CONSERVATION BIOLOGY OF FRESHWATER TURTLES AND TORTOISES

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Anders G.J. Rhodin, John B. Iverson, Peter Paul van Dijk,
Craig B. Stanford, Eric V. Goode, Kurt A. Buhlmann, and Russell A. Mittermeier



***Sacalia bealei* (Gray 1831) –**
Beale's Eyed Turtle

Liu Lin, Jinzhong Fu, Huai-Qing Chen, and Hai-Tao Shi

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Sacalia bealei (Gray 1831) – Beale's Eyed Turtle

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Summary. – Beale's Eyed Turtle, *Sacalia bealei* (family Geoemydidae) is a small freshwater turtle species endemic to southeastern China. The species inhabits mountain streams with high vegetation cover, deep stream pools, abundant stone caves, high fruit abundance, and high benthic species diversity and abundance. The species has a diverse diet, consisting of plant material, fruits, insects, benthic algae, and carrion. The species typically occupies a small home range averaging 0.626 ha, and females exhibit a larger home range than males during the nesting season. Nesting occurs from the middle of April to the middle of June, mainly in May. Females lay one clutch of eggs per year, with an average clutch size of 2.2 eggs (range, 1-3). The hard-shelled eggs are elongate, with an average length of 45.5 mm, width of 23.2 mm, and weight of 14.8 g. The incubation period in the wild is ca. 85–108 days at incubation temperatures of ca. 17.5–29.6°C (average 25.1°C). Poaching, illegal trade, and habitat loss are major ongoing threats to wild *S. bealei* populations, and the species is extremely rare in the wild. Conservation measures for the species remain limited, but are urgently needed. A conservation action plan has recently been developed and needs to be increasingly implemented.

Distribution. – China. Endemic to southeastern China, including the provinces of Guangdong, Fujian, Jiangxi, Anhui, Hunan, and Guizhou, as well as Hong Kong.

Synonymy. – *Cistuda bealei* Gray 1831, *Emys (Pyxidemys) bealei, Emys bealei, Clemmys bealei, Cistudo bealei, Sacalia bealei, Mauremys bealei, Sacalia bealei bealei, Emys bealii* Gray 1834 *(nomen novum), Clemmys bealii, Sacalia bealii, Cistudo bealii, Clemmys bealii bealii*.

Subspecies. – None currently recognized; *Sacalia quadriocellata* was at times in the past considered a subspecies of *S. bealei*, but is now considered a separate species.

Status. – IUCN 2026 Red List: Endangered (EN, A1d+2d [ver. 2.3]; 2000); TFTSG Provisional Red List: Critically Endangered (CR; 2011); CITES: Appendix II (2013); China Red List: Critically Endangered (2020); China: Class II State Key Protected Wild Animals of China (2021, wild populations).

Taxonomy. — Beale's Eyed Turtle was originally described as *Cistuda bealei* by Gray (1831) from "China," based on two syntypes in the British Museum of Natural History (1947.3.4.33, 1947.3.4.42; Iverson 2022; TTWG 2025). Subsequently, Gray (1834) reassigned the species as *Emys bealii* (but *bealii* was an unjustified emendation of *bealei*) and later established it as the monotypic type species of a new genus, *Sacalia* (Gray 1870). However, for a long time, the species was referred to as *Clemmys bealei* (Boulenger 1889; Smith 1931; Pope 1935) and for a while also as *Mauremys bealei* (Wermuth and Mertens 1977), before being generally accepted as *Sacalia bealei* (McDowell 1964; Pritchard 1979; Iverson 1992; Fritz and Havaš 2007; TTWG 2007, 2025). The specific epithet has frequently been misspelled as *bealii*, first perpetrated by Gray (1834), but this was an invalid emendation (TTWG 2025), and the common name has occasionally been incorrectly rendered as Beal's Eyed Turtle.

Iverson and McCord (1992) demonstrated that the syntypes of *Cistuda bealei* were morphometrically most similar to specimens from the Chinese mainland, particularly ones from Fujian and eastern Guangdong provinces and from Hong Kong, and they suggested restricting the type locality of *Sacalia bealei* to the Fuzhou region of Fujian Province, China. However, the syntypes were obtained by Thomas Beale (1775–1842), a naturalist and merchant who lived and worked in China in Macao, so the type locality may more likely have been in the Macao region, as estimated and suggested by TTWG (2025).

Assignment of Beale's Eyed Turtle to the Palaearctic genus *Emys* was clearly untenable, although it was attributed to that genus by Duméril and Bibron (1835) and by Günther (1864). This stems from the time when



Figure 1. Adult female Beale's Eyed Turtle, *Sacalia bealei,* from China. Note the yellow neck stripes. Photo by Cris Hagen.

the genus *Emys* had a far broader content (i.e., virtually all freshwater chelonians) than it does today. The subsequent use of *Clemmys* reflects the long-standing but now largely refuted opinion, except by Ye (1994), that several Asiatic pond turtles, now mostly assigned to *Mauremys*, were congeneric with the North American turtles of the genus *Clemmys*. McDowell (1964) demonstrated that, with a few exceptions, the New World and Old World pond turtles belonged to different subfamilies (now considered families). McDowell therefore revived Gray's 1870 genus *Sacalia* to include only the species *bealei*, and he listed in a lengthy table the features by which *Sacalia* differed from both *Mauremys* and *Clemmys*. The key features are listed below under Description. Although *Cistuda* Fleming 1822 is an older name than *Sacalia* Gray 1870, the type species of the former was an American Box Turtle (*Terrapene carolina*), and it is thus unavailable for *bealei*, even though *bealei* was described as a *Cistuda*.

Subsequent work by Merkle (1975) on protein electrophoresis confirmed McDowell's conclusion that *Sacalia* and *Mauremys* were separate and closely related, but differed significantly from *Clemmys*. Additional work by Bickham (1975) documented that the karyotypes of *Sacalia* and *Mauremys* are both 2n = 52, as opposed to species in the *Clemmys* complex (= *Clemmys, Actinemys, Glyptemys*) with a karyotype of 2n = 50. The karyotypic relationships between these genera within the suborder Cryptodira and specifically within the subfamily Batagurinae were further elucidated and confirmed by Bickham and Carr (1983), Bickham and Baker (1976), and Carr and Bickham (1986).

Recent work on the phylogeography and genetics of the *S. bealei* has progressed stepwise from a single mitochondrial locus to genome-wide population genomics, and now provides a robust framework for both taxonomy and conservation. Shi et al. (2008) conducted the first phylogeographic survey of the genus *Sacalia* using field-collected and trade

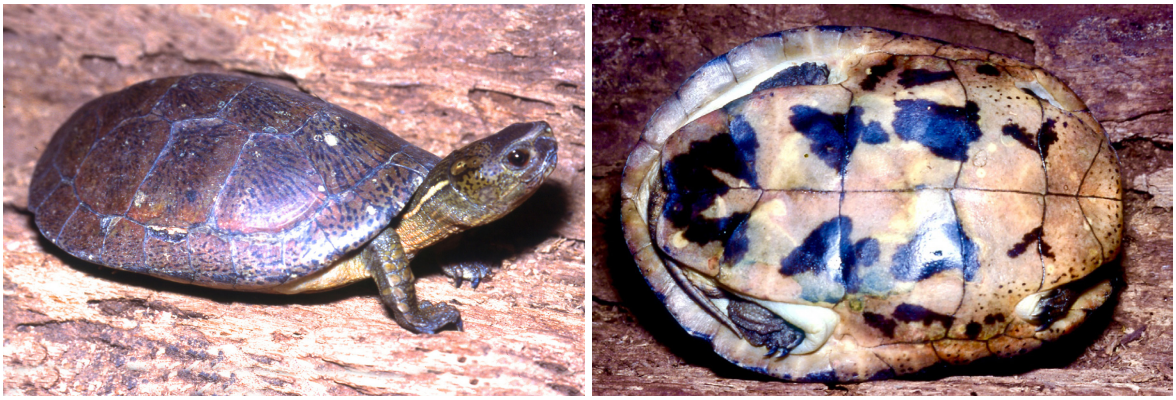


Figure 2. Adult female Beale's Eyed Turtle, *Sacalia bealei,* from China. Photo by John B. Iverson.



Figure 3. Adult male Beale's Eyed Turtle, *Sacalia bealei,* from China. Note the red neck stripes. Photo by Cris Hagen.

specimens with mitochondrial cytochrome b (*CytB*). They confirmed *S. bealei* as a genetically distinct, monophyletic lineage (uncorrected divergence from *S. quadriocellata* of 9.0–9.7%) and, importantly, demonstrated low intraspecific variation in this species.

Lin et al. (2020) characterized and compared the complete mitogenomes of the "eyed" turtle species, including *S. bealei* (16,564 bp). This comparison supported the distinct species status of *S. bealei* and provided a genomic reference for the species. In a subsequent range-wide study of the genus, Lin et al. (2022) combined mitochondrial *CytB* gene with 16 nuclear loci and recovered *S. bealei* as a single clade endemic to southeastern China, which they described as near-panmictic with low genetic diversity and little population structure.

Most recently, Lee et al. (2026) used genome-wide ddRADseq SNPs on 75 *S. bealei* individuals (from Fujian, two Hong Kong sites, and a captive colony). In line with Lin et al. (2022), they confirmed low genetic diversity in the species, but the higher resolution of genome-wide markers and population-level sampling allowed them to go further, recovering distinct geographic clusters with weak yet significant differentiation—including restricted gene flow between the two nearby Hong Kong populations and a captive colony of mixed, mostly hybrid origin.

Description. — *Sacalia bealei* is a small freshwater turtle with a mean shell size of 127.5 mm straight-line carapace length (SCL) in adult males and 139.4 mm in adult females (Lin et al. 2017). Maximum sizes recorded for males and females are 141 and 156 mm SCL, respectively (Pope 1935; Iverson and McCord 1992; TTWG 2025).The average body weight of male *S. bealei* is 268.2 g (n = 28), while that of females is 356.4 g (n = 40); the heaviest female recorded had a mass of 1,010.5 g (Lin / Hainan Normal University, unpubl. data). Females also exhibit a longer plastron, deeper carapace, and wider head (Lin et al. 2017).

The species is most easily identified by the presence of two pairs of prominent, black-centered light ocelli on the dorsum of the head; they are very conspicuous except when the head is partially or completely retracted. Generally, *S. bealei* has many small black dots on its head and the two pairs of eye-like spots are connected, with the anterior pair often being more obscure and posterior pair being brighter, especially in males (Lin et al. 2022).

The carapace is oval, moderately wide, slightly broader posteriorly than anteriorly, with a slight median ridge, especially in the young, but essentially unkeeled except possibly slightly towards the rear. In fully mature animals the shell is usually completely smooth, but shallow annular sculpturing may be evident in younger specimens. The shell margin is smooth or very slightly sinuous towards the rear. There is no nuchal notch, and the nuchal scute is small and very variable in shape, but typically the sides are posteriorly slightly divergent. The sulcus between the supracaudal scutes may be slightly elevated. The five vertebral scutes are broad, with unusually long sulci between elements in the series. The costo-peripheral sulcus line is almost even, or with very slight elevations at the points of contact with the intercostal sulci.



Figure 4. Adult female (*left*) and male (*right*) Beale's Eyed Turtle, *Sacalia bealei*, from China. Photos by Hai-Tao Shi.



Figure 5. Hatchling Beale's Eyed Turtle, *Sacalia bealei*, from Fujian, China. Photos by Liu Lin.

The plastron is large and wide, and the bridge is long. Anteriorly, the plastron is smoothly rounded or slightly truncated, and the anal notch may be obtuse and shallow or (rarely) rather deep and angled. The abdominals have the longest sulcus along the midline, and the gulars or the humerals the shortest. The axillary scutes are moderate, the inguinals very small.

The neck is rather long and the head narrow, strikingly flat-topped. The snout is short and truncated, and the upper jaw is strongly notched at the midline. The skin of the crown and the rear of the head is smooth and unbroken. The neck displays 5–7 longitudinal stripes, with the most prominent three stripes situated on the dorsal side. The female's stripes are yellow, whereas the male's turn red after sexual maturation. There is a strip of granular scales between the lower rear corner of the orbit and the tympanum. The forelimbs have a few very large scales, without intervening granules. The digits are fully webbed. The tail is noticeably elongate in juveniles, moderately long in adults.

The carapace is chocolate-brown in mature specimens, with a variable degree of black speckling that is most often concentrated anteriorly. The plastron is usually yellowish, with black spots in males or patches in females, but much fewer as compared to *S. quadriocellata*. Some individuals have a pure yellowish plastron without any spots or patches.

Neonates have a soft, reddish brown carapace with curled margins that gradually flatten after several days, an orange plastron and skin, and bright yellow stripes on the neck. Four bright-green eye-spots are obvious on the head, with the two spots on the same side linked together. A black dot can be seen in every eye-spot (Lin et al. 2018).

Distribution. — *Sacalia bealei* is endemic to southeastern China, including the provinces of Guangdong, Fujian, Jiangxi, Anhui, Hunan, and Guizhou, as well as Hong Kong (Lin et al. 2022; TTWG 2025). Recent surveys and sampling records indicate that *S. bealei* is concentrated in mountainous areas of southeastern China (Schilde 2004; Shi et al. 2008; Fong and Qiao 2010). In addition, there appear to be two isolated disjunct populations, one in Anhui and one near the border area between Hunan and Guizhou provinces (Lin et al. 2022; TTWG 2025). The reason for this apparent distribution gap is unclear, possibly due to insufficient sampling effort, but these disjunct populations may have been isolated by natural or anthropogenic factors during human population expansion (Lin et al. 2022). Further sampling efforts in the areas between the main



Figure 6. Hatchling Beale's Eyed Turtle, *Sacalia bealei*, at the Turtle Survival Center, South Carolina, USA, showing marked variation in plastral coloration and pattern. Photos by Cris Hagen.

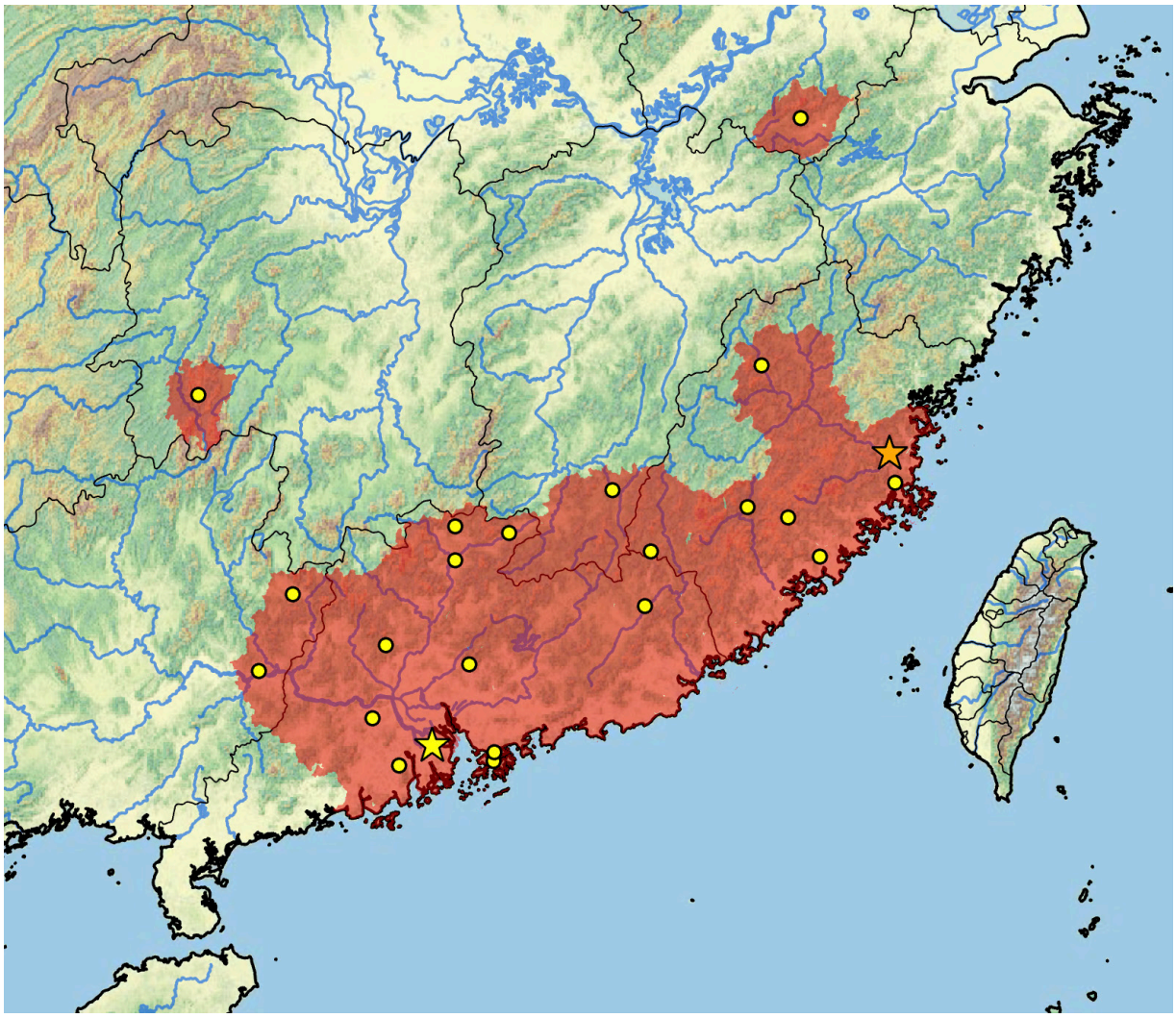


Figure 7. Estimated historical indigenous distribution of *Sacalia bealei* in China. Yellow dots = museum and current and historical occurrence records of presumed native populations based on literature and online records (TTWG 2025); yellow star = recently estimated type locality for *Cistuda bealei* Gray 1831 (TTWG 2025); orange star = previously estimated type locality for *Cistuda bealei* Gray 1831 (Iverson and McCord 1992). Colored shading = estimated historical indigenous range. Distribution is based on fine-scaled GIS-defined level 12 HUCs (hydrologic unit compartments) constructed around localities and then adding HUCs that connect point localities in the same watershed or physiographic region, and similar habitats and elevations as verified HUCs, based on TTWG (2025) and adjusted based on subsequent data (TTWG, in prep.) and from the authors. Map by Chelonian Research Foundation.

population and the disjunct ones are still required to elucidate this question.

Habitat and Ecology. — *Sacalia bealei* prefers primary tributary mountain streams at low altitudes (200–400 m). These mountain streams usually have high vegetation cover, with deep stream pools, abundant stone caves, fruit abundance, and high benthic species diversity and abundance. Seasonal variations in habitat use are evident, with breeding habitats characterized by lower woody plant density, thinner leaf litter, higher elevations, and increased stone cave availability (Hu et al. 2016; Yuan et al. 2025a).While mostly aquatic, the species occasionally rests or basks on exposed land above water (Luo et al. 2023).

Diet. — *Sacalia bealei* has a diverse diet, consisting of plant materials, fruits, insects, and occasionally carrion, reflecting its role in nutrient cycling within its ecosystem (Sung et al. 2021). Captive individuals readily accept commercial turtle feeds, but Fong et al. (2020) suggested that a diet including more fruits may better mimic a diet in the wild and enhance gut microbiota diversity, potentially improving reproductive success.

Behavior. — The species generally occupies a small home range. The linear home range size (LHR), home range area (HR), and core home range area (CHR) are about 185 m, 0.626 ha, and 0.089 ha, respectively, with no significant sex-based differences (Yuan et al. 2025b). However, during the nesting season, females exhibit significantly larger HR and CHR areas than males, reflecting increased movement for nesting purposes (Yuan et al. 2025b).

Reproduction. — The nesting period of female *S. bealei* in the wild is from the middle of April to the middle of



Figure 8. Preferred habitats of Beale's Eyed Turtle, *Sacalia bealei*, in mountain streams, Fujian, China. Photos by Liu Lin.

June, mainly in May (Hu 2016). Females lay one clutch per year, with an average clutch size of 2.2 eggs (1–3; *n* = 6), which they deposit in nests dug into the soil near water bodies (Lin et al. 2018). Females in captivity also lay clutches of 1–3 eggs (Hennig 2020; C. Hagen / Turtle Survival Alliance, unpubl. data). They prefer to nest and lay eggs on rainy days. Females tend to choose stream banks with low vegetation density, lower shrub height, and low herb density as nesting sites. Nests are well camouflaged by leaves and soil, making them difficult to find. The shape of nests is hemispherical, with a diameter of ca. 7.0–10.0 cm and depth of ca. 5.5–7.0 cm. Due to the relatively shallow depth, eggs are often half-buried by soil and then covered by leaves. In captivity in the USA, nests were 2.5–5.0 cm deep and eggs barely, if at all, covered by soil, or occasionally deposited at the base of plants (C. Hagen / Turtle Survival Alliance, unpubl. data).

The hard-shelled eggs are elongate, with an average length of 45.5 mm, width of 23.2 mm, and weight of 14.8 g (*n* = 13; Lin et al. 2018). Eggs in captivity had lengths from 38.9 to 52.0 mm, widths from 21.3 to 25.7 mm, and mass of 11.4 to 21.9 g (*n* = 80) (C. Hagen / Turtle Survival Alliance, unpubl. data). Gad (1994) described the ultrastructure of *S. bealei* eggshells. Relative clutch mass (clutch mass/gravid female mass) is estimated to be 9.9% (Iverson et al. 2025).



Figure 9. Nests of *Sacalia bealei*, Fujian, China. Surface leaves have been pulled to the side to expose the eggs. Photos by Qingru Hu.

No mating behavior of *S. bealei* has yet been observed in the wild; however, observations under captive conditions indicate that *S. bealei* exhibits mating activity from March to November, with relatively frequent mating activity occurring in March and April (accounting for approximately 75%) (Gong et al. 2017b).

The mean incubation period for eggs in the wild is 95 days (ca. 85–108 days) and the temperature range during incubation is 17.5–29.6°C (mean 25.1°C) (Lin et al. 2018). However, in captive environments, the incubation period is 70–91 days when incubated at 28 vs. 25°C, respectively (Schilde 2004; Hennig 2020). In captivity in the USA, when incubated at a constant temperature of 25.5ºC (78ºF), eggs hatched between 82 and 92 days. At a constant temperature of 27.8ºC (82ºF), eggs hatched between 70 and 78 days. At fluctuating temperatures (14 hours at 26.7ºC [80ºF] during the day and 10 hours at 23.3)C [74ºF] at night), eggs hatched between 79 and 89 days (C. Hagen / Turtle Survival Alliance, unpubl. data).

Hatchlings have a mean SCL of 40.1 mm (37–42 mm, $n = 7$], carapace width of 33.3 mm, carapace depth of 17.4 mm, plastron length of 31.6 mm, plastron width of 25.4 mm, and body weight of 9.7 g (8–12 g, $n = 7$] (Lin et al. 2018). Hatchlings in captivity ranged in weight from 7.8 to 12.9 g ($n = 41$) (C. Hagen / Turtle Survival Alliance, unpubl. data).

Population Status. — The species is currently extremely rare in the wild (Gong et al. 2017; Lin et al. 2018) as well as in the trade (van Dijk et al. 2000; Lin et al. 2022). Hu et al. (2016) applied cage-trapping methodology in Huboliao National Nature Reserve, Fujian Province, between 2014–2015, and found that the relative population density of *S. bealei* was 0.003/trap-day in this reserve. Fong et al. (2020) estimated the wild population in Hong Kong to be no more than 100 individuals.

Threats to Survival. — Poaching is the greatest threat to wild freshwater turtles in many parts of Asia (Lau and Shi 2000). The unusual head ocelli, small body size, and sexually dimorphic coloration make *Sacalia* turtles attractive in the pet market, while turtle farms and private collectors create continued demand for wild-caught founders and replacement stock. Traps used for poaching have been periodically uncovered in Fujian and Hong Kong, where *S. bealei* occurs. Evidence shows that illegal possession and harvesting from national protected areas still occurs in China (Hu 2016; Gong et al. 2017a). The illicit trade of *Sacalia* turtles remains prevalent, which often involves long-distance and cross-border transportation (Lin et al. 2022; Sung et al. 2025).

Legal and management gaps further aggravate these threats. In China, *S. bealei* and *S. quadriocellata* were added to the National Key Protected Wild Animal list in 2021, but protection is specified only for wild populations. Because wild-caught and captive-bred *Sacalia* individuals cannot be reliably distinguished by enforcement officers without origin documentation or molecular and isotope testing, this legal wording weakens practical enforcement (Sung et al. 2025). Existing farms and private holdings therefore require auditing to prevent laundering of wild-caught animals. Moreover, in 2022, China's conviction criteria on wildlife crime changed from the numbers of individual animals involved in a given offense to their monetary value. The switch to monetary conviction standards has led to marked increases in convictable individual numbers, and has resulted in a tangible weakening of the legal protection of wildlife, particularly for species vulnerable to wildlife crime (Hu et al. 2025).

Forest fragmentation and human encroachment upon the species' habitat constitute progressively increasing threats to *S. bealei* populations (Yuan et al. 2025). In addition, genetic contamination is another threat because it is a common practice in China to mix different geographical populations, and even different species of *Sacalia* turtles, which can lead to genetic contamination of *ex-situ* populations, jeopardizing their suitability for future reintroductions (Lin et al. 2022; Lee et al. 2026). Additionally, genetic pollution from released exotic turtle species poses a risk, as hybrids between Beale's

Eyed Turtles and *Cyclemys* sp. have been discovered in the wild in Hong Kong (Sung et al. 2021)

Conservation Measures Taken. — *Sacalia bealei* has been listed on the IUCN Red List since 1996, first as Vulnerable (VU) (TFTSG *in* Baillie and Groombridge 1996), then uplisted in 2000 to Endangered (EN A1d+2d) (ATTWG 2000), and more recently provisionally further uplisted to Critically Endangered in 2011 by the IUCN SSC Tortoise and Freshwater Turtle Specialist Group (Rhodin et al. 2018; TTWG 2025). The species urgently needs to be officially reassessed and updated for the IUCN Red List.

The species is also listed as Critically Endangered in the Red List of China Vertebrates (Ministry of Ecology and Environment and Chinese Academy of Sciences 2023), and Class II State Key Protected Wild Animals of China (2021, but only for wild populations) .

In-situ conservation measures for this species are still very few. Its habitats in Hong Kong are mainly located and protected in country parks that are not listed here to protect the wild populations. In June 2024, a conservation planning workshop was convened by Ocean Park, Hong Kong, to develop a coordinated and integrated conservation strategy for this and other Chinese species (CPSG and Ocean Park 2025). The strategy combines *in-situ* and *ex-situ* approaches and is structured for adaptive implementation to safeguard the species' future.

Conservation Measures Proposed. —The inclusion of the species in long-term ecological and monitoring studies is crucial for monitoring its population status and to respond to potential worsening threats and to further develop its conservation needs. Law enforcement should be strictly implemented to continuously and more successfully interdict illegal wildlife trade. Regulation of the turtle farming industry needs to be tightened, with improved qualification management and reform of the current lax regulatory system and arbitrary licensing practices. Furthermore, the existing Wildlife Protection Law should be amended to repeal the provision that protects only wild populations for numerous species, such as *Sacalia* turtles, and the unreasonable practice of using the total case value as the standard for conviction should be corrected. At the same time, conservation efforts for natural habitats must be further strengthened.

Captive Husbandry. — *Ex-situ* breeding programs have been conducted in Guangdong, Hainan, Hong Kong, and the USA. Captive individuals readily accept commercial turtle feeds, but Fong et al. (2020) suggested that a diet including more fruits may better mimic a diet in the wild and enhance gut microbiota diversity, potentially improving reproductive success. The diversity of the gut microbiota in wild individuals compared to those in captivity indicates the importance of dietary variety in maintaining health and fertility (Fong et al. 2020). In captivity, *S. bealei* exhibits diurnal activity with a bimodal circadian rhythm, showing distinct activity peaks at 0500–0900 and 1600–1900 hrs. There are also significant differences in seasonal activity patterns, with shorter active durations in spring, autumn, and winter, while summer activity is the longest, lasting up to seven hours daily (Zhang 2016).

A total of 14 kinds of postures and 73 acts by *S. bealei* were recorded and distinguished to build an ethogram and PAE (Posture-Act-Environment) coding system to help understand the relationships between ecological function, behavior and environment in captivity (Luo et al. 2023).

Li et al. (2026) showed that plasma analyses of captive *S. bealei* demonstrated seasonal and sexual variations in testosterone, 17β-estradiol, and progesterone. Both sexes display pronounced seasonal reproductive cycles. Males showed bimodal testosterone peaks in May and August, suggesting a dissociated reproductive strategy featuring "postnuptial" (= postbreeding) spermatogenesis. Females had a single spring peak of 17β-estradiol associated with annual Type I vitellogenesis. Their testosterone peaked in April and August corresponding to ovarian growth and recrudescence, respectively, while progesterone peaked in June, coinciding with ovulation.

At the Turtle Survival Alliance's Turtle Survival Center, located in Cross, South Carolina, USA, an adult group of wild-origin and captive-bred *S. bealei* live outdoors year-round under natural climate conditions (C. Hagen / Turtle Survival Alliance, unpubl. data). Each adult is housed individually most of the year and only paired for breeding encounters for one or two weeks in the fall (September or October) and in the spring (March or April). Nesting occurred primarily in May, but occasionally in June. Size and incubation data on eggs (n = 80) and hatchlings (n = 41) are presented in the text under Reproduction.

Current Research. — Currently, field investigations on *S. bealei* have and are being carried out in Fujian and Hong Kong, China. Recent research has focused on the species' natural habitat, population density, dietary composition, home range, microhabitat preferences, and foraging behavior (Hu et al. 2016; Lin et al. 2017, 2018; Sung et al. 2021; Yuan et al. 2025a,b; Chan et al. 2026). Simultaneously, the primary threats to its survival, such as illegal hunting, the pet trade, and habitat degradation, have been identified. Nevertheless, long-term monitoring research and in-situ conservation initiatives for this species remain insufficient, and are urgently needed.

Preliminary studies have also been performed recently on the captive breeding and rearing of *S. bealei*, resulting in fundamental data regarding its circadian rhythm, seasonal rhythm, reproductive behavior, diet, gut microbial community, stable isotope analysis, and annual gonadal hormone fluctuation (Zhang 2016; Gong et al. 2017b; Fong et al. 2020; Sung et al. 2025; Li et al. 2026). In addition, recent research efforts have concentrated on the phylogeny, taxonomy, and genetic structure of the genus

Sacalia (Shi et al. 2008; Li et al. 2014; Lin et al. 2020, 2022; Lee et al. 2026).

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Literature Cited

ATTWG [Asian Turtle Trade Working Group]. 2000. *Sacalia bealei*. The IUCN Red List of Threatened Species 2000: e.T19796A9016239.

Baillie, J. and Groombridge, B. 1996. The 1996 IUCN Red List of Threatened Animals. Gland, Switzerland: IUCN, 368 pp.

Bickham, J.W. 1975. A cytosystematic study of turtles in the genera *Clemmys, Mauremys* and *Sacalia*. Herpetologica 31:198–204.

Bickham, J.W. and Baker, R.J. 1976. Chromosome homology and evolution of emydid turtles. Chromosoma 54:201–219.

Bickham, J.W. and Carr, J.L. 1983. Taxonomy and phylogeny of the higher categories of cryptodiran turtles based on a cladistic analysis of chromosomal data. Copeia 1983:918–932.

Boulenger, G.A. 1889. Catalogue of the Chelonians, Rhynchocephalians, and Crocodiles in the British Museum (Natural History). London: Trustees of the Museum, 311 pp.

Carr, J.L. and Bickham, J.W. 1986. Phylogenetic implications of karyotypic variation in the Batagurinae (Testudines: Emydidae). Genetica 70:89–106.

Chan W.S., Fong J.J., Bonebrake T., and Sung, Y.H. 2026. Movement and space use patterns of the Beale's Eyed Turtle (*Sacalia bealei*) suggest sensitivity to environmental changes and poaching. Wildlife Letters 0:e70037.

CPSG [Conservation Planning Specialist Group] and Ocean Park. 2025. In: Kwok, A., Bamford, P., Rocha, F.L., and Agriculture, Fisheries and Conservation Department (Eds.). Integrated Conservation Strategy for the Beale's Eyed Turtle in Hong Kong – 2025–2030. CPSG: Hong Kong, 50 pp. https://www.cpsg.org/sites/default/files/2026-02/Integrated%20Conservation%20Strategy%20for%20the%20Beale%27s%20Eyed%20Turtle.pdf.

Duméril, A.M.C. and Bibron, G. 1835. Erpétologie Générale ou Histoire Naturelle Complète des Reptiles. Tome Second. Paris: Roret, 680 pp.

Fleming, J. 1822. The Philosophy of Zoology; or a General View of the Structure, Functions, and Classification of Animals. Vol. II. Edinburgh: Archibald Constable and Co., 618 pp.

Fong, J.J. and Qiao, G.X. 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, J.J., Sung, Y.H., and Ding, L. 2020. Comparative analysis of the fecal microbiota of wild and captive Beale's Eyed Turtle (*Sacalia bealei*) by 16S rRNA gene sequencing. Frontiers in Microbiology 11:2732.

Fritz, U. and Havaš, P. 2007. Checklist of chelonians of the world. Vertebrate Zoology 57:149–368.

Gad, J. 1994. Die Ultrastruktur der Eischalen von *Geoemyda spengleri*, *Indotestudo elongata* und *Sacalia bealei* (Testudines). Salamandra 30:277–280.

Gong, S.P., Shi, H.T., Jiang, A.W., Fong, J.J., Gaillard, D., and Wang, J.C. 2017a. Disappearance of endangered turtles within China's nature reserves. Current Biology 27(5):R170–R171.

Gong, S.P., Zhong, X.J., Tao, J., Chen, Y., Deng, J.M., Ge, Y., and Wei, Y.F. 2017b. Preliminary report on the captive breeding of Beale's Eyed Turtle (*Sacalia bealei*), an endangered species endemic to China. Chinese Journal of Zoology 52(2):359–360. (in Chinese).

Gray, J.E. 1831. Synopsis Reptilium; or Short Descriptions of the Species of Reptiles. Part I.—Cataphracta. Tortoises, Crocodiles, and Enaliosaurians. London: Treuttel, Wurz, and Co., 85 pp.

Gray, J.E. 1834. Characters of several new species of freshwater tortoises (*Emys*) from India and China. Proceedings of the Zoological Society of London 1834(2):53–54.

Gray, J.E. 1870. Supplement to the Catalogue of Shield Reptiles in the Collection of the British Museum. Part I. Testudinata (Tortoises). London: British Museum, 120 pp.

Günther, A.C.L.G. 1864. The Reptiles of British India. London: Ray Society, Robert Hardwicke, 452 pp.

Hennig, A. 2020. Incubating Chelonian Eggs. Frankfurt, Germany: Edition Chimaira, 253 pp.

Hu, Q.R. 2016. Ecological research of the Beal's Eyed Turtle (*Sacalia bealei*) at Huboliao National Nature Reserve, Fujian, China. Master's Thesis, Hainan Normal University. (in Chinese).

Hu, Q.R., Yang, J.B., Lin, L., Xiao, F.R., Wang, J.C., and Shi H.T. 2016. Habitat selection factors of the Beal's Eyed Turtle (*Sacalia bealei*) at Huboliao National Nature Reserve, Fujian Province. Chinese Journal of Zoology 51(4):517–528. (in Chinese).

Hu, R., Liu, S., Xiao, L., Zhu, Z., Dou, Y., Zhang, S., Ren, X., Hua, F., and Lu, Z. 2025.Toward science-based conviction criteria to deter wildlife crime. Science 390:993–995.

Iverson, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately printed, 363 pp.

Iverson, J.B. 2022. A review of chelonian type specimens (Order Testudines). Megataxa 007(1):1–85.

Iverson, J.B. and McCord, W.P. 1992. A new Chinese Eyed Turtle of the genus *Sacalia* (Batagurinae: Testudines). Proceedings of the Biological Society of Washington 105:426–432.

Iverson, J.B., Ennen, J., and Lovich, J. 2025. Life-history and ecology data for the turtles of the world. Chelonian Conservation and Biology 24:136–141.

Lau, M. and Shi, H.T. 2000. Conservation and trade of terrestrial and freshwater turtles and tortoises in the People's Republic of China. In: van Dijk P.P., Stuart B.L., and Rhodin A.G.J. (Eds.). Asian Turtle Trade: Proceedings of a Workshop on Conservation and Trade of Freshwater Turtles and Tortoises in Asia. Chelonian Research Monographs 2:30–38.

Lee, W.H., Sung, Y.H., Low, B.W., and Fong, J.J. 2026. Population genomics identifies genetic structure and admixture in the endangered Beale's Eyed Turtle (*Sacalia bealei*), and implications for aquatic ecology and ex situ breeding. Marine Life Science and Technology 8:446–458.

Li, W.Y., Gong, S.P., and Hua, L. (2014). Isolation and characterization of microsatellite markers from the Chinese

endemic species, Beal's-eyed turtle (*Sacalia bealei*). Conservation Genetic Resources 6:437–438.

Lin, L., Gaillard, D., Hu, Q.R., Yang, J.B., Chen, Z.D., Zhou, F.Y., Xiao, F.R., and Shi, H.T. 2017. Sexual dimorphism in body size and shape of Beal's Eyed Turtle (*Sacalia bealei*). Chelonian Conservation and Biology 16:180–184.

Lin, L., Hu, Q.R., Fong, J.J., Yang, J.B., Chen, Z.D., Wang, J.C., Xiao, F.R., and Shi, H.T. 2018. Reproductive ecology of the endangered Beal's-Eyed Turtle, *Sacalia bealei*. PeerJ 6:e4997.

Lin, L., Chen, H.Q., Wang, Z., Gaillard, D., Zhai, X.F., and Shi, H.T. 2020. Characterization and comparison of mitogenomes of three 'eyed' turtles *Sacalia* spp. Mitochondrial DNA Part B 5(3):3206–3208.

Lin, L., Chen, H.Q., Gaillard, D., Shi, H.T., and Luo, S.J. 2022. Phylogeography of the endangered "eyed" turtles (genus *Sacalia*) and the discovery of a lineage derived from natural interspecific hybridization. Ecology and Evolution12:e9545.

Luo, M.L., Hu, L.J., Shi, H.T., and Lin, L. 2023. Ethogram and PAE coding system of captive Beale's Eyed Turtle (*Sacalia bealei*). Sichuan Journal of Zoology 42:294–302. (in Chinese).

McDowell, S.B. 1964. Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae. Proceedings of the Zoological Society of London 143:239–279.

Merkle, D.A. 1975. A taxonomic analysis of the *Clemmys* complex (Reptilia: Testudines) utilizing starch gel electrophoresis. Herpetologica 31:162–166.

Ministry of Ecology and Environment and Chinese Academy of Sciences. 2023. Red List of China's Biodiversity – Vertebrates (2020). Beijing: Ministry of Ecology and Environment. https://www.mee.gov.cn/xxgk2018/xxgk/xxgk01/202305/t20230522_1030745.html.

National Forestry and Grassland Administration of China and Ministry of Agriculture and Rural Affairs of China. 2021. List of State Key Protected Wild Animals (2021). https://www.forestry.gov.cn/c/www/gkzfwj/546057.jhtml.

Pope, C.H. 1935. The Reptiles of China. New York: American Museum of Natural History, Natural History of Central Asia, Vol. 10, 604 pp.

Pritchard, P.C.H. 1979. Encyclopedia of Turtles. Neptune, NJ: TFH Publications, 895 pp.

Rhodin, A.G.J., Stanford, C.B., van Dijk, P.P., Eisemberg, C., Luiselli, L., Mittermeier, R.A., Hudson, R., Horne, B.D., Goode, E.V., Kuchling, G., Walde, A., Baard, E.H.W., Berry, K.H., Bertolero, A., Blanck, T.E.G., Bour, R., Buhlmann, K.A., Cayot, L.J., Collett, S., Currylow, A., Das, I., Diagne, T., Ennen, J.R., Forero-Medina, G., Frankel, M.G., Fritz, U., García, G., Gibbons, J.W., Gibbons, P.M., Gong, S., Guntoro, J., Hofmeyr, M.D., Iverson, J.B., Kiester, A.R., Lau, M., Lawson, D.P., Lovich, J.E., Moll, E.O., Páez, V.P., Palomo-Ramos, R., Platt, K., Platt, S.G., Pritchard, P.C.H., Quinn, H.R., Rahman, S.C., Randrianjafizanaka, S.T., Schaffer, J., Selman, W., Shaffer, H.B., Sharma, D.S.K., Shi, H., Singh, S., Spencer, R., Stannard, K., Sutcliffe, S., Thomson, S., and Vogt, R.C. 2018b. Global conservation status of turtles and tortoises (Order Testudines). Chelonian Conservation and Biology 17(2):135–161.

Schilde, M. 2004. Asiatische Sumpfschildkröte. Die Familie Geoemydidae in Südostasien, China und Japan. Natur und Tier Verlag, 189 pp.

Shi, H.T., Fong, J J., Parham, J.F., Pang, J., Wang, J.C., Hong, M.L., and Zhang, Y.P. 2008. Mitochondrial variation of the "eyed" turtles (*Sacalia*) based on known-locality and trade specimens. Molecular Phylogenetic Evolution 49:1025–1029.

Smith, M.A. 1931. The Fauna of British India, including Ceylon and Burma. Reptilia and Amphibia. Vol. I. Loricata, Testudines. London: Taylor and Francis, 185 pp.

Sung, Y., Liew, J.H., Chan, H K., Lee, W., Wong, B.H., Dingle, C., Karraker, N.E., Spencer, R., and Fong, J.J. 2021. Assessing the diet of the endangered Beale's Eyed Turtle (*Sacalia bealei*) using faecal content and stable isotope analyses: Implications for conservation. Aquatic Conservation 31:2804–2813.

Sung, Y.H., Chong, K.Y.W., Lee, W.H., Lau, M.W.N., Lau, A., Wong, P., Dingle, C., Yeung, H.Y., and Fong, J.J. 2021. Species list and distribution of non-native freshwater turtles in Hong Kong. BioInvasions Records 10:647–662.

Sung, Y.H., Liew, J.H., Chan, W.S., Fok, A.W.L., Leung, J., Wong, H.F., Baker, D.M., Bonebrake, T.C., Dingle, C., Dudgeon, D., Karraker, N.E., Lau, A., Colon, V.A., Magouras, I., Ades, G., Crow, P., Rose-Jeffreys, L., Spencer, R., and Fong, J.J. 2025. Stable isotope analysis successfully identifies wild-caught individuals of threatened Asian freshwater turtles in illegal trade. Global Ecology and Conservation 64:e03947.

TTWG [Turtle Taxonomy Working Group: Bickham, J.W., Iverson, J.B., Parham, J.F., Philippen, H.D., Rhodin, A.G.J., Shaffer, H.B., Spinks, P.Q., and van Dijk, P.P.]. 2007. An annotated list of modern turtle terminal taxa with comments on areas of taxonomic instability and recent change. Chelonian Research Monographs 4:173–199.

TTWG [Turtle Taxonomy Working Group: Rhodin, A.G.J., Iverson, J.B., Fritz, U., Gallego-García, N., Georges, A., Shaffer, H.B., and van Dijk, P.P.]. 2025. Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status (10th Ed.). Chelonian Research Monographs 10:1–575.

van Dijk, P.P., Stuart, B.L., and Rhodin, A.G.J. (Eds.). 2000. Asian Turtle Trade: Proceedings of a Workshop on Conservation and Trade of Freshwater Turtles and Tortoises in Asia. Chelonian Research Monographs 2:1–164.

Wermuth, H. and Mertens, R. 1977. Liste der rezenten Amphibien und Reptilien: Testudines, Crocodylia, Rhynchocephalia. Tierreich 100:1–174.

Ye, X. 1994. Fossil and Recent Turtles of China. Beijing: Science Press, 112 pp.

Yuan, X.Y., Hu, Q.R., Bu, R.P., Yang, J.B., Lin, L., and Shi, H.T. 2025a. Microhabitat selection by the Beale's eyed turtle (*Sacalia bealei*) and conservation implications. Global Ecology and Conservation 60:e03607.

Yuan, X.Y., Hu, Q.R., Bu, R.P., Yang, J.B., Lin, L., and Shi, H.T. 2025b. Home range of the endangered Beale's Eyed Turtle (*Sacalia bealei*) and the implications for conservation. Ecology and Evolution 15:e71520.

Zhang, Q. 2016. Activity rhythm and time allocation study of captive Beale's EyedTurtle *Sacalia bealei*. Bachelor's Thesis, Hainan Normal University. (in Chinese).

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