Ecological notes on the Cát Bà gecko *Goniurosaurus catbaensis*, a species endemic to the limestone karst islands of northern Vietnam

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ABSTRACT - The Cát Bà gecko *Goniurosaurus catbaensis* is endemic to Cát Bà and Ha Long islands of Vietnam. The ecology of this species is still scarcely studied but previous reports have suggested that the species is Endangered due to small population size and low ecological plasticity. We studied aspects of the ecology of this species between May 2019 and June 2020, along seven transects on Cát Bà island. At least 173 different individuals (possibly as many as 189) were recorded, with an equal sexratio and apparently no intersexual differences in adult body size. The species was clearly more widely distributed than previously supposed. We were able to confirm that *G. catbaensis* is a limestone karst microhabitat specialist, as the farthest sighting from a karst area was only 10 m. Geckos were observed at a mean height of 45 cm but up to 500 cm above ground, with males perching significantly higher than females. We observed these geckos at altitudes ranging from 11 to 228 m a.s.l.; much higher than previously recorded. Overall, our study revealed that this endemic gecko is certainly less threatened than previously feared.

INTRODUCTION

The genus *Goniurosaurus* (Eublepharidae) has a restricted range in Asia and consists of about 24 species that are characterised by predominantly nocturnal and terrestrial habits (Chen et al., 2014; Grismer et al., 1994; Honda & Ota, 2017; Ngo et al., 2016, 2019; Nguyen, 2011; Orlov et al., 2008; Vu et al., 2006; Wang et al., 2010; Zhou et al., 2018; Ziegler et al., 2008; Zhu et al., 2018, 2020; Qi et al., 2020; Uetz et al., 2020). Among them, five species of this genus occur in Vietnam (Nguyen, 2011), including the Cát Bà gecko *Goniurosaurus catbaensis* Ziegler, Truong, Schmitz, Stenke, Rösler, 2008.

The Cát Bà gecko is currently only known from two islands in northern Vietnam, Cát Bà, where it was discovered in 2008 (Ziegler et al., 2008), and Ha Long island. Since discovery there have been a few field surveys to define the ecology and conservation status of this species (Nguyen et al., 2016; Ngo et al., 2019a, 2019b) but little is known about its ecology. Due to a colourful appearance (Fig. 1), this gecko is threatened by pet trade exploitation, but also by habitat fragmentation due to agricultural development and the expansion of tourism (Ngo et al., 2019b), and it shown as Endangered (EN) in the IUCN Red List (2020). In order to guide future conservation/ management action we have undertaken further field research to examine aspects of population ecology and habitat use.

MATERIALS & METHODS

Our survey was undertaken on Cát Bà Island (20° 47'19.46" N, 106° 59'14.56" E), one of 366 islands in the Cát Bà Archipelago, Ha Long Bay, north-eastern Vietnam. The island covers an area of 140 km² and roughly half of this is protected by the Cát Bà National Park where the survey was undertaken. The island has a limestone karst landscape which has allowed the creation of caves that are the preferred shelters of the Cát Bà gecko.

Our surveys were undertaken from 19:10 h to 23:40 h (Hanoi standard time), as previous reports indicated that the Cát Bà gecko is a nocturnal species (Ngo et al., 2019a). We searched for lizards along seven line transects that were designed using i) topographic and vegetation maps with 1/25,000 scale, ii) previous reports on the local distribution of the study species (Ngo et al., 2019a, 2019b), and iii) interviews with local people. We also used existing or newly created trails passing through different habitat types to facilitate transect surveys. In particular, we designed transects that passed through areas with caves and cliffs and valleys between limestone cliffs in the forest, where the probability of encountering Cát Bà geckos was thought to be high. The length of line transects ranged from 2.5 to 6.5 km depending on the topography. For each transect, we marked the starting point, the end point and the traveling distance by hand-held GPS. The locations of the seven line transects used in this

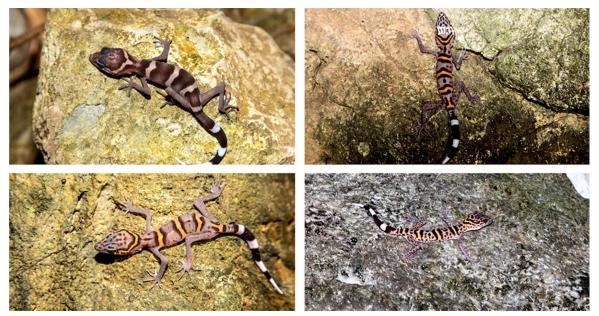


Figure 1. Some individual Cát Bà geckos observed during the study, note the upper left photograph is of a juvenile and lacks the dorsal yellow bars

study were: 1) Cát Bà National Park Center - Cát Bà Ngu Lam Peak, 2) Eo Bua ranger station - Ang Co, 3) Trung Trang cave - Uy Ban – Hospital cave, 4) Cát Bà - Ang Cu Ru, 5) Viet Hai village - Tien Duc cave - Ang Kho, 6) Gio Cung ranger station - Ang Ca Vuoc, and 7) Gio Cung ranger station - Ang Can. Five of these transects (#1, 2, 4, 6 & 7) had not previously been surveyed for geckos.

There were a total of 39 surveys in the period June 2019 to May 2020, although surveys were suspended in March 2020 due to Covid-19 lockdown. Survey effort varied by transect. Transects # 1, 2, and 3 were surveyed monthly, apart from March 2020. Transects #4, 6, and 7 only once (in April 2020), and transect # 5 once in November 2019 and twice in December 2019. Each survey had 3 - 4 surveyors (in most cases three).

We captured geckos by hand. Each captured gecko was measured in the field with electronic digital calipers (\pm 0.01mm) for snout-vent length (SVL), tail length (TL), head length from tip of snout to the posterior edge of ear (HL), and head width (HW) and weighed using an electronic balance (\pm 0.01g). The gender of each individual was determined based on external morphology: the adult males usually had a larger bulging tail base than females and had the anterior part of the vent more pronounced while females typically carried eggs (Ziegler et al., 2008). In order to tell the life stages apart, we considered as adults those individuals with SVL \geq 105 mm, subadults those with 85 < SVL < 104.9 mm, and juveniles those with SVL \leq 85 mm (Ziegler et al., 2008).

For each observed gecko, we recorded the temperature and humidity of where it was sighted with an electronic thermo-hygrometer (Extech 445702). We also noted: i) altitude of each record (m a.s.l.); ii) one of five habitat types (see below); iii) type of substrate used by the lizard (three categories: cliffs and rocks, branches, soil); iv) height of the animal from the ground (cm); v) location of the lizard when associated with a cave (either inside or outside). Each gecko record was assigned to one of the following five habitat types: (i) Secondary forest on limestone hills (LHF): this is evergreen forest that was destroyed many years ago but is now being restored. The vegetation consisted of multi-tier canopy with pioneer trees, vines and large trees with DBH (diameter at breast height) >> 50 cm. This type of vegetation growing on ultramafic soil is different from the original evergreen forest. Indeed, in the past much of the forest area has been destroyed for charcoal and logging, including legal logging for timber by the Vietnamese government. The main vegetation includes *Burretiodendron hsienmu, Anogeissus acuminata, Streblus ilicifolius* and *Nageia fleuryi*.

(ii) Medium secondary forest on limestone hills (MHF) is similar to LHF, but with tree vegetation less well restored. The mean DBH was about 50 cm.

(iii) Poor secondary forest on limestone hills (PHF): has much less soil cover than LHF and very poor floral diversity. The canopy is more open than in LHF and trees are smaller (DBH << 50 cm).

(iv) Bamboo forests (BAF) consists of a monoculture of bamboos without any trees.

(v) Scrub grassland (SCR) is an open-bushy herbaceous area, with small regenerating trees (DBH < 6 cm).

(vi) Caves are widely distributed across the study area due to the limestone characteristics of the island.

We marked each individual on the head with semipermanent paint using a code that records the line transect and the number of the individual, e.g. III.2 indicates Line transect # 3, 2nd individual encountered (Fig. 2). In addition, at the location where each gecko was captured, we marked nearby rock by painting the same symbol as that used for marking the head. Each captured gecko and capture location was photographed for easy re-identification in subsequent surveys. In some cases, we were unable to capture the geckos as they moved too quickly. In those cases, we recorded the GPS coordinates, altitude, air temperature, humidity, habitat type, and height of the animal's position relative to the ground.



Figure 2. A marked Cát Bà gecko on a rock showing the same symbol painted on its head and on the rock

Sex-ratio departure from equality and the frequency of gecko observations between different habitats were assessed by observed-versus-expected χ^2 tests. Intersexual differences in the means of morphometric traits (SVL and weight) were analyzed by Student t-test. For intersexual morphological comparisons, since all morphometric measurements were autocorrelated (P < 0.05), we used only SVL and weight as proxies of body size of each individual. Intersexual comparisons for associated mean humidity (%), mean ambient temperature, and mean height above ground were made by Mann-Whitney U-test, since the respective variables were not normally distributed (Shapiro Wilk test, p < 0.001). In the text, we presented means \pm standard deviation and set the threshold for statistical significance at $p \le 5$ %.

RESULTS

During the field investigation, we recorded 24 species of reptiles, belonging to 9 families (see Supplementary materials, Table S1). We recorded *G. catbaensis* individuals at all the seven surveyed transects (Fig. 2) and at four sites more than 20 individuals were observed (Fig. 2). It should be noted that Figure 2 shows eight location records even though there were only seven transects. This is because in transect #3 we recorded geckos at two distinct and relatively distant points, Trung Trang Cave and at Hospital Cave.

A minimum of 173 individuals were recorded, but for an additional 16 individuals we were unsure whether they were recaptures because their identification marks were illegible. Thus, it is possible that we may have recorded 189 different individuals. Of the different individuals (n = 173), 105 were adults, 38 sub-adults and 46 hatchlings; 69 were males, 90 females. A further 29 could not be sexed as either they were juveniles and/or because they could not be captured.

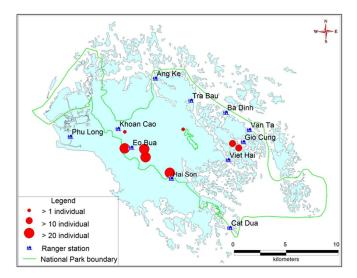


Figure 3. The magnitude of Cát Bà gecko counts at each of 7 transects – note that one of the transects (#3) is represented by two relatively distant records (see text for details)

Table 1. Summary morphometrics for adult male and female Cát Bàgeckos, SVL = snout-vent-length

	Mean ±sd and (range)			
Gender	n	SVL (mm)	n	Weight (g)
Female	79	107.8±7.2 (80.7-119.6)	71	19.9±4.1 (6.7-25.8)
Male	56	109.1±5.4 (90.6-121.8)	46	20.3±3.0 (12.7-27.8)

Body measurements were taken from 90 females, 69 males and 15 juveniles of unknown sex (a full listing is given in Supplementary Material, Table S2). A summary of the SVLs and weights of adult male and female geckos is given in Table 1. The females and males were similar with respect to both SVL (t = 1.1, df = 132, p = 0.279) and weight (t = 0.55, df = 114, p = 0.581). Adult sex-ratio appeared to be skewed to female but was not statistically significant (χ^2 = 3.02, df = 1, p = 0.082). Unfortunately, the number of recaptures was too low to calculate a population size for the study area.

Although G. catbaensis individuals were observed in different types of habitats, there was an uneven frequency of sightings across habitats ($\chi^2 = 205.4$, df = 6, p < 0.0001): the majority of observations were in PHF (47.1% of sightings, total n = 189), followed by BAF (19 %) and caves (15.9 %). LHF contributed to 10.1 % of the sightings, MHF with 6.9 % and SCR with just 1 %. In most cases, however, geckos were observed at less than 10 m away from a nearby karst rock, even if in different microhabitats. Geckos were observed up to a height of 5 m above the ground but were rarely seen at these heights and only in cave entrance areas. Instead they were on average 45 ± 77 cm (median = 15 cm) from the ground and 36.5 % of all the sightings (n = 189) were at ground level. On average males perched at an average of 51.3 ± 67.4 cm above ground while females perched on average of only 28.9 ± 73.5 cm, this difference was statistically significant (Mann-Whitney U-test: z = 4.07, U = 1989, p < 0.0001). These geckos were observed at an altitudinal range from 11 - 228 m a.s.l., with 76 individuals (46 %) being observed at 11 - 100 m, 86 (40 %) at 101-200 m, and 27 (14 %) at more than 200 m a.s.l..

In terms of microclimatic conditions, we recorded geckos at 20.6 - 30.5°C and at 67 - 90 % relative humidity. The mean activity temperature was not different between sexes (females: 27.1 ± 1.9°C, n = 91; males: 27 ± 1.9°C, n = 69; Mann-Whitney U-test: z = 0.326, U = 3044.5, p = 0.745), and the same was true as for the relative humidity (females: 82.9 ± 4.2 %, n = 91; males: 81.9 ± 4.7 %, n = 69; Mann-Whitney U-test: z = 1.42, U = 3884.5, p = 0.155). Outside of these ranges of temperature and humidity, geckos were observed very rarely, particularly in the dry season from December to February (note that in March there were no field surveys) when the weather was dry and cold. Our observation rate of Cát Bà geckos from April to November was relatively stable but fell dramatically in December before beginning to rise again from February and was apparently restored by May (Fig. 4).

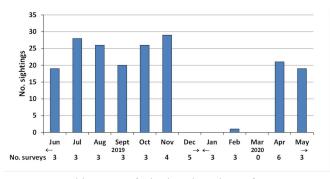


Figure 4. Monthly counts of Cát Bà gecko sightings from 7 transects on Cát Bà island – note there were no surveys in March 2020 due to COVID-19 lockdown and the transects surveyed varied by month (see text for details)

DISCUSSION

Previous studies have concluded that there are only small populations of *G. catbaensis*, that there are very few sites where the species is present, and that they occur in a narrow altitudinal range. Indeed, using capture-mark-recapture protocols in 2014-2015, population size of *G. catbaensis* in the whole of Cát Bà island was estimated to be around 16-24 adults (Ngo et al., 2016), and on Ha Long island (Quang Ninh province) in July 2017 and April 2018 to be about 124 - 129 individuals, with the abundance of sub-populations that had been impacted by anthropogenic pressures consisting of just 2 - 10 individuals (Ngo et al., 2019b).

Concerning the local distribution, Ziegler et al. (2008) recorded *G. catbaensis* in only three small areas (Ong Bi near Tra Bau ranger station, Trung Trang cave and Ang Dai area), and Ngo et al. (2016) recorded it in Viet Hai commune, Kim Giao area, May Bau area and Trung Trang cave area and Hospital cave. In addition, both Ziegler et al. (2008) and Nguyen (2011) indicated that this species is found only between 10-70 m a.s.l.. Our study adds considerably to previous data as it shows that the Cát Bà gecko is much more widely distributed on Cát Bà island, with clearly greater population sizes than previously estimated (Ngo et al., 2019b). Moreover, our research shows that this species has a large altitudinal range from 11 - 228 m a.s.l., and that, at an altitude of over 200

m, we were still able to capture 27 different individuals. Thus, we provide clear evidence that *G. catbaensis* is not as rare/threatened as previously supposed. We speculate that the inconsistencies among studies were mainly related to different field efforts: for instance, Ngo et al. (2016) recorded only 48 individuals in Cát Bà National Park but their study was only conducted for three months: June and August 2014 and May 2015. Ngo et al. (2016) first warned that there may be a serious conservation problem for the Cát Bà gecko, and therefore we decided to investigate the issue further. Based on the results obtained in the present study, we suggest that further studies on this, or other endemic geckos with narrow distribution, should be carried out over longer timespans in order to avoid underestimations of their abundance and distribution within a given study area.

Although the Cát Bà gecko is more widespread and abundant than previously estimated, our results confirmed earlier studies suggesting that G. catbaensis is a karst microhabitat specialist, as the greatest distance a sighting was made from a karst area was only about 10 m. However, these geckos may inhabit a suite of different habitats in proximity to limestone, thus our study widens the knowledge available on the habitat requirements of this species. For instance, G. catbaensis was previously reported to inhabit only the surroundings of large caves covered in part by primary forest vegetation and in the vicinity of primary shrub vegetation on limestone (Ngo et al., 2019a), whereas we found it in a much wider range of habitats. We also found that G. catbaensis can be found on relatively high perches (one individual was 5 m above ground), thus suggesting that further studies should better explore the vertical niche characteristics of this species. Furthermore, we demonstrated that males perched at significantly greater heights than females; this is similar to certain other species of lizards, for instance the African species Agama agama (Anibaldi et al., 1998; Amadi et al., 2021). In A. agama the intersexual differences in perching height is related to hierarchic/territorial behaviours, with dominant males patrolling females from above. We speculate that the same behaviour may occur also in G. catbaensis but since agamids are diurnal (but see Amadi et al., 2021) they may see much better from an elevated perch than geckos would see at night.

In terms of body size and sexual size dimorphism, our study showed that there were no significant differences between males and females. This finding is consistent with data of Ngo et al. (in press) (mean SVL \pm SE - adult males 112.3 \pm 0.8 mm, n=80; adult female 111.8 \pm 0.8 mm, n=93).

The absence of sightings from December to February showed that the above-ground activity of these geckos was affected by low temperatures (22.1-24.1 °C) and/or dry weather (humidity of 75-78 %). Indeed, our data on the temperature and relative humidity values during the period when the geckos were active corroborate those already reported (Ngo et al., 2019a; means of 26 °C and 84.9 %). It is likely that the apparent preference of this species for caves (Ngo et al., 2019a) may also be linked to a need, or preference for, stable microclimatic conditions, that may explain the relatively narrow range of temperatures and humidity at which active geckos were found.

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REFERENCES

- Amadi, N., Luiselli, L., Belema, R., Nyiwale, G.A., Wala, C., Urubia, N. & Meek, R. (2021). From diurnal to nocturnal activity: a case study of night-light niche expansion in *Agama agama* lizards. *Ethology Ecology & Evolution*. DOI: 10.1080/03949370.2021.1883120
- Anibaldi, C., Luiselli, L. & Angelici, F.M. (1998). Notes on the ecology of a suburban population of rainbow lizards in coastal Kenya. *African Journal of Ecology* 36: 199–206.
- Chen, T.-B., Meng, Y.-J., Jiang, K., Li, P.-P., Wen, B.-H., Lu, W., Lazell, J. & Hou, M. (2014). New record of the leopard gecko *Goniurosaurus araneus* (Squamata: Eublepharidae) for China and habitat partitioning between geographically and phylogenetically close leopard geckos. *Reptiles & Amphibians* 21: 16–27.
- Grismer, L.L., Ota, H. & Tanaka, S. (1994). Phylogeny, classification, and biogeography of *Goniurosaurus kuroiwae* (Squamata: Eublepharidae) from the Ryukyu Archipelago, Japan, with description of a new subspecies. *Zoological Science* 11: 319-335.
- Honda, M. & Ota, H. (2017). On the live coloration and partial mitochondrial DNA sequences in the topotypic population of *Goniurosaurus kuroiwae orientalis* (Squamata: Eublepharidae), with description of a new subspecies from Tokashikijima Island, Ryukyu Archipelago, Japan. *Asian Herpetological Research* 8: 96–107.
- IUCN (2020). The IUCN Red List of Threatened Species. Available at www.iucnredlist.org (last accessed: 25 February 2021).
- Ngo, H.N., Ziegler, T., Nguyen, T.Q., Pham, C.T., Nguyen, T.T., Le, M.D. & van Schingen, M. (2016). First population assessment of two cryptic Tiger Geckos (*Goniurosaurus*) from northern Vietnam: Implications for conservation. *Amphibian & Reptile Conservation* 10: 34–45 (e120).
- Ngo, H.N., Le, Q.T., Nguyen, Q.T., Le, D.M., van Schingen, M. & Ziegler, T. (2019a). First record of the Cát Bà tiger gecko, *Goniurosaurus catbaensis*, from Ha Long Bay, Quang Ninh Province, Vietnam: Microhabitat selection, potential distribution, and threat evaluation. *Amphibian & Reptile Conservation* 13: 1-13.

- Ngo, H.N., Nguyen, T.Q., Phan, T.Q., van Schingen, M. & Ziegler, T. (2019b). A case study on trade in threatened Tiger Geckos (*Goniurosaurus*) in Vietnam including updated information on the abundance of the Endangered *G. catbaensis. Nature Conservation* 33: 1-19.
- Ngo, H.N., Nguyen, H.Q, Tran, H.M, Ngo, H.T, Le, D.M., Gewiss, L.R., van Schingen-Khan, M., Nguyen, T.Q. & Ziegler, T. (2021). A morphological and molecular review of the genus *Goniurosaurus*, including an identification key. *European Journal of Taxonomy* (in press).
- Nguyen, Q.T., Ngo, N.H., Van Schingen, M. & Ziegler, T. (2016). Goniurosaurus catbaensis. The IUCN Red List of Threatened Species 2016: e.T18917684A18917688. DOI: 10.2305/IUCN.UK.2016-2.RLTS.T18917684A18917688. en. Downloaded on 25 February 2021.
- Nguyen, T. (2011). Systematics, ecology, and conservation of the lizard fauna in northeastern Vietnam, with special focus on *Pseudocalotes* (Agamidae), *Goniurosaurus* (Eublepharidae), *Sphenomorphus* and *Tropidophorus* (Scincidae) from this country. Unpublished Thesis, Bonn University, Germany.
- Nguyen, T.Q., Stenke, R., Nguyen, H.X. & Ziegler, T. (2011). The terrestrial reptilian fauna of the Biosphere Reserve Cát Bà Archipelago, Hai Phong, Vietnam. In: *Tropical Vertebrates in a Changing World*, 99-115 pp. Schuchmann, K-L. (Ed.). Bonner Zoologische Monographien, 57.
- Qi, S., Grismer, L.L., Lyu, Z.-T., Zhang, L., Li, P.-P., Wang, Y.-Y. (2020). A definition of the *Goniurosaurus yingdeensis* group (Squamata, Eublepharidae) with the description of a new species. *ZooKeys* 986: 127-155.
- Uetz, P., Freed, P. & Hošek, J.(Eds.) (2020). The Reptile Database, available at http://www.reptile-database.org (last accessed: 27 February 2021).
- Van Schingen, M. (2014). Population status and autecology of *Shinisaurus crocodilurus* Ahl, 1930 in northeastern Vietnam. Unpublished MS Thesis, Cologne University, Germany.
- Vu, N.T., Nguyen, Q.T., Grismer, L.L. & Ziegler, T. (2006). Fist record of the Chinese Leopard Gecko, *Goniurosaurus luii* (Reptilia: Eublepharidae) from Vietnam. *Current Herpetology* 25: 93–95.
- Yang, J.H. & Chan, B.P. (2015). Two new species of the genus Goniurosaurus (Squâmta: Sauria: Eublepharidae) from southern China. Zootaxa 3980: 067-080.
- Zhou, R.-B., Ning, W., Bei, C. & Bin, L. (2018). Morphological evidence uncovers a new species of *Goniurosaurus* (Squamata: Eublepharidae) from the Hainan Island, China. *Zootaxa* 4369: 281–291.
- Zhu, X.-Y., Chu-Ze S., Yun-Fei L., Lin, C., Zheng, L., & Zhu-Qing,
 H. (2020). A new species of *Goniurosaurus* from Hainan Island, China based on molecular and morphological data (Squamata: Sauria: Eublepharidae). *Zootaxa* 4772: 349– 360
- Ziegler, T., Truong, N.Q., Schmitz, A., Stenke, R. & Rösler, H.
 (2008). A new species of *Goniurosaurus* from Cát Bà Island, Hai Phong, northern Vietnam (Squamata: Eublepharidae). *Zootaxa* 1771: 16–30.

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