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Coming home to roost: comments on individual sleep-site fidelity, sleep-site choice, and sleeping positions in *Anolis* (*Norops*) *leditzigorum* (Köhler et al., 2014) in Costa Rica (Squamata: Dactyloidae)

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Anolis is a highly diverse radiation of New World tropical and subtropical lizards. With multiple species often present in any given habitat, these lizards present a cornucopia of study systems to behavioural ecologists (e.g., Roughgarden, 1995; Losos, 2009). As a consequence, their territorial and home-range behaviours are among the feats that have been documented in a variety of species (e.g., Johnson et al., 2010; Ord et al., 2013), but with very few exceptions (e.g., Kästle, 1963; Rand, 1967; Kattan, 1984) sleep behaviour at an individual level is still understudied (Singhal et al., 2007; Frank and Flanders, 2016) – as is our understanding of how individual lizards may act in their environments (e.g., Clark and Gillingham, 1990; Shew et al., 2002; Poche et al., 2005; Singhal et al., 2007; Brown and Arrivillaga, 2008; Cabrera-Guzmán and Reynoso, 2010; Storks and Leal, 2020). Key areas of territorial and home-range behaviour include (1) access to breeding sites, (2) access to mates, (3) access to foraging area and food resources, and (4) predator avoidance (Stamps, 1983; Kattan, 1984; Jenssen et al., 1995; Lima et al., 2005). It therefore behooves an animal to sleep in a manner consistent with these requirements and, once such a place has been identified, it would be an optimal strategy to use it repeatedly until conditions change.

In this study we focus on the sleeping habits of the Costa Rican Cloud Forest Anole, *Anolis* (*Norops*) *leditzigorum*[3] (Fig. 1), by examining where and how individuals of this species sleep on plants at night. *Anolis leditzigorum* are medium-sized (maximum snout–vent length in both sexes 60 mm) diurnal lizards that are generalist and opportunistic insectivores (Fitch, 1972; Köhler et al., 2014; Leenders, 2019). *Anolis leditzigorum* foraging behaviour consists of perching head-down on stems and tree trunks and visually searching for leaf-litter prey. These lizards are suitable study subjects due to their restricted home ranges and perch fidelity (Leenders, 2019), and the unique dorsal colour pattern of individual lizards allows easy differentiation not only from the sympatric *Anolis* (*Norops*) species *A. intermedius, A. woodi*, and *A. monteverde*, but also from each other.

Materials and Methods

Observations of individual sleeping *A. leditzigorum* were made by the first author from 17 April–25 May 1987 between 19:00 h and midnight at the Monteverde Cloud Forest Biological Reserve in Monteverde, Costa Rica. Inside the reserve, the banks of the Sendero River (*El Río* Trail) and part of the *Bosque Nuboso* Trail (ca. 10.30°N, 84.79W, elevation ca. 1400 m) were initially censused for sleeping *A. leditzigorum*. All occupied sleep sites were carefully marked with flagging tape, avoiding any disturbance of lizards or the vegetation. A headlamp was used to locate sleeping lizards during walks along these trails. There appeared to be no difference in lizard occupancy between these paths, but no formal assessment was conducted as the habitat was very similar in both places. None of the encountered individuals was marked but a thorough description of each was recorded by sketching and written notes[4].

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[3] In many publications, certainly those appearing before 2014, this species would be considered as a member of *A. tropidolepis*.

[4] With a study conducted in the 1980s, before digital cameras and mobile phones facilitated this type of observation, this is how the work had to be conducted.

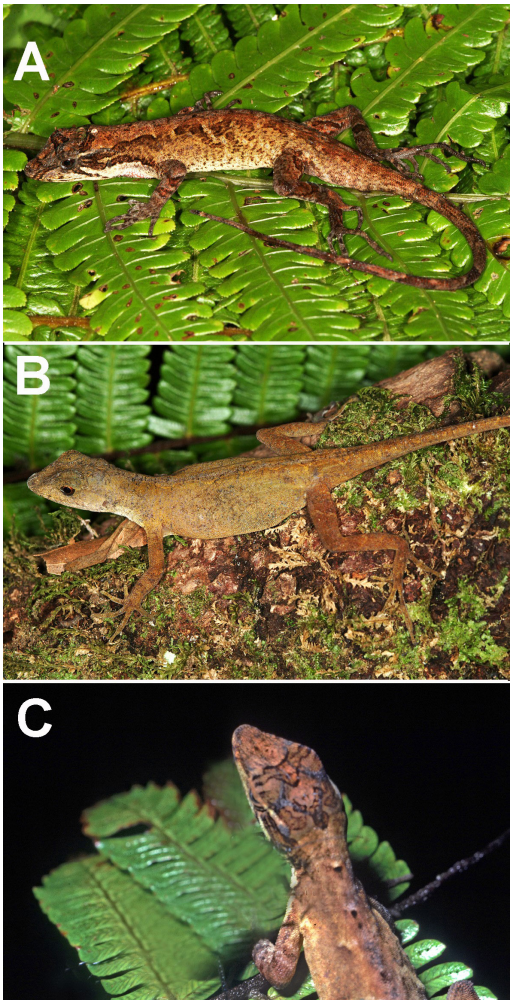

Figure 1. Three individuals of *Anolis leditzigorum* from the Monteverde area, Puntarenas Province, Costa Rica. (A) This awake male (SMF 85532) is shown in the most typical sleeping position, with its body oriented towards the stem of a fern leaf. (B) A female (SMF 85533), showing the relatively plain colouration. (C) View of the head of a male, showing some of the individual characteristics useful for identification, including the specific head pattern, presence or absence of dark lines or crossbars in the neck region, and the pattern of dark spots on head and body. Images in (A) and (B) are from Köhler et al. (2014) and are used under a CC BY-ND 4.0 license and by permission from Gunther Köhler. The image in (C) was taken by Paul Freed.

Individual size, colour, and dorsal pattern varied considerably in the observed *A. leditzigorum* population and these three unique identifiers allowed specific identification of individuals throughout the study period. Thus, in contrast to other studies (e.g., Gilson, 2010), marking individuals was deemed unnecessary and factored out any unnatural response due to handling (see also Wagner et al., 2017). Throughout the study only marked sleep-sites were checked to determine whether individuals were returning, and we did not attempt to quantify or analyse the position of a sleep site relative to the ground but focused strictly on occupancy. A complete recensus of the trails was done approximately weekly during the study period in order to allow sufficient time for lizards to disperse should they choose to do so. A final, fifth census was not conducted due to time constraints and the presence of a large feline predator.

Results

Basics.—Nocturnal temperatures were quite constant, ranging from 14–17°C (mean = 16°C). There was generally little precipitation and only very light wind during the observation time. No observable relationship between lizard activity or position and weather conditions was found.

Sleeping at home.—At a total of 36 sleep sites, 45 *A. leditzigorum* were observed. Twenty of 36 sleep sites (55%) were not revisited by their original occupants. Of the remaining 16 sleep sites, 13 had the same individual returning, but at ten of these sites a gap in occupancy occurred (i.e., a census night when a sleep site was vacant, with a lizard returning during a subsequent census). No sleep sites with returning occupants were vacant for more than one census night. At seven sleep sites, occupants changed at some time during the observation period. Thus, *A. leditzigorum* returned to their identical sleep site, even given a one-week absence, 30% of the time.

Site and position.—Aside from occupancy rates, observations also indicated some level of preference for sleeping position and the type of plant used for sleep sites. Fern leaves were used as sleep sites 71% of the time compared to non-fern leaves, and this is a proportion significantly different from random occupancy (Copas and Lee, 1997). Sleeping *A. leditzigorum* were mostly observed with their snouts facing the basal end of their sleeping leaf (73%) and only 18% of the time with their snouts facing the apical end of the leaf, indicating a non-random choice of sleeping position (sensu Salisbury and Peters, 2019). Only three individuals slept in a transverse position on the leaf, and one slept on the plant stem itself, facing the top of the plant. We consider the observations of these last four individual unusual and likely not part of the ordinary sleep position repertoire for *A. leditzigorum*.

Discussion

Our data indicate that one-third of the observed *A. leditzigorum* did indeed exhibit nocturnal sleep-site fidelity. Whereas some individuals faithfully returned to the same sleep site and were located during each census, many of the sleep sites were used only once. Also, a small number of the sleep sites were used sequentially, but by more than one individual.

Foremost among the reasons why sleep-site fidelity is not higher in *A. leditzigorum* is the basic individuality of each lizard (i.e., its reaction to the immediate ecological conditions impacting it; Lapiedra et al., 2018), which includes serendipitous parameters, such as travel distance to reliable food resources. If food is found away from the sleep site, it might be difficult for a lizard to return at night to a preferred sleep-site, even if their daily activity radius is not very large. With both food and safe sleep-site keys to lizard survival, natural selection may balance these two needs, with sleep-site fidelity having less importance given the many options of sleep-sites in the Monteverde forest. Furthermore, nocturnal predators, including bats and rodents, may become familiar with sleep-sites and pick off naïve occupants, so a lizard with a safe sleep-site may have a distinct advantage. Individual preference may ultimately be the reason why in some anole species there is essentially no sleep-site fidelity nor lizard choice for predation-safe perches (e.g., *A. aeneus*, *A. richardii* – Poche et al., 2005; *A. occultus* – Storks and Leal, 2020), and why in some observations mixed results were observed, with some individuals displaying sleep-site fidelity and others not displaying it (*A. gingivinus*; Shew et al., 2002). On the other hand, in some species sleep-site fidelity may be exceptionally high (up to 98% in *A. cristatellus* and *A. gundlachi*; Clark and Gillingham, 1990). Such extremes indicate that species-specific behaviours, presumably directed by the forces of natural selection, may overrule what would appear to be 'common sense' or individual preference.

Our results show nevertheless that there appear to be some restrictions on where roughly one-third of the observed *A. leditzigorum* slept. The fact that different individuals reappeared at formerly occupied sleep-sites, surrounded by what appears to be a large number of alternative suitable sleep-sites, suggests that there may indeed be a limited number of favoured sites. Fern leaves in particular played a large role in the sleeping habits of *A. leditzigorum*, of which a significant majority preferred sleeping on fern leaves facing the petiole. We do not know why fern leaves might be preferred or if they perhaps play a role in predator avoidance by being more irregularly shaped than regular leaves. A possible reason for sleeping in a position facing the petiole may be related to the escape process, whereby lizards may elude predators by being able to quickly run down into the lower protective layers of the plant and into the leaf litter (e.g., Cabrera-Guzmán and Reynoso, 2010). If sleeping facing the apical end of the fern, the only escape is by a jump from the plant, which carries greater risk than the more protected race into the leaf litter.

We are aware that our sample size is small and does not lend itself to broad interpretations regarding the behaviours related to sleep-site choice of *A. leditzigorum*. However, to the best of our knowledge there exists no published study focused on how individual anoles sleep, as opposed to population-level analyses, for which a number of studies exist.

In some species of anoles, such as the three sympatric species *Anolis lineatopus*, *A. grahami*, and *A. valencienni*, no signs of sleep-site fidelity were reported, and lizards occupied different niches in their respective microhabitats (Singhal et al., 2007). In contrast, *A. aquaticus* were reported to return to the same sleep-sites in the Las Cruces Biological Research Station, Puntarenas, Costa Rica (Frank and Flanders, 2016), but individual lizards and exact sleep-sites were not documented by these authors. A variety of studies exist that documenting how species of *Anolis* sleep on a variety of plants, both on leaves and branches, but in those studies (e.g., Singhal et. al., 2007; Cabrera-Guzmán and Reynoso, 2010) sleep-site fidelity was not studied or does not exist.

Additional recent studies have documented that, sleeping aside, some anoles generally show a high degree of site fidelity in terms of where they can be found over a breeding season. In *A. sagrei* both sexes dispersed less than 2.5 m on average (Calsbeek, 2009), whereas in *A. limifrons* this distance was a little greater (3–5 m; Andrews and Rand, 1983). This suggests that sleep-site fidelity probably occurs as well, but more field behaviour studies are clearly needed to determine whether individuals return to a sleeping site.

Considering the advances in how field studies can be conducted nowadays, there are possible improvements for a study like this. Recognition of individuals can be easily done by scrolling through the photo gallery on a mobile phone (Wagner et al., 2017). Even though the results we present rely on memory, sketches, and written descriptions, we are confident in the data since the observations cover only a finite number of individuals and there was always ample time to consult notes when encountering stationary, sleeping lizards. Nevertheless, a

larger sample size and a broader sampling design would be necessary to determine nocturnal sleep-site fidelity more fully, and documenting a vastly increased lizard number would certainly benefit from GPS-located lizard photographs. In addition, longer observation times, additional sites, and perhaps manipulative experiments (using large, habitat-simulation enclosures) could be useful approaches to examine sleep-site fidelity. Regardless of the approach taken in the future, our limited data show in a snapshot that some lizards really do select and utilise a "home, sweet home."

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