



Preliminary observations on the circadian variation in site fidelity in *Atelopus hoogmoedi* (Lescure, 1974) (Anura, Bufonidae)

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The genus *Atelopus* (Bufonidae) is mostly composed of conspicuously colored species, several of which are known to secrete toxins (Fuhrman 1969; Yotsu-Yamashita and Tateki 2010). The genus has recently received increased attention due to severe decline in population numbers, often suggested to have revealed extinctions (La Marca et al. 2005; Pounds et al. 2006; Wake and Vredenburg 2008; but see Luger et al. 2008 for the Guianas). This mass decline has been attributed to multiple factors such as habitat loss, pollution, introduced species, and the chytrid fungus *Batrachochytrium dendrobatidis* (La Marca et al. 2005). One of the most widespread, and probably less threatened species in the genus is *Atelopus hoogmoedi* (Fig. 1 A–B), which is found in French Guiana, Suriname, Guyana, and northern Brazil (Noonan and Gaucher 2005; Kok and Kalamandeen 2008; Luger et al. 2008; Segalla et al. 2014). Two color morphs co-occur syntopically in Iwokrama (Guyana), an orange and a yellow morph (Fig. 1 A–B). This diurnal toad exhibits spatio-temporal segregation of sexes, with males usually found near streams, while females are found deeper in the forest, away from water bodies (Luger et al. 2009). During the breeding season, which mostly occurs in the dry season (see below), females migrate to streams for mating (Fig. 1 C, Luger et al. 2009). Similar reproductive strategies are observed in other anurans and are often characterized by site fidelity in which the males remain in the vicinity of the same perching site for the duration of the breeding period (e.g., Roithmair 1992; Ringler et al. 2009).

Several studies have investigated homing behavior and site fidelity in some *Atelopus* species (e.g., Crump 1986), including *A. hoogmoedi* (Luger et al. 2009). It has been suggested that site fidelity increases the probability of finding a suitable mate by improving the detection either by males through an increased field of vision, or by females as a result of a more conspicuous male perch (Himmel 2013). However, the occurrence of site fidelity outside of the reproductive season makes the mate detection hypothesis unlikely (Crump 1986; Luger et al. 2009). Alternatively, site fidelity may provide better knowledge of the local microenvironment making foraging more efficient, as well as providing means of protection from predation e.g., by good knowledge on possible escape routes (Luger et al. 2009). Previous studies have focused on diurnal site fidelity, and investigations pertaining to circadian variation in site fidelity are lacking. Since protection from predation is a plausible hypothesis explaining site fidelity, nocturnal behavior (when the diurnal animal is most vulnerable and an optimal protective perch likely required) deserves further attention. If protection is indeed a major driver for site fidelity, scarcity of optimal refuges might lead to increased site fidelity.

This hypothesis was briefly tested during fieldwork conducted in the Iwokrama Forest Reserve, central Guyana. Iwokrama is mostly covered by tropical moist lowland forest (Holdridge 1967), with some of the Iwokrama Mountains reaching ca. 900 m asl (MPFITRF 2009). Climate in Iwokrama is tropical, with an annual mean temperature of 25 °C and a mean rainfall of 3,000 mm

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Fig. 1. (A) Orange and (B) Yellow color morphs of *Atelopus hoogmoedi*, both encountered at the studied locality in the Iwokrama Mountains, Guyana. (C) Typical breeding habitat of *A. hoogmoedi* in the Iwokrama Mountains. Photos by PJRK.

in the north of the reserve and 1,400 mm in the south of the reserve (MPFITRF 2009). Wet season usually extends from May to August and again from November to February (MPFITRF 2009), although this has seemed more irregular in recent years, especially during El Niño events (reported as particularly strong in 2015, and the months of November and December 2015 were very dry in Iwokrama).

Fourteen *Atelopus hoogmoedi* males were “marked” (see below) and “recaptured” in order to track their circadian variation in site fidelity. All individuals were spotted along a portion of the trail between Turu Falls and the Linden-Lethem road (between N 4°24.74' W 58°47.13' and N 4°24.63' W 58°47.30'; WGS 84; Fig. 2). Elevation ranged between 92 and 120 m asl. The trail was walked twice a day, once at 13h (daylight) and once at

18h (shortly after nightfall) between November 27 and December 1, 2015. Color pattern is individual-specific in this species (see Fig. 1 A–B), and individuals were identified based on photographs of the dorsal pattern taken in situ using a digital camera (Canon® Eos 7D). To limit physical interaction, ventral patterns were not examined (no specimen was manipulated during this study). The use of color pattern for identification in this species is an appropriate alternative to invasive marking techniques such as toeclipping (Luger et al. 2009). Locations of observations were recorded using a Garmin eTrex 30® GPS, and marked with colored flagging tape at the site of first detection, allowing immediate recognition of the site. For each observation three parameters were recorded: (1) height above ground; (2) perch type (categorized as leaf litter, shrub, or rock); and (3) distance from

original diurnal or nocturnal perch site. Distances were measured using a 50-m measuring tape. In order to standardize the procedure, an individual was considered to be present if three investigators were able to track it within a three-meter radius from the original perch site within three minutes. We used independent *t*-tests to compare the observation probabilities between different days and different sampling times. Additionally, Fisher's exact test was used to determine whether any of the two most common substrates (shrub or leaf litter) was used more than the other. All statistical analyses were done using IBM SPSS® v20.0.0.

Observation probabilities did not differ significantly between days ($t = 1.14$, $P = 0.26$), nor did they differ significantly between daylight (62%) and night (69%) ($t = 0.71$, $P = 0.54$). More individuals did, however, return to the original perch site at night than during the day (distance from original perch site = 0; $P = 0.08$). Finally, a difference in perching substrate use was found at different times of the day (Fig. 3). While this difference between substrate use was not significant during daylight ($P = 0.25$), a significant difference was found at night when most frogs were present on shrubs ($P =$

0.00). Unlike Luger et al. (2009), who detected *A. hoogmoedi* in leaf litter only 14% of the time, in our study leaf litter was the most used microhabitat, especially during daylight (64%). After dark most individuals were found perching in shrubs, at heights between 10–130 cm.

Most *Atelopus* species, including *A. hoogmoedi*, mate close to streams, and occurrences of flashfloods have been reported to wash away entire *Atelopus* populations (Duellman and Trueb 1986). As a result, high perching sites were explained as a strategy against such sudden water rises (e.g., Duellman and Trueb 1986; Luger et al. 2009). This could explain the differences in observations between our study and previous studies (Luger et al. 2009). Our study, in which individuals were often found on the ground, was conducted during the dry season (see above), in contrast with previous studies that were conducted during the wet season (protection from sudden water rises is likely more necessary during the latter). Furthermore, as reproductive interactions occur in the leaf litter (observation of amplexus during our fieldwork), male individuals are more likely to perch on the leaf litter during breeding season to increase the chance of inter-sexual interactions. Alternatively, differences

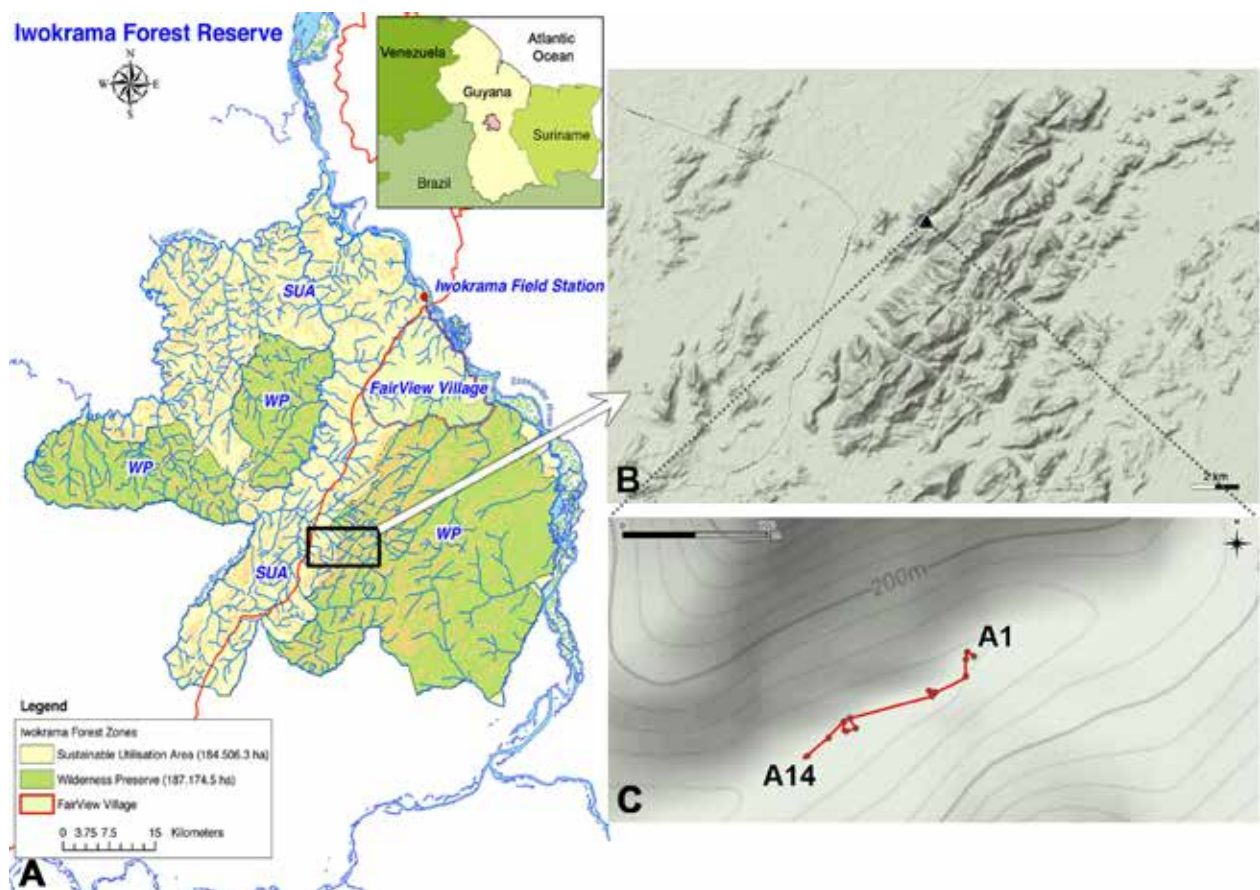


Fig. 2. Geographical overview of the study area. (A) Map of the Iwokrama Forest Reserve and its location in Guyana (top right corner). The red line crossing Iwokrama corresponds to the Linden-Lethem Road. (B) Relief map of the Iwokrama Mountains with Turu Falls represented by a black triangle (N 4°24.770' W 58°47.061'). (C) Portion of the trail between Turu Falls camp and the Linden-Lethem Road monitored, with dots corresponding to *Atelopus* individuals (from A1 - N 4°24.742', W 58°47.130' to A14 - N 4°24.750', W 58°47.128'). A and B from Kok et al. (2013).

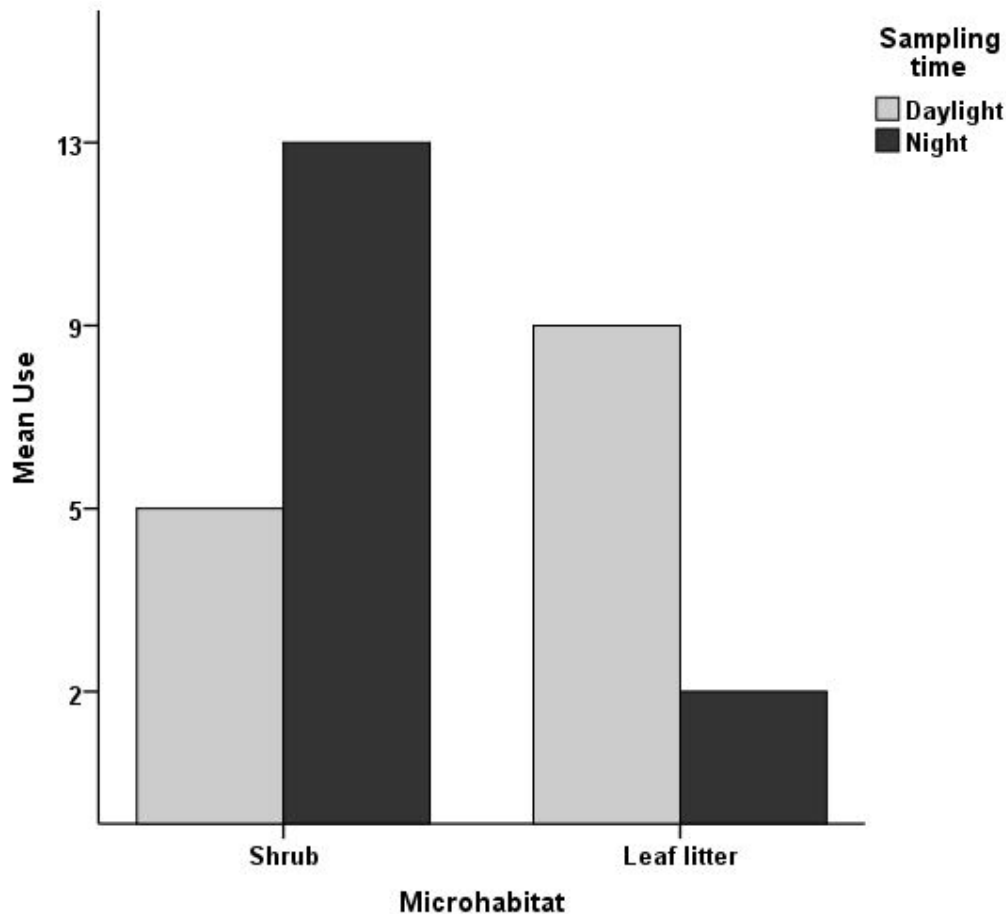


Fig. 3. Substrate (shrub or leaf litter) use in *Atelopus hoogmoedi* during the day (light grey) and night (dark grey) at Turu Falls, Guyana. As indicated, substrate use was significantly different after dark.

with Luger et al. (2009) might be explained by different abiotic and biotic factors between the two study sites. As previous studies indicated that perching on shrubs occurred during both breeding and non-breeding season (Crump 1986; Luger et al. 2009), it is unlikely that this elevated perching plays a major role in mating. The fact that the frogs leave these perch sites diurnally, when they are actively reproducing, further corroborates the hypothesis that elevated perching is not reproduction related. In other *Atelopus* species, such as *A. zeteki*, higher nocturnal perches are proposed to be a safe retreat from predators for this diurnal frog, shifting vigilance from visual to tactile (Lindquist et al. 2007). Some perches serve as better retreats than other perches, and difference in perch quality could drive both diurnal and nocturnal site fidelity. Our preliminary data indeed show that there was no significant difference in site fidelity between night and day as would be expected when site fidelity is linked to lower predation pressure. Furthermore, individuals returned more to the original nocturnal perching site than to the original diurnal perching site. This indicates that site fidelity might actually be linked to nocturnal perching site rather than to diurnal perching site. As both foraging and breeding occur during the day, the protection

hypothesis provides a good explanation for this nocturnal site fidelity, and site fidelity in general.

Some species of *Atelopus* are known to have lived over ten years in the wild (La Marca 1984), and at least one individual was recorded on the same boulder two years after the previous observation (Crump 1986). Such life history strategies make *Atelopus* ideal organisms for study of long-term site fidelity. Future studies are encouraged to expand our preliminary findings by increasing the length of the study, and if possible the number of recaptures.

In conclusion our observations, although sparse, seem to confirm that *Atelopus hoogmoedi* does indeed show strong diurnal and nocturnal site fidelity, during breeding and non-breeding seasons. Although several hypotheses may explain this, the fact that perch site return rate is the highest after dark supports the predation evasion hypothesis.

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