

# Geographical and elevational distributions of the Black-breasted Leaf Turtle, *Geoemyda spengleri* (Gmelin, 1789) (Testudines: Geoemydidae)

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**Abstract.**—Knowledge of the spatial distributions of species is vital for protecting the planet’s biodiversity. Turtles are currently among the most threatened vertebrate groups, resulting in the need for studies of turtle distributions. However, the distributions of many turtle species remain poorly known, particularly for those in Southeast and East Asia. *Geoemyda spengleri* is a small terrestrial turtle found in montane forests of China, Laos, and Vietnam. Here, we update the geographical distribution of this species based on reliable occurrence data and discuss some questionable records. We also present the elevational distribution of *G. spengleri* from localities across its geographical distribution. Compared to prior studies, this work increases the number of verified localities for *G. spengleri* ( $n = 51$ ), but we also consider some previously accepted localities (e.g., central Vietnam) to be unreliable. The total estimated area for the geographical distribution of *G. spengleri* is 227,641 km<sup>2</sup>. Our results also show that the species inhabits an elevation range of 530–1,548 m. A latitudinal gradient in elevation is apparent, with the tendency for more southerly occurrences to be located at higher elevations than more northerly occurrences. The geographical and elevational distributions of *G. spengleri* have implications for the conservation of this species, and additional research involving these topics is encouraged.

**Keywords.** Asia, biogeography, chelonian, conservation, China, Endangered, Laos, montane, threatened species, Vietnam

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## Introduction

Detailed knowledge of the spatial distributions of species is fundamental for studies in biogeography, ecology, and conservation biology. However, information on most species distributions remains incomplete. This deficiency, the Wallacean shortfall, hinders our ability to understand and protect biodiversity on a rapidly changing planet (Lomolino 2004; Richardson and Whittaker 2010).

Turtles (order Testudines) are currently one of the world’s most threatened clades of vertebrates (Rhodin et

al. 2018; Stanford et al. 2020). The creation of distribution maps for turtle species, while certainly not new (e.g., Iverson 1992), has received much attention in recent years due to the conservation status of this group. Buhlmann et al. (2009) described a method of constructing turtle distribution maps based on species occurrence data and hydrologic unit compartments (HUCs). Subsequently revised by the TTWG (2017) using finer resolution HUCs, the resulting maps represent the most current, accurate, and thorough study of turtle distributions to date. These maps have already been used for studies of turtle biogeography,

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macroecology, evolution, and conservation prioritization (Rodrigues and Diniz-Filho 2017; Rodrigues et al. 2017; Ennen et al. 2020).

Despite these advances, the distributions of many turtle species continue to be poorly known. This is especially true for Southeast and East Asian species, which unfortunately are also among the most threatened (van Dijk et al. 2000). The reasons for this information gap include limited field surveying, the massive and widespread trade in turtles, the extreme rarity of some species, and inaccessibility of the scientific literature and museum specimens in the region. Many localities for Asian turtles were based on specimens purchased from markets or introduced through trade, and the uncritical acceptance of these records has resulted in considerable confusion regarding species distributions (Parham and Li 1999; Fong et al. 2002; Stuart and Platt 2004; Zhou et al. 2008; Fong and Qiao 2010).

The Black-breasted Leaf Turtle, *Geoemyda spengleri* (Gmelin, 1789), is a small terrestrial turtle inhabiting montane forests in southern China, Laos, and Vietnam. Under threat from trade and habitat destruction, *G. spengleri* is currently assessed as Endangered for the *IUCN Red List of Threatened Species* (Rhodin et al. 2018; Fong et al. 2020). Although *G. spengleri* remains relatively enigmatic in the wild, basic information on the biology and ecology of the species has been provided by recent field studies in Vietnam (Pham et al. 2018, 2020) and ongoing research in China (Dawson et al. 2019). This field work has also furnished additional locality data for *G. spengleri*. Herein, we use these occurrences to update the geographical distribution of *G. spengleri* and discuss some questionable historical and modern records. We also present the elevational distribution of *G. spengleri* from localities across the geographical distribution. Although elevation is extremely important for montane species, elevational data have seldom been reported for *G. spengleri*, particularly for populations in China.

## Materials and Methods

**Dataset.** We assembled the records of *G. spengleri* from our own field work, museum collections, scientific literature, interviews of local people, and unpublished data from other researchers. Our field work included specific surveys for *G. spengleri* and incidental finds during other projects. For each turtle located in the field, we recorded the position (latitude, longitude, elevation; WGS84) using a handheld GPS receiver. We compiled published records from a search of the primary and secondary literature in Chinese, English, French, German, and Vietnamese. When possible, we authenticated records in the secondary literature with primary sources. We examined museum holdings using online collection databases (VertNet 2015; NSTI 2017; GBIF 2020) and contacted several institutions to obtain additional data or photographs of select specimens.

Interviews of turtle hunters, traders, consumers, and other individuals were typically semi-structured in design and conducted by interviewers fluent in the local language. Details of our interview methodology can be found in Gong et al. (2009a), Gaillard et al. (2017), and Pham et al. (2018, 2020). For records lacking coordinates but with textual descriptions, we geocoded the place names using detailed local maps and satellite imagery in Google Earth Pro (version 7.3, Google LLC, Mountain View, California, USA).

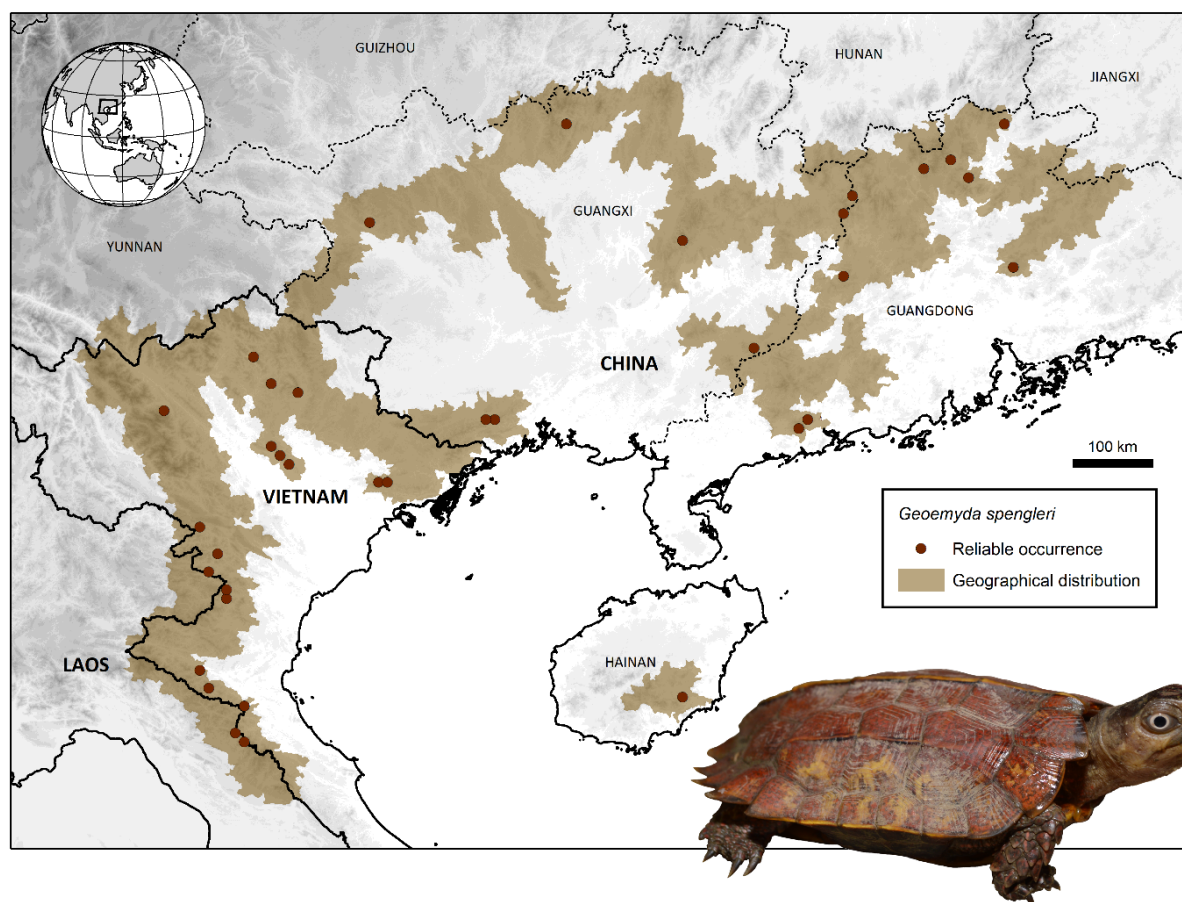
**Data verification.** We critically evaluated the quality of each record in the dataset, and confirmed species identification using a specimen, photograph, or description. Based on qualitative data and expert opinion, we characterized the source as either natural or anthropogenic (i.e., based on trade/introduction). We incorporated uncertainty in horizontal position as an attribute as follows: coordinates from GPS were classified as low error (record position < 1 km from the true location), while geocoded coordinates were categorized as either medium ( $\leq 10$  km from the true location) or high ( $> 10$  km from the true location) errors. We selected this cutoff distance based on the resolution of Level 10 HUCs (mean area =  $143.7 \pm 85.1$  km<sup>2</sup> or  $\sim 12$  km  $\times$  12 km) in the study area, between approximately 16–26°N and 104–114°E. We considered individual records to be reliable occurrences if a correct species identification was established, the source was natural, and the positional error was low or medium. When any of these conditions was not met or missing data prevented verification, we considered the record to be questionable and excluded it from the geographical distribution. For elevational analyses, we retained only reliable occurrences with low positional error.

**Geographical distribution mapping.** To construct a distribution map based on HUCs, we followed the method of Buhlmann et al. (2009) but utilized HUCs of finer resolution, as performed by TTWG (2017). We obtained a polygon shapefile of Level 10 HUCs from the HydroBASINS dataset (Lehner and Grill 2013) and extracted a digital elevation model from the Global Multi-Resolution Terrain Elevation Data 2010 (GMTED2010) 30 arc-second systematic subsample product (Danielson and Gesch 2011). In ArcGIS Desktop (version 10.8.1, ERSI, Redlands, California, USA), we added a point layer of reliable occurrences to the GMTED2010 elevation raster and the HUCs vector layer. Initially, we selected the localities of the HUCs containing occurrence points, followed by the addition of neighboring HUCs at similar elevations and adjacent HUCs within the same larger watershed or physiographic region, until all the HUCs were connected. For comparison to our results, we obtained polygon shapefiles of the distributions created by Buhlmann et al. (2009) and the updated version by TTWG (2017).

**Area calculations, statistical analyses, and data presentation.** We estimated the area of the geographical distribution using the equal-area Behrmann cylindrical map projection (Yildirim and Kaya 2008) and the Calculate Geometry tool in ArcGIS Desktop. We defined statistical significance as  $p \leq 0.05$  and evaluated relationships of elevation to latitude and longitude using Kendall's rank correlation (using the `cor.test` function in the `stats` package of R: a language and environment for statistical computing, version 4.0.3, R Core Team, Vienna, Austria). Mean values are given  $\pm 1$  standard deviation. The release of precise locality information can inadvertently increase the threats to species, such as by facilitating exploitation (Fong et al. 2002; Fong and Qiao 2010). *Geoemyda spengleri* is highly vulnerable to exploitation over its entire geographical distribution, and the public availability of precise locality data could further jeopardize some populations. To reduce the risk of data misuse, we generalized the localities presented here by rounding coordinates to the nearest 0.1 degree (Chapman and Grafton 2008) and withheld some localities from the map. Finer resolution data may be obtained for approved uses under the terms of a data license agreement by contacting the corresponding author.

## Results

**Geographical distribution.** Of the 244 total records in our dataset, we considered 77 to be reliable occurrences. Fifty-one HUCs were localities containing reliable occurrences, with a mean of  $1.5 \pm 1.5$  occurrences per hydrologic unit (range = 1–9). Reliable occurrences by Fang (1930) and KFBG (2002a) for Liuzhou City, Guangxi Autonomous Region, China (25.2°N), formed the northernmost recorded locality for *G. spengleri*. The southernmost reliable occurrences were in Khamkeut District, Bolikhamxay Province, Laos (18.3°N), and consisted of the locality in Stuart et al. (2011) and a previously unpublished nearby record (an adult *G. spengleri* photographed in the field by C. Nanthavong and S. Sayavong on 26 March 2007). Most of the reliable occurrences ( $n = 65$ ) formed an arc of localities that connect to create a geographical distribution extending from the Nanling Mountains of southern China to the northern Annamite Range of Vietnam and Laos. Twelve insular occurrences in Hainan Province, China, were disjunct from the mainland geographical distribution (Fig. 1). We estimated the total area of the geographical distribution of *G. spengleri* to be 227,641 km<sup>2</sup> (Table 1).



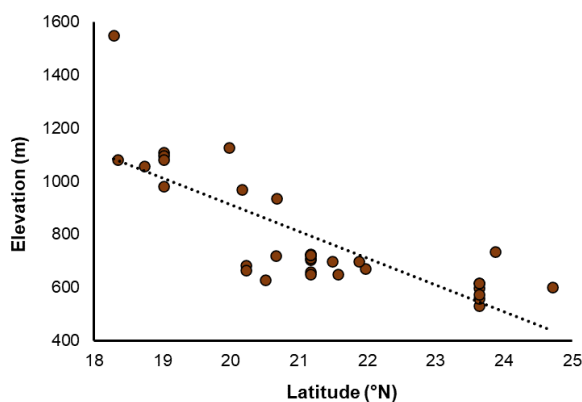
**Fig. 1.** Geographical distribution of *Geoemyda spengleri* based on hydrologic unit compartments (Level 10 HUCs). Positions of the reliable occurrences ( $n = 77$ ) are approximate, as the coordinates were generalized by rounding (see text for details). Multiple symbols may overlap and appear as a single point. Not all localities are shown to protect particularly sensitive populations. Inset: Adult male *Geoemyda spengleri* from Guangxi Autonomous Region, China. Photo by Jeffrey E. Dawson.

## Distribution of Black-breasted Leaf Turtle, *Geoemyda spengleri*

**Table 1.** Area estimates (km<sup>2</sup>) for the geographical distribution of *Geoemyda spengleri*. The sum for areas of the political divisions may not equal the total area due to rounding and because the coarse resolution HUCs used by Buhlmann et al. (2009) were not perfectly aligned with political and natural boundaries.

| Location  | Buhlmann et al. (2009) | TTWG (2017) | This study |
|-----------|------------------------|-------------|------------|
| Total     | 452,934                | 273,018     | 227,641    |
| China     | 229,058                | 182,222     | 140,804    |
| Guangdong | 71,898                 | 58,416      | 52,405     |
| Guangxi   | 131,480                | 110,050     | 75,765     |
| Guizhou   | –                      | –           | 1,029      |
| Hainan    | 7,721                  | 8,382       | 4,111      |
| Hunan     | –                      | 2,436       | 2,506      |
| Jiangxi   | –                      | 2,936       | 1,393      |
| Yunnan    | 17,958                 | –           | 3,594      |
| Laos      | 68,334                 | 3,833       | 13,293     |
| Vietnam   | 155,259                | 86,962      | 73,508     |

**Elevational distribution.** Elevations were available for 33 reliable occurrences of *G. spengleri* with low positional error. The mean elevation of these occurrences was  $791.6 \pm 229.6$  m. No association was found between elevation and longitude (Kendall's  $\tau = -0.22$ ,  $p$  value = 0.70). However, a negative correlation between elevation and latitude was highly significant (Kendall's  $\tau = -0.61$ ,  $p < 0.001$ ). The lowest recorded elevation was an occurrence in Huizhou City, Guangdong Province, China (23.6°N), which is near the north-eastern extent of the geographical distribution. The mean elevation of occurrences at this locality was  $582.2 \pm 34.4$  m (range = 530–618 m;  $n = 6$ ). Moving southward along the geographical distribution, the elevations of occurrences increased (Fig. 2). The highest recorded elevation (1,548 m) was also the southernmost reliable occurrence in Khamkeut District, Bolikhamxay Province, Laos (18.3°N). The mean elevation of the disjunct occurrences in Qiongzong County, Hainan Province, China (18.8°N), was  $1,064.4 \pm 51.1$  m (range = 980–1,110 m;  $n = 5$ ).



**Fig. 2.** Relationship between elevation and latitude of reliable *Geoemyda spengleri* occurrences with low positional error ( $n = 33$ ).

## Discussion

Early reports on the geographical distribution of *G. spengleri* included a number of spurious localities, such as the Mascarene Islands of Africa and the archipelagos of Indonesia and the Philippines (e.g., Duméril and Bibron 1835; Boulenger 1889; Castro de Elera 1895; Shelford 1901; De Rooij 1915; Smith 1931; Pope 1935). These erroneous records were apparently based on misidentified, mislabelled, or translocated specimens (Strauch 1865; Iverson 1992; Yasukawa and Ota 2010). As *G. spengleri* has been subjected to extensive exploitation since the 1980s, recent localities must also be carefully scrutinized. Records for some locations, including Anhui Province (Yao and Liu 1995) and Macau (Zhao and Leung 1999) in China, appear to be based on specimens released or purchased from trade (Shi 2005).

Uncertainty still remains for a number of other localities for *G. spengleri*, particularly in China. Pierlioni (2016) published images of a specimen photographed during the filming of a television documentary in extreme western Yunnan Province, China. We attempted to obtain additional locality data through contact with the media company, but the only recollection of the photographer was that a ranger purportedly caught the turtle in Gaoligongshan National Nature Reserve and released it afterward (B. Morrison, pers. comm.). However, the location of the reserve is over 650 km from the nearest reliable occurrence record in Van Ban District, Lao Cai Province, Vietnam. Lacking any further information, we excluded this locality from the geographical distribution. It is more probable that *G. spengleri* occurs in eastern Yunnan Province. According to Li and Wang (1999), wildlife traders asserted that some specimens in the markets of Yunnan originated from areas of the province close to the border with Vietnam. Although we were unable to confirm any localities during this study, J. Wang (pers. comm.) has provided us with information on

one possible site in eastern Yunnan. *Geoemyda spengleri* has been included in the herpetofauna of Hunan Province (Zhao 1986; Zhao and Adler 1993). However, no specimens or details from Hunan have been documented thus far, and the occurrence of the species there remains unconfirmed (Shen et al. 1998). The current study also did not substantiate a possible locality in Jiangxi Province listed by Schaefer (2005) and TTWG (2017). Field work should be undertaken in the parts of Yunnan, Hunan, Jiangxi, and Guizhou provinces near reliable occurrences to establish whether *G. spengleri* is present.

Although numerous occurrences exist in Guangxi Autonomous Region, China, there are very few localities in the western one-third of the region. Furthermore, some records in this area are equivocal. Fang (1930) provided a locality (“Tung-kwai, Lungchow”) for two specimens from Chongzuo City, on the border with Vietnam, in southwestern Guangxi. However, the terrain of this area consists of karst hills that are generally less than 400 m in elevation. Based on the recorded elevational distribution of *G. spengleri*, that area appears largely unsuitable for the species. More recent records for the area include a literature report on Nonggang National Nature Reserve (Long 1988, in KFBG 2002b) and specimens with collection dates from the late 1990s held by Anhui Normal University (NSTI 2017). However, no specimens have been found during field surveys of Nonggang National Nature Reserve since 1998, and local people have not reported the species during interviews. *Cuora mouhotii* occurs in the area, and the *G. spengleri* record for the reserve may be based on misidentified juveniles of *C. mouhotii* (B. Chan, pers. comm.). It seems highly plausible that the museum specimens from the 1990s could have originated elsewhere. The Guangxi-Vietnam border was at the epicenter of the trade in wildlife, including *G. spengleri*, entering southern China at that time (Li and Li 1998). While there could be a localized population in southwestern Guangxi, as suggested by the specimens of Fang (1930), records for the area should be considered questionable until further evidence becomes available.

The southern extent of the geographical distribution of *G. spengleri* is also unclear (Fong et al. 2020). Many authors have included a locality for the species in Quang Nam Province (15–16°N) in central Vietnam (e.g., Pope 1935; Bourret 1941; Iverson 1992; Le 2000; Le and Nguyen 2002; Schaeffer 2005; Nguyen et al. 2005, 2009; Yasukawa and Ota 2010; TTWG 2017). A single specimen with a reported locality from the area (“Chang Nam, C. Annam”), was collected by Hans Fruhstorfer around 1900 and deposited in the Natural History Museum, London, United Kingdom. Photographs show that the specimen (NHMUK 1903.7.2.2) is correctly identified as *G. spengleri* and that it was collected as a hatchling, still bearing a slight plastral indentation from attachment of the yolk sac (approximate maximum straight carapace length = 38 mm). However, to our knowledge, no other

specimens have since been substantiated from Quang Nam. While we can neither confirm nor deny the exact provenance of the Fruhstorfer specimen, we considered this record to be unreliable given the likelihood of high positional error, in combination with its early collection date and the lack of any subsequent verifiable specimens.

The only other indication for the possible occurrence of *G. spengleri* in Quang Nam appears to be information from turtle traders. Based on surveys of the turtle trade in Vietnam during 1993, Le and Broad (1995) listed *G. spengleri* as occurring in Quang Nam and the neighboring municipality of Da Nang. Unfortunately, Le and Broad (1995) did not publish any photographs which would enable their species identification to be confirmed. Even if *G. spengleri* was correctly identified, it remains uncertain whether the traded turtles actually originated from either locality. Yasukawa and Ota (2007) suggested that Da Nang may have been a distribution center for the selling or shipping of turtles, rather than a true occurrence of the species. Moreover, the sources for the information in Le and Broad (1995) came from four provinces to the north of Quang Nam. Reliable occurrences for *G. spengleri* exist in two of these provinces (Nghe An and Thanh Hoa), and another (Ha Tinh) is adjacent to reliable occurrences in Laos. Therefore, if *G. spengleri* were traded in these provinces, the turtles could have all originated locally, rather than being sourced from Quang Nam and Da Nang.

*Geoemyda spengleri* has not been observed in Quang Nam during multiple surveys in recent years by the Asian Turtle Program (data not shown). As the nearest reliable occurrence is over 350 km to the north, in Khamkeut District, Bolikhamxay Province, Laos (18.3°N), the reports for Quang Nam and Da Nang should probably be treated with skepticism. Tordoff et al. (2003) noted that *G. spengleri* was unconfirmed in the region of Quang Nam and listed the species as provisionally occurring there. We followed the opposite approach, by omitting the area south of approximately 17.5°N from the geographical distribution of the species, until additional support for its occurrence can be firmly established. However, we also note that portions of the Annamite Range remain relatively unstudied by scientists, and that *G. spengleri* was not confirmed from Laos until quite recently (Stuart et al. 2011). Therefore, it is conceivable that *G. spengleri* could occur in Quang Nam or the surrounding area, and field surveys should be undertaken to thoroughly investigate this possibility.

The availability of locality data for *G. spengleri* has increased greatly over time. Iverson (1992) mapped seven localities for the species (excluding specimens belonging to a taxon now recognized as a separate species, *G. japonica*), while Buhlmann et al. (2009) used four. The map of Yasukawa and Ota (2010) included 16 localities, and the TTWG (2017) incorporated 27 localities. As discussed above, some of these locality records for *G. spengleri* may not represent reliable occurrences.

However, despite our use of a relatively conservative methodology that excluded some records previously accepted by other authors, we increased the number of different verified localities for *G. spengleri* to 51 (i.e., the number of HUCs containing reliable occurrences) in the current study.

By incorporating more localities, our map and estimates for the geographical distribution area of *G. spengleri* are more refined than previous estimates (Table 1). Buhlmann et al. (2009) used coarse resolution Level 6 HUCs, which contributed to an apparent overinflation of the geographical distribution. In particular, the estimated areas in Laos and Yunnan Province, China, are five times larger than the estimates in this study. In total, the geographical distribution area calculated by Buhlmann et al. (2009) is double our total estimated area. The TTWG (2017) utilized the same finer resolution HUCs as the present study, and their total area is closer (20% higher) to our estimate. In comparison, their work seems to have overestimated the area in Jiangxi Province, China, and underestimated the area in Laos. Both Buhlmann et al. (2009) and TTWG (2017) appear to have inflated the disjunct geographical distribution of *G. spengleri* in Hainan Province, China. The area calculated for Hainan by TTWG (2017) is actually larger than that in Buhlmann et al. (2009) and roughly double our estimate.

The results of our elevational analyses confirm that *G. spengleri* occurs in upland areas. Previous reports on the elevational distribution of the species were mostly qualitative. Fang (1930) reported that a specimen was “collected from the hill-side” in northern Guangxi Autonomous Region, China. According to Fan (1931), mountain peaks surrounding an area for *G. spengleri* in north-eastern Guangxi were “no less than 3,000 ft” to “7,000 ft” (914–2,133 m), but the elevations of the exact collection sites were not specified. Pope (1935) interpreted these accounts to mean that *G. spengleri* preferred “wild, wooded, mountainous country.” Bourret (1941) wrote that the species occurred at mid-elevations (“moyenne altitude”) in forested montane regions of Vietnam. Based on reports and photographs of *G. spengleri* habitat, Schaefer (2005) inferred that it ranged from 400–1,200 m in elevation.

More recently, a few studies have provided quantitative elevational data for *G. spengleri* encountered in the field, but these measurements were restricted to only a few localities (Stuart et al. 2011; Pham et al. 2018, 2020). Our data are more comprehensive and indicate that while *G. spengleri* is a montane species over its entire geographical distribution, the species seems to occur at higher elevations at lower latitudes. This relationship is likely due to the spatial distribution of suitable climatic conditions, particularly temperature, over the elevational and latitudinal gradients (Bickford et al. 2010). This pattern could have implications for the vulnerability of *G. spengleri* to climate change. Small terrestrial herpetofauna species have limited capacity for dispersal,

constraining their ability to follow poleward shifts in suitable conditions (Bickford et al. 2010). Valleys between upland areas and anthropogenic habitat fragmentation serve as further obstacles to latitudinal movements by montane species, such as *G. spengleri*. Instead, as the global average temperature continues to rise, the elevational distributions of some montane herpetofauna species in Southeast Asia appear to be shifting upward (Bickford et al. 2010). However, populations of *G. spengleri* that already occupy the uppermost elevations of mountains may not be able to move higher to track suitable environmental conditions, increasing the level of threat to the species in these areas. As countries confront climate change, conservation measures for *G. spengleri* should include the creation of corridors to link isolated reserves into larger contiguous protected areas, thereby permitting movements by the species. More radical and potentially risky interventions, such as assisted migration across dispersal barriers, should also be considered as last resorts.

## Conclusions

Our study provides a better understanding of the geographical and elevational distributions of *G. spengleri* compared to previous works. However, there are some caveats to our findings. The survey effort has not been equal across all localities or elevations. Many reliable occurrence records are based on incidental finds, rather than standardized surveys. Even in areas of relatively good surveying, the species is difficult to detect due to its small size and secretive nature. No doubt, additional field work will result in occurrence records at new localities, and interpretations of the geographical and elevational distributions for *G. spengleri* will continue to change. For example, unlike the continuous distribution on our map, the mainland geographical distribution of *G. spengleri* from southern China to Vietnam and Laos is likely broken into disjunct segments. Little to no connectivity among some populations would explain the phylogeographic pattern previously seen in *G. spengleri* (Gong et al. 2009b), and would have considerable implications for the conservation of the species. Continued research (including additional field surveys, genetic analyses, and distribution modeling) is strongly encouraged, as these efforts will be vital to further the knowledge and conservation of the species. Until then, this work represents the most accurate and thorough assessment of the geographical and elevational distributions of *G. spengleri*.

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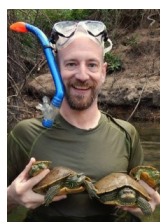
## Literature Cited

- Bickford D, Howard SD, Ng DJJ, Sheridan JA. 2010. Impacts of climate change on the amphibians and reptiles of Southeast Asia. *Biodiversity and Conservation* 19: 1,043–1,062.
- Boulenger GA. 1889. *Catalogue of the Chelonians, Rhynchocephalians, and Crocodiles in the British Museum (Natural History)*. British Museum (Natural History), London, United Kingdom. 311 p.
- Bourret RL. 1941. *Les Tortues de l'Indochine*. Institut Océanographique Indochine, Hanoi, Vietnam. 235 p.
- Buhlmann KA, Akre TS, Iverson JB, Karapatakis D, Mittermeier RA, Georges A, Rhodin AGJ, van Dijk PP, Gibbons JW. 2009. A global analysis of tortoise and freshwater turtle distributions with identification of priority conservation areas. *Chelonian Conservation and Biology* 8: 116–149.
- Casto de Elera F. 1895. *Catálogo Sistemático de Toda la Fauna de Filipinas Conocida hasta el Presente, y á la Ves el de la Colección Zoológica del Museo de PP. Volumen I, Vertebrados*. Dominicos del Colegio-Universidad de Santo Tomás de Manila, Manila, Philippines. 701 p.
- Chapman AD, Grafton O. 2008. *Guide to Best Practices for Generalizing Primary Species-Occurrence Data, version 1.0*. Global Biodiversity Information Facility, Copenhagen, Denmark. 27 p.
- Danielson JJ, Gesch DB. 2011. *Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010): U.S. Geological Survey Open-File Report 2011-1073*. United States Geological Survey, Reston, Virginia, USA. 26 p. Available: <http://topotools.cr.usgs.gov> [Accessed: 3 November 2020].
- Dawson J, Gaillard D, Shi H, Lin L, Gong S, Anders B. 2019. A vision for conserving the Black-breasted Leaf Turtle in China. *Turtle Survival* 2019: 40–41.
- De Rooij N. 1915. *The Reptiles of the Indo-Australian Archipelago. I. Lacertilia, Chelonia, Emydosauria*. Brill, Leiden, Netherlands. 384 p.
- Duméril AMC, Bibron G. 1835. *Erpétologie Générale ou Histoire Naturelle Complète des Reptiles. Tome Second*. Roret, Paris, France. 680 p.
- Ennen JR, Agha M, Sweat SC, Matamoros WA, Lovich JE, Rhodin AGJ, Iverson JB, Hoagstrom CW. 2020. Turtle biogeography: global regionalization and conservation priorities. *Biological Conservation* 241: 108323.
- Fan TH. 1931. Preliminary report of reptiles from Yaoshan, Kwangsi, China. *Bulletin of the Department of Biology, College of Science, Sun Yatsen University, Canton* 11: 1–154.
- Fang PW. 1930. Notes on chelonians of Kwangsi, China. *Sinensia* 1: 95–135.
- Fong JJ, Qiao G. 2010. New localities of endangered Chinese turtles from museum specimens and the practical and ethical challenges using and reporting natural history collection data. *Zootaxa* 2393: 59–68.
- Fong JJ, Parham JF, Fu J. 2002. A reassessment of the distribution of *Cuora flavomarginata* Gray 1863 on mainland China. *Russian Journal of Herpetology* 9: 9–14.
- Fong J, Hoang H, Li P, McCormack T, Rao D-Q, Timmins RJ, Wang L. 2020. *Geoemyda spengleri*. The IUCN Red List of Threatened Species 2020: e.T39552A2929166.
- Gaillard D, Lin L, Shi H, Luo S. 2017. Turtle soup: local usage and demand for wild caught turtles in Qiongzong County, Hainan Island. *Herpetological Conservation and Biology* 12: 33–40.
- GBIF. 2020. *GBIF Occurrence Download*. Available: <http://doi.org/10.15468/dl.dymf5z> [Accessed: 13 November 2020].
- Gong S, Shi H, Fong JJ, Lau M. 2009a. Recent records of freshwater turtles from Guangdong, China. *Turtle and Tortoise Newsletter* 13: 24–27.
- Gong S, Shi H, Mo Y, Auer M, Vargas-Ramírez M, Hundsdoerfer AK, Fritz U. 2009b. Phylogeography of the endangered Black-breasted Leaf Turtle (*Geoemyda spengleri*) and conservation implications for other chelonians. *Amphibia-Reptilia* 30: 57–62.
- Iverson JB. 1992. *A Revised Checklist with Distribution Maps of the Turtles of the World*. Privately printed,

- Richmond, Indiana, USA. 363 p.
- KFBG [Kadoorie Farm and Botanic Garden]. 2002a. *Report of a Rapid Biodiversity Assessment at Jiuwanshan Headwater Forest Nature Reserve, North Guangxi, China, 24 to 27 July 1998*. South China Forest Biodiversity Survey Report Series (Online Simplified Version), Number 14. KFBG, Hong Kong SAR, China. 18 p.
- KFBG [Kadoorie Farm and Botanic Garden]. 2002b. *Report of Rapid Biodiversity Assessments at Nonggang National Nature Reserve, Southwest Guangxi, China, 19 to 27 May 1998*. South China Forest Biodiversity Survey Report Series (Online Simplified Version), Number 10. KFBG, Hong Kong SAR, China. 34 p.
- Le DD, Broad S. 1995. *Investigations into Tortoise and Freshwater Turtle Trade in Vietnam*. IUCN Species Survival Commission, Gland, Switzerland and Cambridge, United Kingdom. 34 p.
- Le KV. 2000. The biodiversity of the terrestrial vertebrates in Ba Na Natural Reserve (Quang Nam Province and Da Nang City). *Journal of Biology, Hanoi* 22(15): 154–164.
- Le KV, Nguyen SV. 2003. Species composition of reptiles and amphibians from Ba Na area (Hoa Vang district, Da Nang city). *Journal of Organism Issues of Science* 2003: 638–642.
- Lehner B, Grill G. 2013. Global river hydrography and network routing: baseline data and new approaches to study the world's large river systems. *Hydrological Processes* 27: 2,171–2,186, plus Data (version 1.c, format 1). Available: <http://www.hydrosheds.org>.
- Li Y, Li D. 1998. The dynamics of trade in live wildlife across the Guangxi border between China and Vietnam during 1993–1996 and its control strategies. *Biodiversity and Conservation* 7: 895–914.
- Li W, Wang H. 1999. Wildlife trade in Yunnan Province, China, at the border with Vietnam. *TRAFFIC Bulletin* 18(1): 21–30.
- Lomolino MV. 2004. Conservation biogeography. Pp. 293–296 In: *Frontiers of Biogeography: New Directions in the Geography of Nature*. Editors, Lomolino MV, Heaney LR. Sinauer Associates, Sunderland, Massachusetts, USA. 436 p.
- Nguyen SV, Ho CT, Nguyen TQ. 2005. *A Checklist of Amphibians and Reptiles of Vietnam*. Agricultural Publishing House, Hanoi, Vietnam, 180 p.
- Nguyen SV, Ho CT, Nguyen TQ. 2009. *Herpetofauna of Vietnam*. Edition Chimaira, Frankfurt am Main, Germany. 768 p.
- NSTI [National Science and Technology Infrastructure]. 2017. National Specimen Information Infrastructure of China. Available: <http://www.nsii.org.cn> [Accessed: 14 November 2020].
- Parham JF, Li D. 1999. A new locality for *Cuora pani* Song, 1984 with comments on its known range. *Asiatic Herpetological Research* 8: 111–113.
- Pham TV, Vu TT, Dawson JE, Bui TT, Leprince B. 2018. Natural history observations on the Endangered turtle *Geoemyda spengleri* in Tay Yen Tu Nature Reserve (Vietnam), with notes on other sympatric species. *Herpetological Bulletin* 146: 1–7.
- Pham TV, Le Duc O, Leprince B, Bodres C, Zuklin T, Ducotterd C, Quang VL, Lo OV, Nguyen AT, Fa JE, Luiselli L. 2020. Unexpected high forest turtle diversity in hill forests in northern Vietnam. *Biodiversity and Conservation* 29: 4,019–4,033.
- Pierlioni A. 2016. *Black-breasted Leaf Turtles: The Natural History, Captive Care, and Breeding of Geoemyda spengleri and Geoemyda japonica*. Turtles of the World, Geoemydidae, Number 1. Living Art Publishing, Ada, Oklahoma, USA. 114 p.
- Pope CH. 1935. *Natural History of Central Asia, Volume 10. The Reptiles of China*. American Museum of Natural History, New York, New York, USA. 604 p.
- Rhodin AGJ, Stanford CB, van Dijk PP, Eisemberg C, Luiselli L, Mittermeier RA, Hudson R, Horne BD, Goode EV, Vogt RC, et al. 2018. Global conservation status of turtles and tortoises (Order Testudines). *Chelonian Conservation and Biology* 17: 135–161.
- Richardson DM, Whittaker RJ. 2010. Conservation biogeography: foundations, concepts, and challenges. *Diversity and Distributions* 16: 313–320.
- Rodrigues JFM, Diniz-Filho JAF. 2017. Dispersal is more important than climate in structuring turtle communities across different biogeographical realms. *Journal of Biogeography* 44: 2,109–2,120.
- Rodrigues JFM, Olalla-Tárraga MÁ, Iverson JB, Akre TSB, Diniz-Filho JAF. 2017. Time and environment explain the current richness distribution of non-marine turtles worldwide. *Ecography* 40: 1,402–1,411.
- Schaefer I. 2005. *Zackenerdschildkröten: Die Gattung Geoemyda*. Natur und Tier Verlag, Münster, Germany. 143 p.
- Shelford BA. 1901. A list of the reptiles of Borneo. *Journal of the Straits Branch of the Royal Asiatic Society* 1901(35): 43–68.
- Shen Y, Mo X, Deng X. 1998. Testudinata in Hunan Province. *Chinese Journal of Zoology* 33: 16–18.
- Shi H. 2005. Distribution of the Black-breasted Leaf Turtle (*Geoemyda spengleri*) on Hainan Island, China. *Chelonian Conservation and Biology* 4: 954–956.
- Smith MA. 1931. *The Fauna of British India, including Ceylon and Burma. Reptilia and Amphibia, Volume I, Loricata, Testudines*. Taylor and Francis, London, United Kingdom. 179 p.
- Stanford CB, Iverson JB, Rhodin AGJ, van Dijk PP, Mittermeier RA, Kuchling G, Berry KH, Bertolero A, Bjorndal KA, Blanck TEG, et al. 2020. Turtles and tortoises are in trouble. *Current Biology* 30: R721–R735.
- Strauch A. 1865. Die Vertheilung der Schildkröten über den Erdball. Ein zoogeographischer Versuch. *Mémoires de l'Académie Impériale des Sciences de St.-Petersbourg* 8(13): 1–207.



- Stuart BL, Platt SG. 2004. Recent records of turtles and tortoises from Laos, Cambodia, and Vietnam. *Asiatic Herpetological Research* 10: 129–150.
- Stuart BL, Hallam CD, Sayavong S, Nanthavong C, Sayaleng S, Vongsa O, Robichaud WG. 2011. Two additions to the turtle fauna of Laos. *Chelonian Conservation and Biology* 10: 113–116.
- Tordoff A, Timmins R, Smith R, Vinh MK. 2003. *A Biological Assessment of the Central Truong Son Landscape*. Central Truong Son Initiative Report Number 1. WWF Indochina, Hanoi, Vietnam. 135 p.
- TTWG [Turtle Taxonomy Working Group: Rhodin AGJ, Iverson JB, Bour R, Fritz U, Georges A, Shaffer HB, van Dijk PP]. 2017. *Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status (8th Edition)*. Chelonian Research Monographs, Number 7. Chelonian Research Foundation and Turtle Conservancy, Lunenburg, Massachusetts, USA. 292 p.
- van Dijk PP, Stuart BL, Rhodin AGJ. 2000. *Asian Turtle Trade: Proceedings of a Workshop on Conservation and Trade of Freshwater Turtles and Tortoises in Asia*. Chelonian Research Monographs, Number 2. Chelonian Research Foundation, Lunenburg, Massachusetts, USA. 164 p.
- VertNet. 2015. VertNet Search Portal. Available: <http://portal.vertnet.org/search> [Accessed: 8 January 2015].
- Yao W, Liu Z. 1995. [Preliminary observation on *Geoemyda spengleri*, a record new to Anhui Province]. *Chinese Journal of Zoology* 30(3): 22–24. [In Chinese].
- Yasukawa Y, Ota H. 2010. *Geoemyda spengleri* (Gmelin, 1789) – Black-breasted Leaf Turtle. Pp. 047.1–047.6 In: *Conservation Biology of Freshwater Turtles and Tortoises: a Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group*. Editors, Rhodin AGJ, Pritchard PCH, van Dijk PP, Saumure RA, Buhlmann KA, Iverson JB, Mittermeier RA. Chelonian Research Monographs, Number 5. Chelonian Research Foundation, Lunenburg, Massachusetts, USA.
- Yildirim F, Kaya A. 2008. Selecting map projections in minimizing area distortions in GIS applications. *Sensors* 8: 7,809–7,817.
- Zhao E. 1986. A revised catalogue of Chinese tortoises. *Acta Herpetologica Sinica* 5: 145–148.
- Zhao E, Adler K. 1993. *Herpetology of China*. Society for the Study of Amphibians and Reptiles, Oxford, Ohio, USA. 522 p.
- Zhao E, Leung V. 1999. Notes on amphibians and reptiles of Macau. *Sichuan Journal of Zoology* 18: 147–150.
- Zhou T, Blanck T, McCord WP, Li P-P. 2008. Tracking *Cuora mccordi* Ernst, 1988: the first record of its natural habitat; a redescription, with data on captive populations and its vulnerability. *Hamadryad* 32: 57–69.



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## Distribution of Black-breasted Leaf Turtle, *Geoemyda spengleri*



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