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Watch out where you sleep: Nocturnal sleeping behaviour of Bay Island lizards

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Sleeping strategies in Bay Island lizards
LAY SUMMARY

Animals, like lizards, are exposed to predators while sleeping at night. In order to escape predation, these animals show several behavioural adaptations. We studied such an adaptation in two Bay Island lizard species that co-occur in the Andaman Islands. There was no competition between species in choices of sleeping perches and they chose perches that provided tactile and visual cues of an approaching predator. The study provides insights into a behaviour rarely studied in reptiles and its significance.

ABSTRACT

Sleeping exposes lizards to predation. Therefore, sleeping strategies must be directed towards avoiding predation and might vary among syntopic species. We studied sleeping site characteristics of two syntopic, congeneric lizards - the Bay Island forest lizard, Coryphophylax subcristatus and the short-tailed Bay Island lizard, C. brevicaudus and evaluated inter-specific differences. We measured structural, microclimatic and potential predator avoidance at the sleeping perches of 386 C. subcristatus and 185 C. brevicaudus. Contrary to our expectation, we found similar perch use in both species. The lizards appeared to use narrow girth perch plants and accessed perches by moving both vertically and horizontally. Most lizards slept on leaves, with their heads directed towards the potential path of a predator approaching from the plant base. There was no inter-specific competition in the choices of sleeping perches. These choices indicate an anti-predator strategy involving both tactile and visual cues. This study provides insight into a rarely studied behaviour in reptiles and its adaptive significance.
INTRODUCTION

Sleep, a highly prevalent behavioural state across the animal kingdom (Siegel 2008), has been hypothesised to serve many roles, including energy conservation (Christian et al. 1984), neural restoration (Siegel 2003) and predator avoidance (Meddis 1975; Lima et al. 2005). The long periods of immobility during sleep, along with high intensity of stimulus required for arousal, can make an organism vulnerable to predation. The choice of where an individual sleeps is as important as the phases and duration of sleep (Lima et al. 2005).

Sleeping strategies have received relatively less attention than wakeful behaviours (Siegel 2003; Lima et al. 2005) and have been largely limited to laboratory experiments with mammals (Stuber 2014). Sleep is characterized by a typical sleep posture, behavioural quiescence, high intensity of stimulus required for arousal and quick reversibility to active state (Tobler 1985), and is known to occur in reptiles (Flanigan 1973, 1974). Sleeping strategies of ectotherms, such as reptiles, are studied infrequently and mostly by electro-physiological experiments (Ayala-Guirrero 1991, 2008). Observational studies have been dominated by the polychrotid genus Anolis (Goto and Osborne 1989; Clark and Gillingham 1990; Shew et al. 2002, Singhal et al. 2007; Cabrera-Guzmán and Reynoso 2010;). These studies have focused on a few perch characteristics (; Goto and Osborne 1989; Poche et al. 2005; Reaney and Whiting 2003; Sabo 2003; Singhal et al. 2007; Razafimahatratra et al. 2008; Ikeuchi et al. 2012).

From the limited studies on sleeping behaviour of lizards, it is apparent that sleeping sites can vary across species and local conditions, though a synthesis is lacking. For example, use of sleeping perches which are narrower and less stable than diurnal perches (Anolis species, Singhal et al. 2007) or higher than diurnal perches (Acanthocercus atricollis atricollis, Reaney and Whiting 2003); perches on leaf and branch tips, which may aid in tactile detection of predators
(Lygodactylus tolampyae, Ikeuchi et al. 2012) and sex-specific choice of thermal microenvironment (Sabo 2003) have been reported. Differences in sleep sites between two syntopic species (Anolis spp., Goto and Osborne 1989) or lack thereof (Anolis spp., Poche et al. 2005) are also known. The positive relationship of body size to perch height and diameter (Brookesia decaryi, Razafimahatratra et al. 2008); the association of diurnal niches and nocturnal sleeping perches (Singhal et al. 2007); variable head position and orientation with respect to ground (Poche et al. 2005; Cabrera-Guzmán and Reynoso 2010) have been found.

The influence of predation risk on sleeping strategies (e.g. the choice of sleeping perches) of animals has been inferred through theoretical models (Acerbi and Nunn 2011) field observations, (Singhal et al. 2007; Ramakrishnan and Coss 2001) and laboratory experiments (Stuber 2014). Experimental studies, on the role of predation in reptilian sleep, have also been limited (Mathews et al. 2006; Revell and Hayes 2009). Apart from its importance in enhancing fitness of an individual, the choice of sleeping perches might lead to competition between syntopic and congeneric species. The preference of species for particular types of sleep sites, such as, structurally unstable perches, high perches or warm perches has been reported. Such preferences, could lead to limitation of usable perches and competition. Such competition could impose selection pressures that in turn could result in resource partitioning (Schoener 1974). The agamid lizard genus Coryphophylax is endemic to the Andaman and Nicobar Islands and has two species, C. subcristatus and C. brevicaudus. The syntopic diurnal lizards are semi-arboreal and also occupy the forest floor. During the day, they generally perch vertically with respect to the ground, on both narrow and broad tree trunks. Males use diurnal perches to display as part of their territorial and sexual behaviour. Coryphophylax subcristatus is found throughout the Andaman and Nicobar Islands, in most forest types including human disturbed areas, while C.
brevicaudus occurs only in the Andaman archipelago and is limited to dense evergreen and semi-evergreen forests (Das 1999; Harikrishnan et al. 2012). Among diurnal lizards, Coryphophylax subcristatus is the most abundant in the Andaman archipelago, attaining a density of 650 lizards ha\(^{-1}\), followed by C. brevicaudus at 90 lizards ha\(^{-1}\) (Harikrishnan and Vasudevan 2015). Coryphophylax subcristatus is also 1.35 times larger than C. brevicaudus (Harikrishnan et al. 2012). Potential nocturnal predators of the lizards include the Andaman cat snake (Boiga andamanensis), Andaman pit viper (Trimeresurus andersonii), Bay Island wolf snake (Lycodon hypsirhinoiodes), Andaman krait (Bungarus andamanensis), and Andaman cobra (Naja sagittifera). Potential avian predators are the Andaman barn owl (Tyto (alba) deroepstorffii), Andaman scops-owl (Otus balli), Oriental scops-owl (Otus sunia), Hume’s hawk owl (Ninox (scutulata) obscura), and Andaman hawk owl (Ninox affinis) (Grimmett et al. 2011). Other potential predators include giant centipedes (Scolopendra gigantea) and rodents (Cricidura spp.).

We conducted an observational study, to understand sleeping perch characteristics of the genus Coryphophylax by considering an exhaustive set of structural, micro climatic and potential predator avoidance measures. We evaluated inter- and intra-specific variations in sleeping perches and preliminarily investigated site fidelity of Coryphophylax subcristatus. Additional natural history observations were also recorded.

METHODS

Study area and effort
We walked 53 trails in eight sites across three islands of the Andaman archipelago: South Andaman, Little Andaman and Rutland, with a total effort of 313.23 man hours (Fig.1; Table 1). We located and measured the sleeping perch characteristics of Coryphophylax subcristatus and C. brevicaudus. We sampled in the evergreen and semi-evergreen forests representative of the habitats used by the lizards (Fig.2). All the sites had minimal human disturbance, being part of either reserve forests or National Parks. Department of Forests and Wildlife, Andaman and Nicobar Islands provided permit CWLW/WL/134/350 to conduct fieldwork in the Andaman Islands. The study spanned from September 2014 to January 2015. Altitude ranged between ca. 30 - 650 m. The average night time temperature during sampling was 28.35 ± 0.09 °C with wind speed of 0.03 ± 0.018 km hr⁻¹ and percentage humidity at 87.75 ± 0.60. The three islands experienced annual rainfall ranging from 3000 to 3500 mm (Andrews and Sankaran 2002). A group of two to four personnel surveyed the forest trails at night with headlamps, searching for sleeping lizards, from the ground to the canopy. Reliable observations could only be made up to a height of 4 m. Forest trails were separated by a minimum distance of 100 m. Searches were not repeated on these trails. We carried out one or more two hour long visual encounter surveys per night, between 1800 hrs to 0200 hrs. We did not sample on nights when it rained, as it hampered detection of lizards and accurate measurement. A sleeping lizard was considered as an observational unit.

Perch characteristics and use

On locating a sleeping lizard (Fig.2), we memorized the perch location, orientation with respect to the ground and head direction of the lizard, to avoid losing data in case the lizard escaped. Then, we proceeded to capture the lizard and marked the head position on the perch. Immediately afterwards, one team member recorded microclimatic measures of the perch, i.e.
temperature (°C), percentage humidity and wind speed (km/h), using a pocket weather meter (Kestrel 3000). Simultaneously, one member noted down body size measurements of the lizard, i.e. snout to vent length (SVL), tail length and weight, using a Vernier calliper of 0.01 mm precision and a Pesola spring balance of 0.2 g precision. All lizards were placed at their original sleeping perch, on completion of the measurements. As there is considerable sexual dimorphism in adult *C. subcristatus* (Harikrishnan et al. 2012), we determined the sex of adult *C. subcristatus* based on morphological features, such as, the presence of dorsal crest in males, size of nuchal crest and colour. Due to poor differentiation in morphology of sexes in *C. brevicaudus* (Harikrishnan et al. 2012), it was not possible to identify the sexes of this species. We did not attempt sexing by evertting hemipenis, as all personnel could not carry out the task with equal efficiency. We measured structural parameters of the perch, i.e., height, leaf length and width (maximum values), maximum girth of trunk (hereafter, girth), branch circumference (at the base of the petiole when the substrate was a leaf) and distance to trunk (non-linear). We noted the orientation of the perching substrate with respect to the ground (horizontal, vertical or angular) and the head direction (inward, outward or perpendicular) of the lizards. We classified the head direction (Fig. 3) with respect to the trunk when the perching substrate was a branch (e.g., inward = head towards the trunk), with respect to the petiole when the substrate was a leaf (e.g., outward = away from the petiole/plant base; perpendicular = across the leaf axis), and with respect to the ground if the substrate was the trunk (e.g., outward = away from the ground). We measured distance to nearest plant in the escape direction of the individual. The escape direction of an individual was assumed to be between 0° to 180° in front of its head (NPM and SH personal observations). The nearest point on the adjacent plant was considered to be on the same plane as or below the lizard. We measured all distances using a measuring tape with 0.1 cm precision.
We also recorded additional variables such as presence of water bodies within a 10 m radius of the perch plant, and plant species (Appendix 1). In this study, selection of sleep sites was not investigated and therefore, availability of sleeping perches was not quantified.

**Site fidelity**

To understand fidelity of lizards towards their sleeping site, we marked ten *C. subcristatus* (of all size classes) with roman numerals using blue nail paint. We marked their sleeping sites (on the night of capture) by tying a ribbon (red, 150 mm x 10 mm) to the nearest plant on the left of the perch plant, so as not to change the visual setting. This part of the study was limited to the campus of Andaman and Nicobar Islands’ Environmental Team, South Andaman Island, which has a cover of naturally growing and planted forest. We could not mark *Coryphophylax brevicaudus* as they were unavailable at the site. We searched the area (~1 ha) for the marked lizards for 13 nights and recorded the distance between each night’s perch and the perch where we had captured them initially.

**Analyses**

We performed one-way ANOVAs on normally distributed sleeping perch characteristics (Table 2) to test for differences between the three sampled islands. Kruskal-Wallis rank sum tests were performed to compare variables (Table 2) which did not conform to normal distributions. We pooled the observations from all three islands because the differences were associated with extremely small effect sizes. We assumed that the lizards approached the perch by climbing from the base of the perch plant. Therefore, we computed total distance moved by a lizard as the sum of perch height and distance to trunk. All missing values were left as such and not substituted. As
we had fewer data points with measured microclimatic factors (n = 164), we analysed that subset of the data separately. We conducted one-way ANOVAs to test for differences between the two species and among the sexes of *C. subcristatus*, in terms of structural and microclimatic measures of the perch. Non-normally distributed variables were compared across these groups by employing Kruskal-Wallis rank sum tests. We constructed multiple regression models to test the relationship between body size and distance, while accounting for the girth of perch plants. We controlled for the effect of body size while evaluating the relationship between sexes of *C. subcristatus* and perch characteristics. The statistical comparisons were carried out at a significance level (α) of 0.05.

As the sample size for this study was large (n = 501), we relied on effect sizes to infer patterns of biological significance, rather than merely on the basis of *p* values. For one-way ANOVAs we report effect size - $\eta^2$ (Zar 1999) in percentage.

$$\eta^2 = \frac{\text{Between group SS}}{\text{Total SS}} \times 100$$

Where, SS is sum of squared deviance.

We computed leaf area considering a leaf to be an ellipse. Thus, leaf area = $\pi \times (\text{length } \times 0.5) \times (\text{width } \times 0.5)$

Snout-vent-length was considered as a measure of body size. We calculated effort of a lizard to reach its perch from the base of the plant as, total number of body displacements = total distance moved / SVL.

We report all values in SI units, after converting the raw measurements. We carried out all analyses using the statistical software R (R Core Team 2013).
RESULTS

We encountered 386 sleeping individuals of *C. subcristatus* and 115 of *C. brevicaudus*, during our surveys spanning South Andaman, Little Andaman and Rutland islands (Table 1). The encounter rate of sleeping *C. subcristatus* was $3.60 \pm 0.41 \text{ hr}^{-1}$ in South Andaman, $2.85 \pm 0.42 \text{ hr}^{-1}$ in Rutland and $7.71 \pm 1.16 \text{ hr}^{-1}$ in Little Andaman. Corresponding encounter rates of *C. brevicaudus* in the three islands were $0.98 \pm 0.22 \text{ hr}^{-1}$, $0.81 \pm 0.27 \text{ hr}^{-1}$ and $1.73 \pm 0.94 \text{ hr}^{-1}$ respectively.

Perch characteristics and use

We observed lizards of both species sleeping on different substrates, including leaf, branch, trunk, climber, fallen branch and leaf-branch (body supported by both leaf and branch). We observed both species of lizards on narrow girth (54.8 ± 2.1 mm) perch plants with associated structural, microclimatic and potential predator avoidance measures (Table 2). Most lizards of both the species slept horizontally on leaves, with their head directed ‘inwards’ towards the potential path of an approaching predator (Table 3). A majority of *C. subcristatus* (64.24%) slept on leaves, while 87.82 % of *C. brevicaudus* did so.

Inter-specific and intra-specific variations

We found significant differences in perch characteristics between the two species but effect sizes in all the comparisons were small (Table 2). The two species showed distinct patterns in the way they accessed perches (Fig.4). While both species moved similar distances vertically, *C. subcristatus* accessed perches away from the trunk (Fig.4). In contrast, *C. brevicaudus* used perches close to the trunk (Fig.4).
We found that vertical distance contributed relatively more to the total distance moved than horizontal distance (Fig. 4). After controlling for girth of perch plants, body size positively influenced vertical distance ($R^2 = 0.30$, $\beta = 11.76$, SE = 1.53, $p < 0.001$; Fig. 5) but not horizontal distance ($R^2 = 0.36$, $\beta = 2.08$, SE = 1.53, $p = 0.175$; Fig. 5). We found no difference in effort to reach sleeping perch (i.e. total number of body displacements) between species ($F = 0.254$, df = 476, 1, $p = 0.615$, $\eta^2 = 0.05$). Increasing body size was not associated with increasing effort in *C. brevicaudus* ($R^2 = 0.01$, $\beta = -2.13$, SE = 1.65, $p = 0.19$) and had a statistically significant but small effect size in case of *C. subcristatus* ($R^2 = 0.02$, $r = -0.14$, $\beta = -2.1$, SE = 0.73, $p = 0.004$).

We found no difference between males and females of *C. subcristatus* with respect to girth of perch plant ($F = 0.60$, df = 166, 1, $p = 0.438$, $\eta^2 = 0.003$). After controlling for body size, sex of the lizard did not influence perch height ($R^2 = 0.002$, $\beta = -0.38$, SE = 9.34, $p = 0.966$) and perch distance from trunk ($R^2 < 0.001$, $\beta = -0.73$, SE = 11.05, $p = 0.947$).

**Site fidelity**

We redetected eight out of the ten marked individuals of *C. subcristatus*. The eight individuals were redetected on $3.7 \pm 1.02$ (1 to 11) occasions, during 13 nights of observation. We found one adult male (11 nights) and one juvenile (6 nights), sleeping regularly on a specific perch. On average, individuals were found sleeping within a distance of $1.75 \pm 0.41$ m from their original perch.

**Natural history observations**

Most of the lizards of both species were observed sleeping with their eyes open, though this could be an artefact of disturbance by flashlights and motion of personnel. Upon disturbance, the lizards escaped by dropping to the ground and running. When we released the lizards back on
their perches, many remained limp and immobile for a few minutes before escaping. We have witnessed the Green bronzeback tree snake (*Dendrelaphis andamanensis*) and Andaman pit viper (*Trimeresurus andersonii*) predating on *Coryphophylax* during the day. We have observed an attempted nocturnal predation, by the Andaman pit viper where the snake was first seen climbing a tall sapling along the main stem. At about 2 m above ground, it started climbing on to a horizontal branch, from which a *Coryphophylax subcristatus* was seen jumping to the ground. We also observed two individuals sleeping on one plant, on four occasions (one and three records of *C. brevicaudus* and *C. subcristatus* respectively). On one such occasion, two *C. subcristatus* (an adult female and a sub-adult) were found sleeping on the same leaf. On another occasion two adult female *C. subcristatus* were observed on top of each other. The lighter individual (SVL = 49 mm and weight = 3 g) was found sleeping on top of the other (SVL = 59 mm, weight = 5 g). We have recorded several instances of juvenile bent-toed gecko, *Cyrtodactylus rubidus*, a nocturnal lizard, sleeping on saplings and one case of the diurnal Andaman skink, *Eutropis andamanensis*, sleeping on a *Pandanus sp.*

**DISCUSSION**

*Perch characteristics and use*

This study investigates structural, micro-climatic and potential predator avoidance characteristics of sleeping perches in the most abundant genus of lizards in the Andaman archipelago - *Coryphophylax* (Harikrishnan and Vasudevan 2015). Both species of the genus sleep on narrow girth plants. When compared to their vertical diurnal perches that are mainly on tree trunks, their nocturnal behaviour reveals a tendency to use structurally unstable perches. The narrow girth of perch plants, coupled with extremely thin perch circumference characterize these
‘flimsy’ perches (similar to Shew et al. 2002; Singhal et al. 2007; Ikeuchi et al. 2012). The study sites had a tree (> 100 mm in GBH) density of ca. 950 ha⁻¹ (Mohanty et al. 2016) which would provide many more perches than smaller plants of narrow girth. The almost exclusive use of narrow girth plants (< 100 mm in GBH) by the lizards appears to be more than their availability at the study sites. Though, we did not quantify the availability of sleeping perches, the observed pattern suggests selection. This choice of narrow girth plants may discourage heavy predators from climbing the plant.

Most lizards (79%) move vertically and then horizontally away from the base of the plant, attaining a certain distance in each dimension between them and potential predators approaching from the same plant. The benefit of such movement is two-fold: (i) increase in the search time for predators; (ii) increase access to narrow girth perches (Goto and Osborne 1989). Overall, this sleeping strategy could be explained as a tendency of the lizards to enhance tactile detection and increase search time of predators approaching from the same plant (see Singhal et al. 2007). The striking similarity documented in the sleeping strategies of anoline lizards and Coryphophylax suggests a possible convergence in such adaptation. Greater observed use of leaves than other substrates as sleeping perches (Table 3) could be due to the larger availability of surface area for traction. Alternatively, it could also be due to pliability of leaves resulting in better tactile detection by the lizards perching on them.

All three microclimatic measures (temperature, humidity and wind speed) showed limited variation during the sampling period. While the effect of wind on sleeping perches inside dense evergreen and semi-evergreen forests may be negligible, changes in temperature and humidity during drier months might influence choice of sleep sites.
A significant role of visual cues probably explains the majority of individuals of both species sleeping with their head directed ‘inwards’- towards the direction of approach of potential predators (Clark and Gillingham 1990; Cabrera-Guzmán and Reynoso 2010). The importance of visual cues in avoiding predators in the lizards is reinforced from our observations of most lizards found sleeping with their eyes open. Though we do not have quantified data on the nature of eye closure (both or single eye), such behaviour resulting from uni-hemispherical sleep has been reported in reptiles (Matthews et al. 2006; Revell and Hayes 2009). If such an adaptation occurs, it would allow the lizards to reduce their sleep debt while remaining vigilant (Lima et al. 2005). The distance to nearest plant in the direction of escape was considerably low, as the understory used by the lizards was fairly dense.

**Inter-specific and intra-specific variations**

Contrary to our expectation, we did not find stark differences between species in structural, micro-climatic and predator avoidance measures. However, the two species accessed horizontally located perches differentially (Fig.4). The apparent lack of nocturnal resource partitioning is similar to that observed by Poche et al. (2005) but unlike observations of Singhal et al. (2007) and Goto and Osborne (1989). This suggests that the two species probably partition their niches along other resources, such as, diet and diurnal perches. Specialized use of perches by the two species and both sexes points at an effective sleeping strategy under local conditions.

While there are no biologically meaningful inter-specific differences in perch characteristics, a clear pattern of intra-specific variation emerges. Larger individuals cover greater distances from the base of the plant compared to smaller ones and tend to move more vertically (similar to Clark and Gilingham 1990; Razafimahatratra et al. 2008; Fig. 5), while
there is no difference in horizontal movements. This could be due to the higher energy cost involved in covering greater distances, thereby, forcing small individuals to make fewer vertical displacements than large ones. But, considered along with the fact that horizontal movement is not different across body sizes, the relationship of body size with vertical distance could be due to a better climbing ability of large individuals. A lack of difference in perch use between the sexes of *C. subcristatus*, after accounting for body size, discounts any inter-sexual competition leading to contrasting nocturnal perch characteristics.

Site fidelity

We find evidence of a certain degree of fidelity to sleeping perch in the case of *Coryphophylax subcristatus* (similar to Kennedy 1959; Clark and Gilingham 1990; Reaney and Whiting 2003; Singhal et al. 2007). It is probable that they use multiple locations within a certain range, to which they return every night. Fidelity to sleeping sites has been explained as choosing of limited high quality perches (Clark and Gilingham 1990), which maybe ‘safe’.

Natural history observations

We note a difference in escape strategies during the day and night in both species. Upon disturbance during the day *Coryphophylax spp.* tend to run up tree trunks (SH and NPM personal observations), while at night they usually drop to the ground and escape. This mode of escape is best explained as an avoidance of serpentine predators approaching from the same plant. The option of climbing a great distance up is also curtailed by the narrow -girth perch plants which might be short. Our single observation of an attempted predation on *Coryphophylax* and its escape fits our inference of predator avoidance while sleeping. Our limited observations of
females and sub-adults sleeping on the same plant are probably explained by increased combined vigilance (Dehn 1990) or kinship, but not by social monogamy (Bull 2000; Harrison 2013).

CONCLUSION

Both species of the genus Coryphophylax use structurally and micro-climatically similar sleeping perches. In general, the lizards use perches which are unstable in structure. We infer a role of both tactile and visual cues in detecting and subsequently avoiding nocturnal predators. We did not find evidence of segregation of sleeping perches between the two syntopic and congeneric species and propose investigations on competition for diurnal perch use and food acquisition. While inter-specific and inter-sexual differences are absent, a positive relationship between body size and perch height is apparent. We also found evidence for site fidelity in Coryphophylax subcristatus, which may reflect limited number of ‘safe’ perches in the area. Our study provides new insights into a rarely studied behaviour in lizards, the adaptive significance of sleeping behaviour in predator avoidance and resource partitioning in syntopic and congeneric species. Based on reported negative impacts on lizard population by spotted deer (Axis axis), an invasive mammalian herbivore in the Andaman Islands (Mohanty et al. 2016), our findings lend support to the importance of understory vegetation structure for long-term survival of these endemic lizards in the Islands.

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367  Mohan for providing illustrations for this manuscript.
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FIGURE LEGENDS

Fig. 1  Study area map showing eight sites in three islands - South Andaman, Little Andaman and Rutland, sampled in the Andaman archipelago, from September 2014 to January 2015.

Fig. 2  A sleeping Coryphophylax brevicaudus and its typical habitat in the evergreen forest.

Fig. 3  Depiction of head direction of lizards in their sleeping perches, categorized as ‘inward’, ‘outward’ or ‘perpendicular’ with respect to (a) the petiole, in case of leaf as perch substrate, (b) the trunk, in case of branch as perch substrate and (c) the base of the plant, in case of trunk as perch substrate.

Fig. 4  Relative contribution of horizontal distance (perch distance from trunk) and vertical distance (perch height) to the total distance moved, from the base of the plant to the perch, in (a) Coryphophylax subcristatus (n = 372) and (b) C. brevicaudus (n = 114).

Fig. 5  Relationship between body size (snout to vent length - SVL) of individuals belonging to Coryphophylax subcristatus (A-B) and C. brevicaudus (C-D), with vertical distance and horizontal distance.
Table 1 (on next page)

Table 1

Site-wise sampling effort and number of individuals of *Coryphophylax subcristatus* and *C. brevicaudus* observed, across three islands of the Andaman archipelago – South Andaman, Little Andaman and Rutland.
**Table 1** Site-wise sampling effort and number of individuals of *Coryphophylax subcristatus* and *C. brevicaudus* observed, across three islands of the Andaman archipelago – South Andaman, Little Andaman and Rutland.

<table>
<thead>
<tr>
<th>Site</th>
<th>Island</th>
<th>Man hours</th>
<th>Trails</th>
<th><em>C. subcristatus</em></th>
<th><em>C. brevicaudus</em></th>
<th>No. of observations</th>
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<td>151.5</td>
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<td>142</td>
<td>33</td>
<td>175</td>
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<tr>
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<tr>
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<tr>
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<td>21</td>
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<td>22 km</td>
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</tr>
<tr>
<td>Krishnanalla</td>
<td>Little Andaman</td>
<td>20.25</td>
<td>2</td>
<td>24</td>
<td>36</td>
<td>60</td>
</tr>
<tr>
<td>South Bay</td>
<td>Little Andaman</td>
<td>7.33</td>
<td>2</td>
<td>50</td>
<td>3</td>
<td>53</td>
</tr>
<tr>
<td>Komyo</td>
<td>Rutland</td>
<td>62.78</td>
<td>12</td>
<td>49</td>
<td>26</td>
<td>75</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td><strong>313.23</strong></td>
<td><strong>53</strong></td>
<td><strong>386</strong></td>
<td><strong>115</strong></td>
<td><strong>501</strong></td>
</tr>
</tbody>
</table>
Table 2

Table 2

Descriptive statistics and inter-specific differences in perch characteristics of *Coryphophylax subcristatus* and *C. brevicaudus*. Asterisks denote median values; CI – 95% confidence interval; df – degrees of freedom; *F* – Fisher’s F statistic; *p* – probability value; $\eta^2$ – effect size in percentage.
Table 2 Descriptive statistics and inter-specific differences in perch characteristics of *Coryphophylax subcristatus* and *C. brevicaudus*. Asterisks denote median values; CI – 95% confidence interval; df – degrees of freedom; *F* – Fisher’s F statistic; *p* – probability value; *η*² – effect size in percentage.

<table>
<thead>
<tr>
<th>Characteristics</th>
<th><em>C. subcristatus</em></th>
<th>C. brevicaudus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Girth</td>
<td>5.9 ±0.51</td>
<td>4.15 ±0.5</td>
</tr>
<tr>
<td>Branch circumference</td>
<td>1.2* ±0.14</td>
<td>1.26 ±0.12</td>
</tr>
<tr>
<td>Perch height</td>
<td>110.04 ±5.04</td>
<td>89.3 ±8.27</td>
</tr>
<tr>
<td>Distance to trunk</td>
<td>51.47 ±5.52</td>
<td>35.86 ±7.79</td>
</tr>
<tr>
<td>Leaf area</td>
<td>124.78 ±14.56</td>
<td>74.63 ±8.62</td>
</tr>
<tr>
<td>Temperature</td>
<td>28.6 ±0.22</td>
<td>27.73 ±0.34</td>
</tr>
<tr>
<td>Wind speed</td>
<td>0* ±0.05</td>
<td>0</td>
</tr>
<tr>
<td>% Humidity</td>
<td>88.55* ±1.57</td>
<td>88.01 ±1.25</td>
</tr>
<tr>
<td>Distance to nearest plant</td>
<td>43.78 ±2.69</td>
<td>39.14 ±4.49</td>
</tr>
</tbody>
</table>
Table 3

Percentage of lizards observed sleeping on different substrates with varied orientation with respect to the ground and head direction. ‘L-B’ refers to both leaf and branch; ‘Other’ includes vines, climbers and adventitious roots. The sample sizes (n) refer to observations of ‘orientation’ followed by ‘head direction’.

Table 3 (on next page)
Table 3. Percentage of lizards observed sleeping on different substrates with varied orientation with respect to the ground and head direction. ‘L-B’ refers to both leaf and branch; ‘Other’ includes vines, climbers and adventitious roots. The sample sizes (n) refer to observations of ‘orientation’ followed by ‘head direction’.

<table>
<thead>
<tr>
<th>Orientation</th>
<th>C. subcristatus n = 384, 368</th>
<th>C. brevicaudus n = 112, 111</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Leaf</td>
<td>Branch</td>
</tr>
<tr>
<td>Horizontal</td>
<td>50.78</td>
<td>9.63</td>
</tr>
<tr>
<td>Angular</td>
<td>11.71</td>
<td>7.55</td>
</tr>
<tr>
<td>Vertical</td>
<td>2.08</td>
<td>2.08</td>
</tr>
</tbody>
</table>

**Head direction**

<table>
<thead>
<tr>
<th></th>
<th>C. subcristatus n = 384, 368</th>
<th>C. brevicaudus n = 112, 111</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Inward</td>
<td>Outward</td>
</tr>
<tr>
<td></td>
<td>Leaf</td>
<td>Branch</td>
</tr>
<tr>
<td>Inward</td>
<td>57.88</td>
<td>8.69</td>
</tr>
<tr>
<td>Outward</td>
<td>4.89</td>
<td>10.05</td>
</tr>
<tr>
<td>Perpendicular</td>
<td>4.07</td>
<td>0</td>
</tr>
</tbody>
</table>
**Figure 1** (on next page)

Fig. 1 Study area map showing eight sites in three islands - South Andaman, Little Andaman and Rutland, sampled in the Andaman archipelago, from September 2014 to January 2015.
A sleeping *Coryphophylax brevicaudus* and its typical habitat in the evergreen forest.
Figure 3 (on next page)

Depiction of head direction of lizards in their sleeping perches

Depiction of head direction of lizards in their sleeping perches, categorized as ‘inward’, ‘outward’ or ‘perpendicular’ with respect to (a) the petiole, in case of leaf as perch substrate, (b) the trunk, in case of branch as perch substrate and (c) the base of the plant, in case of trunk as perch substrate.
Relative contribution of horizontal distance (perch distance from trunk) and vertical distance (perch height) to the total distance moved, from the base of the plant to the perch, in (a) *Coryphophylax subcristatus* (n = 372) and (b) *C. brevicaudus* (n = 114).
Figure 5 (on next page)

Relationship between body size with vertical distance and horizontal distance

Relationship between body size (snout to vent length - SVL) of individuals belonging to Coryphophylax subcristatus (A-B) and C. brevicaudus (C-D), with vertical distance and horizontal distance.