *L. nannotis* are known to be active both during the day and at night, but no study has compared the proportion of diurnal and nocturnal activity. The objectives of this study were to describe the daily behavior and use of habitats by *L. nannotis*, specifically how *L. nannotis* divide their activity between the forest and stream habitats, and between nocturnal and diurnal activity.

The study was conducted within a 200-m transect at Python Creek, Tully Gorge, Cardstone (145°35'E, 17°46'S), approximately 40 km northwest of Tully, North Queensland. Python Creek is a relatively fast-flowing lowland rain-forest stream, lined on both sides by simple notophyll vine forest. The creek bed is composed of moderate to large granite boulders (0.5–2.5 m in diameter), that create many short waterfalls. Therefore, Python Creek is considered a prime habitat for *L. nannotis*. Tully Gorge experiences a distinct wet and dry season. Average monthly rainfall increases dramatically between January and April (Fig. 1), often creating floodwaters in Python Creek.

A total of 19 frogs were radiotracked over three survey periods. Three frogs (one male, two female) were radiotracked in the midwet season of 1995 from 16 January to 2 February. Eight frogs (four male, four female) were radiotracked late in the wet season of 1995, from 29 March to 20 April. Eight frogs (four male, four female) were radiotracked during the dry season of 1996, from 2 October to 23 October.

A preliminary radiotracking study conducted at Paluma, North Queensland, suggested that Holohil BD-2A whip transmitters weighing 1.4–1.5 g are small enough to be carried by healthy adult male and female *L. nannotis*, which weigh on average 8.9 g (SE = 0.08, N = 310) and 12.8 g (SE = 0.19, N = 185), respectively. Although relatively heavy (at up to 16% of body weight), the transmitters showed no sign of inhibiting the behavior of *L. nannotis*, because individuals with transmitters were found at exposed positions on waterfalls, often in association with frogs not carrying transmitters. In this study large, healthy male and female frogs were taken from Python Creek to a nearby field station, where they were fitted with soft radiotracking belts. Each radiotracking belt was constructed by gluing a transmitter to a thin gauze bandage strip that was rolled into a belt and tied around the waist of the frog so that it sat on the lower back, above the vent (Fig. 2). Carried in this position, the transmitters appeared to cause minimal inconvenience to

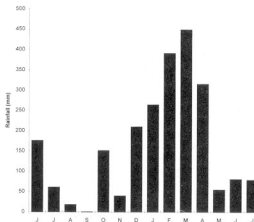


FIG. 1. Monthly rainfall totals recorded at Kareeya Power Station, Tully Gorge between June 1996 and July 1997.

TABLE 1. Summary of data for individual *Litoria nannotis* radiotracked at Python Creek. Data presented as percentage of frogs found in the stream or forest among the diurnal and nocturnal locations.

Season	Sex, individual frog #	Transmitter life (days)	Diurnal			Nocturnal			Initial frog weight	Final frog weight	
			Stream (%)	Forest (%)	No. of fixes	Stream (%)	Forest (%)	No. of fixes			
Wet season 1995	Male 1	30	100	0	8	100	0	10	9.5	9.5	
	Male 2	30	100	0	8	88.89	11.11	9	9	8.25	
	Male 3	22	100	0	1	100	0	2	8.25	—	
	Male 4	23	100	0	8	90	10	10	7	7.25	
	Male 5	16	100	0	5	80	20	5	8	8.5	
	Female 1	18	100	0	5	16.67	83.33	6	10.25	10	
	Female 2	18	100	0	6	100	0	4	12.5	12.5	
	Female 3	23	100	0	4	100	0	6	13	—	
	Female 4	23	100	0	8	81.82	18.18	11	11.5	11.5	
	Female 5	23	100	0	5	75	25	4	14	—	
Female 6	22	100	0	6	88.89	11.11	9	14	15		
Wet season total			100	0	64	84.21	15.79	76			
Dry season 1996	Male 6	10	100	0	10	100	0	5	8.5	8.75	
	Male 7	14	90	10	10	81.82	18.18	11	7.5	7.5	
	Male 8	11	100	0	13	100	0	10	8	—	
	Male 9	16	100	0	11	90.91	9.09	11	9.5	9.25	
	Female 7	9	100	0	9	77.78	22.22	9	13	13.25	
	Female 8	14	100	0	7	57.14	42.86	7	14	13.8	
	Female 9	11	100	0	6	100	0	6	13.5	13.75	
	Female 10	19	100	0	8	87.5	12.5	8	12	12.5	
	Dry season total			98.65	1.35	74	86.57	13.43	67		
	Female total			100	0	64	78.57	21.43	70		
Male total			98.65	1.35	74	91.78	8.22	73			
Total			99.28	0.72	138	85.31	14.69	143			

the frogs. Once fitted with transmitters, the frogs were returned to Python Creek and released at the site of capture.

Signals were received using a hand-held H-frame antenna attached to a Telonics TR-4 receiver. Frogs were located twice every 24 h, once during the day (0700–1900) and once at night (1900–0700). Each time

a frog was located, information on the frogs location was recorded, including the vertical height above water, lateral distance from water, position along the 200-m transect, location in the stream or on vegetation, and whether it was at an exposed or sheltered position. Each frog located was observed for 5 min from a distance of more than 5 m using binoculars.

For each individual, the proportion of fixes in the stream and adjacent forest were compared during the day and at night. Because the number of diurnal and nocturnal fixes were uneven, day and night fixes were examined separately. Seasonal habitat use was compared between the wet and dry season surveys, as was the use of habitats by male and female *L. nannotis*.

Throughout the survey, 281 fixes (138 diurnal, 143 nocturnal) were obtained for 19 *L. nannotis* individuals. Frogs were radiotracked for periods that ranged from nine to 30 days because of variations in transmitter longevity. The frogs displayed distinctly different nocturnal and diurnal behavior. During the day, nearly all frogs (99.3% of fixes) were restricted to the stream environment (Table 1). Most frogs (96.4% of fixes) spent daylight hours sheltering in small refuges behind waterfalls or wedged between rocks in the stream. A small proportion of diurnal fixes (3.6%) located individuals basking in splash zones beside waterfalls (Fig. 3).

At night frog activity increased substantially. A considerable proportion of nocturnal fixes (37.1%) located frogs in exposed positions within the stream and some (14.7%) ventured away from the stream on at least one occasion, and one female was found in

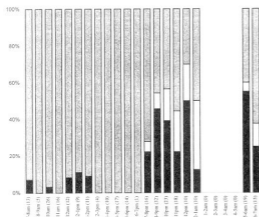


FIG. 3. The proportion of fixes locating frogs in exposed or sheltered positions in the stream and forest for each hour of the day. Closed bars represent exposed stream sites, open bars represent exposed forest sites, and grey bars represent sheltered stream sites.

stream-side vegetation on five separate evenings. Frogs did not venture further than 15 m from the stream and always returned before dawn.

Litoria nannotis appeared to be sedentary for much of the time. Despite the increase in nocturnal activity (with individuals having moved to exposed positions in the stream and forest), frogs were observed moving on only five of 281 occasions. On four occasions, radiotracked and nonradiotracked frogs were observed returning to the stream simultaneously, minutes before dawn. There did not appear to be any seasonal difference in the nocturnal movement of frogs away from the stream. During the dry season, 13.4% of nocturnal fixes located frogs within stream-side vegetation, compared with 15.8% during the wet season (Table 1). Female frogs spent a greater proportion of their time (21.4% of nocturnal fixes) in stream-side vegetation than did males (8.2% of nocturnal fixes).

Four frogs were not recovered because of transmitter failure. A *t*-test conducted on the initial and final weights of the 15 frogs that were recovered suggested that the frogs did not suffer any significant loss of weight, ($t = 0.98$, $N = 15$, $P = 0.34$) and therefore were likely to be in relatively good health (Table 1). The fact that nonradiotracked frogs were frequently seen displaying behavior similar to that observed by frogs with transmitters provides further evidence that the behavior displayed by the radiotracked frogs was representative of that seen in the general population.

Litoria nannotis is unlike many amphibians in that it is not strictly nocturnal. Although most individuals spent daylight hours sheltering among rocks within the stream, a small number of frogs were found basking in sunny, splash zones beside waterfalls during the day. Basking behavior has been reported in other amphibians, including *Rana cascadae*, *Rana septentrionalis*, *Hyla versicolor*, *Hyla californica*, *Bufo canorus*, *Bufo boreas*, *Bufo woodhousei* (Brattstrom, 1963; Lillywhite et al., 1973; Pearson and Bradford, 1976). The higher body temperatures induced by basking facilitate an increase in the rate of digestion, enabling individuals to maximize growth rates and optimize postmetamorphic recruitment success. Despite this, the phenomenon is not common among amphibians, presumably because the detrimental effects of accelerated evaporative water loss experienced while basking outweigh the advantages gained by raising body temperature. Basking behavior tends to be more common in humid tropical regions (Duellman and Trueb, 1986), and many species, including *L. nannotis* reduce the effect of evaporation by basking within wet zones beside waterfalls where they can be continually hydrated by splashing water.

Unlike most stream-breeding frog species that live in the adjacent forest and use the stream habitat for breeding, the stream is the primary habitat for both male and female *L. nannotis* throughout the year. Subsequently, *L. nannotis* is an obligate stream-dwelling and stream-breeding frog. *Litoria nannotis* was not confined to the stream, however, and individual frogs made regular nocturnal excursions for short distances into stream-side vegetation, returning to diurnal shelter sites in the stream before sunrise. Many amphibians exhibit such diel shifts in habitat use, including the stream-dwelling *Rana clamitans* (Martof, 1953) and *Ascaphus truei* (Daugherty and Sheldon, 1982). These

frogs often forage away from the stream at night. Terrestrial frogs including *Pseudacris striata* (Kramer, 1973) and *Eleutherodactylus coqui* (Woolbright, 1985) move from diurnal retreats within leaf litter to nocturnal foraging zones among vegetation. Other frogs such as *Phyllomedusa bicolor* (De Oliveira, 1996) and *Hyla cadaverina* (Harris, 1975) move from arboreal and terrestrial refuges to nocturnal calling and feeding sites in nearby streams.

Nocturnal movement into stream-side vegetation by *L. nannotis* may be motivated by the need to locate more efficient feeding sites, to reduce the risk of predation, or to escape possible aggressive intraspecific (territorial) interactions at the stream. Interestingly, females appeared to move into the forest more frequently than males. Although this may simply be the result of chance (because of the low number of individuals tracked in this study), it may indicate a significant difference in the behavior of males and females that warrants further investigation.

One surprising result was that almost half the nocturnal fixes located frogs in sheltered positions within the stream; hence, many individuals were not sighted. Assuming the radiotracked frogs were not inhibited by the transmitters or by the presence of humans, their behavior suggests that a single visual survey will underestimate the abundance of *L. nannotis*.

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