Assessing habitat associations of critically endangered big-headed turtles to support grassroots river conservation

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Abstract

1. Modern biodiversity conservation relies largely on state-run protected areas and environmental regulations, whereas grassroots initiatives to protect species and ecosystems are underrecognized and receive limited scientific support.

2. We studied critically endangered big-headed turtles (*Platysternon megacephalum*) to support a grassroots river conservation initiative in Southeast Asia's rapidly changing Mekong region. The study area was a montane watershed in northern Thailand, including an ambiguous protected area boundary, national forest reserve lands used and cultivated by local people, and a state-planned (currently suspended) large dam site. Residents have warned that the dam project could threaten the local wild-caught fishery and other freshwater biodiversity, including big-headed turtles, which have been encountered by fishers.

3. We aimed to provide the initiative's leading village council and government-mandated authorities with current information on the turtle population to support species and ecosystem conservation. We trapped for turtles at 250 river and stream pools (494 trap-nights) above the planned dam site in 2024–2025 and assessed how species occurrence and observed body size varied with different pool features.

4. We captured 24 individual turtles (seven juveniles, four subadults, 13 adults) in 22 widely distributed river and stream pools inside and outside of the protected area, as close as ~400 meters to the planned dam reservoir. Species occurrence increased with pool width, depth, and boulder substrate (refugia). Body size was smaller in streams than in the river and correspondingly increased with water pH and decreased with forest canopy closure, possibly reflecting favorable conditions for nesting and/or juvenile survival in stream habitats.

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5. *Practical implication*. Dam construction could diminish a breeding population of big-headed turtles by inundating parts of some turtles' home ranges, blocking species dispersal, and/or disrupting river flow regimes and food webs. Hazardous irrigation (e.g. diversion of freshwater from turtle nesting areas) and fishing practices (e.g. electrofishing, use of explosives) observed by researchers inside and outside of the protected area could also threaten the turtle population. Amidst institutional fragmentation and ongoing land-use intensification and environmental degradation, grassroots initiatives to halt undesirable land development projects and improve local environmental management have key roles in protecting threatened species.

Keywords: ambiguous lands, conservation action, dams, development, ecology, infrastructure, elusive species, endangered species, grassroots conservation, wildlife

INTRODUCTION

Perpetual declines in global biodiversity have illuminated the limitations of modern protected areas (e.g. national parks, wildlife reserves) and related environmental regulations (e.g. legal protection of species) in stabilizing the ongoing mass extinction event (Laurance et al. 2012, Geldmann et al. 2019, Herse et al. 2024). These limitations are particularly evident in the plight of turtles, which are now among the most imperiled vertebrates on Earth due to widespread habitat degradation and overconsumption by people (Lovich et al. 2018, Stanford et al. 2020). Although state-run protected areas and restrictions on hunting and wildlife markets have helped to conserve some turtles in some places (van Dijk et al. 2000, Le 2007, Castello et al. 2013), continued habitat degradation (Dudgeon 2019, Bárcenas-García et al. 2022) and exploitation (Nijman & Shepherd 2015, Luiselli

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et al. 2016, Sung et al. 2021), including inside some protected areas (Gong et al. 2017, Thieme et al. 2020, Hoang et al. 2021), indicate that alternative actions are needed to protect extant species.

Another way of protecting threatened species is by supporting community-led or grassroots environmental initiatives. Grassroots initiatives to protect local lands, livelihoods, and common pool resources are often situated at the interface between primary habitats (e.g. forests, grasslands, wetlands, rivers) and environmentally destructive industrial development projects (e.g. logging, mining, urbanization, agricultural intensification), and thus are typically important for biodiversity conservation (Ghai & Vivian 1995, Perfecto et al. 2019, Walter et al. 2026). For instance, whereas the rapid build-out of large dams across the globe has severely degraded freshwater ecosystems and biodiversity (Lees et al. 2016, Dudgeon 2019, Sor et al. 2023), including turtle populations (Moll and Moll 2004, Bárcenas-García et al. 2022), grassroots initiatives to critically appraise and halt undesirable dam projects have helped to limit potential degradation (Hoogesteger et al. 2023, Vos 2024). Such initiatives are often constrained by various factors, however, including restricted decision-making rights and limited capacity to conduct environmental impact assessments independently of state and private interests (Aguilar-Støen & Hirsch 2015, Arpornsilp 2025).

Here we present the results of a study we established to assist a local community in Phayao Province, northern Thailand, in their efforts to protect a montane riverine ecosystem and aquatic biodiversity, including nationally 'endangered' and globally 'critically endangered' big-headed turtles (*Platysternon megacephalum*) (ONEP 2017, Fong et al. 2021), from a state-planned large dam project, the "Mae Lao Reservoir" (Figs. 1, 2; Supporting Information, Fig. S1; Chiang Mai News 2021, RID et al. 2021). The Mae Lao Reservoir project would involve constructing a 61-m tall, 395-m wide retention dam across the Mae Lao River, ~500 m upriver of the village Ban Khanaeng (Figs. 1, 2), for the stated purpose of mitigating dry-season water shortages and rainy-

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season flooding downriver (Fig. S1). The dam would permanently flood a ~2-km reach of the river and parts of several streams (Figs. 1, 2). Residents of Ban Khanaeng and neighboring villages have contended that existing weirs are sufficient for irrigation and flood control (Transborder News 2021a, b). Residents have also stressed that the dam would threaten village safety, inundate farmlands and the locally recognized guardian spirit of the village weir, and destroy or degrade the local wild-caught fishery. Moreover, residents have warned that the dam could threaten other aquatic biodiversity such as big-headed turtles in the river and its stream tributaries (Living River Association 2023), which originate nearby from inside Tham Sakoen National Park (Fig. 1).

Concerned community members have been limited in their ability to critically appraise or halt the Mae Lao Reservoir because the planned project site is on national forest reserve lands, where local farmers hold usufruct rights to occupy and cultivate state-owned lands under Thai law but lack full land titles or tenure security (Sato 2000, Woods et al. 2011). Concerned residents have opposed dam construction through a subdistrict-level referendum (six of seven participating villages voted against the dam), formal appeals to the district government, and interventions to prevent private pre-development consultants from conducting a preliminary environmental impact assessment (Chiang Mai News 2021, Transborder News 2021a, b), which apparently would not have involved ecological surveys (Fig. S1). The Thai government subsequently suspended the project, but representatives of the Royal Irrigation Department (RID, the state authority in inland water management) have reportedly told residents that construction could still occur eventually (Ban Khanaeng village council, M.R. Herse, personal communication, May 2022).

Besides concerns about the Mae Lao Reservoir, some community leaders in Ban Khanaeng have expressed a more general interest in turtle conservation and welcomed suggestions from researchers for improving local watershed management toward that end (e.g. village head, M.R.

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Herse, N. Khuntong, personal communication, October 2023). Local fishers have reported seeing big-headed turtles in the river and some streams periodically over their lifetimes, including in recent years (Living River Association 2023). However, detailed information on species distribution and habitat use in the watershed does not exist. Indeed, published information on the distribution and ecology of big-headed turtles in Southeast Asia is currently limited to low-resolution encounter data (Pipatsawasdikul et al. 2010, Chaikaew et al. 2025, TTWG 2025) and observations of nine radio-marked individuals in a wildlife sanctuary in Chiang Mai Province, Thailand (Pipatsawasdikul 2009). Information on local distributions and habitat associations of big-headed turtles could be particularly useful for protecting extant populations from ongoing land development and habitat degradation in the region (Ingalls et al. 2018, Struebig et al. 2025).

Our main goal was to provide Ban Khanaeng's village council and government-mandated authorities from Thailand's Department of Fisheries (DOF, the state authority in fishery and freshwater biodiversity management) and Department of National Parks, Wildlife and Plant Conservation (DNP, the state authority in protected area management) with current information on the Mae Lao River turtle population to support species conservation and habitat management. Thus, we trapped for turtles at river and stream pools in 2024–2025 and assessed the spatial distribution of captured turtles relative to the planned dam site and other potentially vulnerable habitats, including an irrigated stream and popular fishing areas. We also assessed the relative effects of different pool features on species occurrence and observed body size to better understand local habitat needs of turtles (Sung et al. 2015a). Finally, we summarized turtle body sizes to elucidate the population's status and check for possible demographic evidence of targeted hunting by people. For instance, if the population has been targeted recently, we expected to find mostly juveniles and few large adults (Sung et al. 2013), or no turtles. Based on our results, we outline

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threats to the population and explore potential strategies for conservation. In the final section, we discuss the role of grassroots conservation initiatives in stabilizing regional and global biodiversity declines in the context of institutional fragmentation and ongoing land-use intensification.

METHODS

Study species

The big-headed turtle (*P. megacephalum*) is the sole member of the monotypic family Platysternidae. In recent years, scientists have typically classified big-headed turtles into three taxa: *P. m. megacephalum* in southcentral China; *P. m. shiui* in Hainan Island/Province, China, and northeast Vietnam; and *P. m. peguense* in Yunnan Province, China, and parts of Cambodia, Lao People's Democratic Republic (PDR), Myanmar (Burma), Thailand, and Vietnam (TTWG 2025). Some biologists have posited that the taxa *megacephalum*, *peguense*, and "*baiseensis*", a previously undescribed lineage in Guangxi Province, China, are distinct species with divergent evolutionary histories (Gong et al. 2023, Liang et al. 2025), whereas some other biologists have contended that taxonomic revision is currently not warranted (TTWG 2025: p. 435). In lieu of a consensus, we follow the existing classification.

Big-headed turtles inhabit rocky mountain rivers and streams characterized by cool clear running water and intermittent waterfalls, pools, and heaps of boulders. The species is mostly aquatic, nocturnal, and elusive, usually hidden underwater beneath rock piles, logs, or leaf litter (Sung et al. 2015a). However, adults are remarkably capable climbers. Space use is typically sedentary within seasons (Sung et al. 2015a), but individuals sometimes cover long distances (> 500 m) across seasons (Pipatsawasdikul 2009) or following translocation (Xiao et al. 2021). In Thailand, the species has been documented between 430 and 1350 m above sea level (MASL)

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(Pipatsawasdikul et al. 2010). Diet consists of plant matter (e.g. fruits) and animals (e.g. insects, mollusks, crabs, fish, frogs) (Sung et al. 2016). Nesting occurs in leaf litter near river or stream edges during rainy seasons (May–October; Pipatsawasdikul 2009, Sung et al. 2014). Mean age to maturation is approximately 8 and 13 years for females and males, respectively (Sung et al. 2015b).

Concentrated space use in pools combined with delayed maturity makes big-headed turtle populations both vulnerable and sensitive to targeted exploitation and can explain population declines in many otherwise suitable habitats (van Dijk et al. 2000, Gong et al. 2006, Sung et al. 2013, Hoang et al. 2021). Habitat degradation from deforestation, damming of rivers, and pollution has likely also contributed to population declines (Lau and Haitao 2000, Pipatsawasdikul et al. 2010). The metapopulation status of big-headed turtles in Thailand is unknown (CITES 2013). However, the species has been recorded in more than 20 localities and all but one northern province since 2006 (Pipatsawasdikul et al. 2010, Chaikaew et al. 2025), indicating that this region could be one of the last strongholds for extant populations.

Study area

The study area was the upper Mae Lao River watershed in between the planned dam site and the river's headwaters inside Tham Sakoen National Park (Fig. 1). The Mae Lao River is a tributary of the Ing River, which feeds into the Mekong River at the Thailand-Lao PDR border. The climate is tropical and marked by monsoonal rains in May–October, winter in November–January, and a hot dry season in February–April (Chaiwino et al. 2025). More than 20 streams feed directly into the upper Mae Lao River (Fig. 1). Water runs in the river year-round at varying levels, whereas streams retract or dry up entirely during the height of the dry season. The areas we studied ranged in elevation from about 630 to 1220 MASL (Table S1).

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Upper areas of the watershed were officially incorporated into Tham Sakoen National Park in 2016 (DNP 2026). Local land cover inside the park comprises mostly secondary mixed deciduous and hill evergreen forest (Gardner et al. 2007). Some of these lands may have been logged during the nineteenth and/or twentieth centuries (Delang 2005). Two Hmong communities also lived along the present-day park boundary during the late twentieth century (RTSD 1993) and used surrounding hills for swidden cultivation, before being relocated by the Thai government. A small group of Hmong now live beside the park, where they manage a local DNP reforestation program and tree nursery.

At least one spring-fed stream inside the park has been irrigated by residents (primarily Khon Mueang, i.e. northern Thai) of Ban Khanaeng for agricultural and household use outside the park via an extensive network of polyvinyl chloride (PVC) tubes (Fig. 2). Ban Khanaeng comprises around 112 households and 350 people (village head, M.R. Herse, N. Khuntong, November 2025, personal communication). Land cover outside the park consists mostly of cash crops (e.g. rubber, coffee, corn, ginger, durian) and rice, whereas strips of secondary forest exist in some steep and rocky riparian areas. These lands outside the park are legally owned by the Thai state, classified as forest reserve irrespective of forest cover, and administered by the Royal Forest Department (RFD, the state authority in forestry management) (Open Development Thailand 2020).

Fishing occurs in most of the river and some streams, particularly in easily accessible areas nearer to the village during winter and dry seasons. Fishing has involved the use of temporary stone weirs and baskets, hand-woven or silicon-mesh funnel traps, suspended nylon-multifilament nets, spears, electricity, and small explosives (Fig. 2). A customary fishing exclusion area spans ~500 m of the river between the village and the local weir (the planned dam site) to protect spawning grounds and limit potential overfishing (Living River Association 2023). Hunting of

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landfowl (Galliformes spp.) and mammals (e.g. wild boar [*Sus scrofa*], barking deer [*Muntiacus muntjak*], Malayan porcupine [*Hystrix brachyura*]) by some residents, laborers, and visitors also occurs in forested and riparian areas inside and outside the park. Some hunters from Ban Khanaeng have described consuming big-headed turtles in the past, whereas others have suggested that doing so could bring bad luck (Living River Association 2023: p. 25). Several hunters have said that they are not aware of anyone from Ban Khanaeng consuming turtles in recent years. However, some fishers have reported capturing turtles in traps incidentally and releasing them alive.

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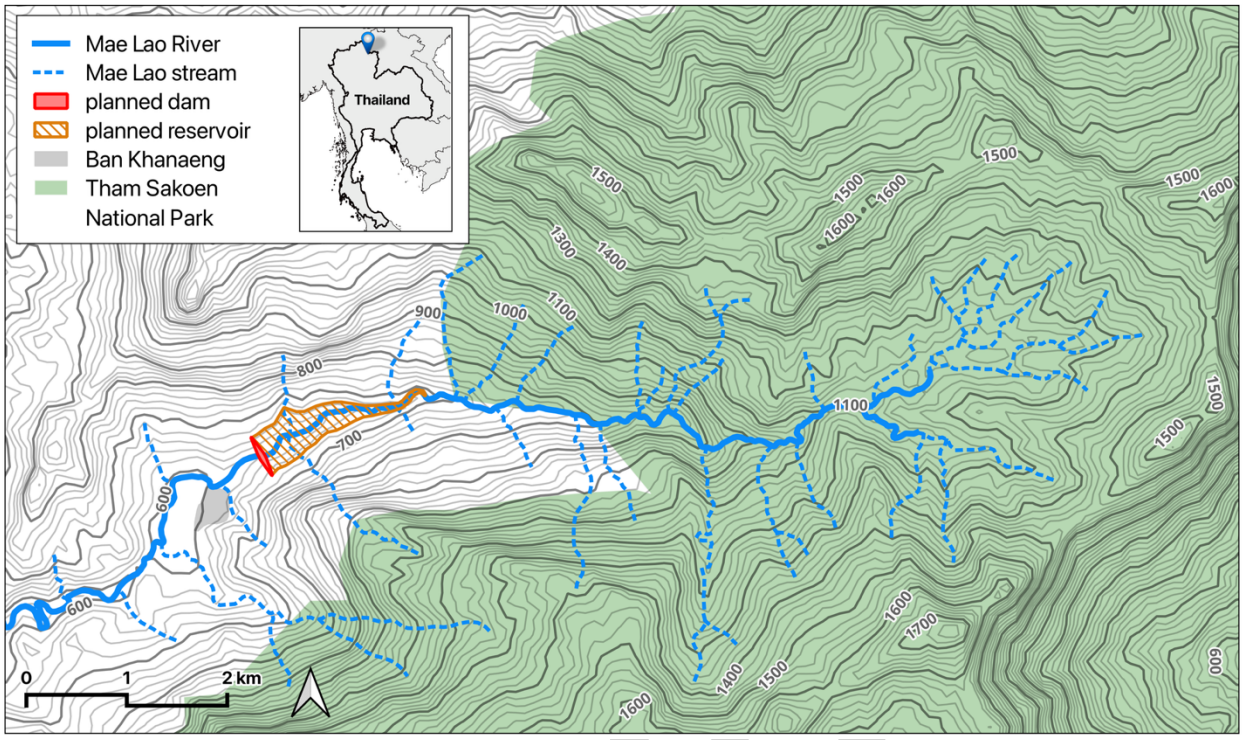


Figure 1. Upper Mae Lao River watershed and planned dam site in Phayao Province, Thailand. Locations of trap sites and turtle captures are excluded to protect the population from potential exploitation. Grey lines are elevation contours (numbers indicate meters above sea level). The first author obtained national park land cover data as part of a separate study (Herse et al. 2024). We drew planned dam and reservoir locations following an official dam project map (see Fig. S1-2), and river and stream locations following Google satellite imagery, topographic maps (RTSD 1993), and direct observations. We made the map in QGIS (QGIS Development Team 2025).

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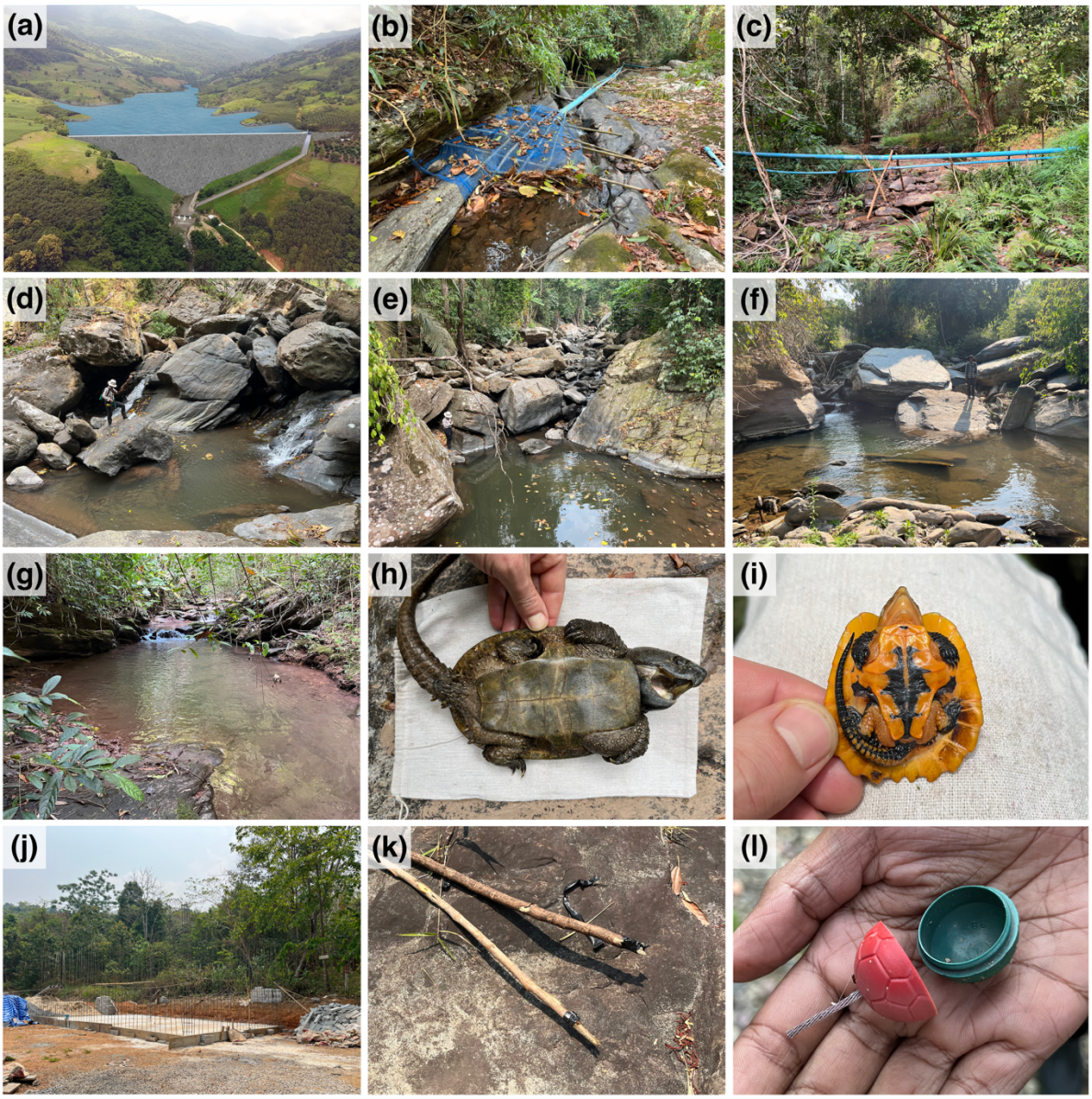


Figure 2. Images: (a) rendering of the planned Mae Lao Reservoir in between the village Ban Khanaeng and Tham Sakoen National Park (© 2025 Pre-Development Consultant Co., Ltd., www.pdc-consultant.com, accessed January 2025); (b, c) Ban Khanaeng's main PVC irrigation line diverting spring water away from a stream inside the national park; (d, e) two river pools where we found adult big-headed turtles; (f) potentially suitable habitat inside the planned dam reservoir area; (g) stream pool where we found juvenile big-headed turtles; (h) large adult male

and (i) small juvenile big-headed turtles; (j) construction site of a large stream-fed water retention tank for supplying a new durian plantation on the immediate edge of the park; (k) discarded sticks fitted with electric tape for electrofishing; (l) discarded casing of an undetonated explosive.

Data collection

We previously searched for turtles during daytime and nighttime along parts of the river and six streams (2.3 km in total) in 2023–2024 (see Supporting Information) and found no turtles, indicating that turtles were extremely rare in search areas, or detection probability during visual searches was extremely low, or both. Thus, we surveyed turtles over a more extensive area using baited traps in 2024–2025. We aimed to survey most (about 6 km) of the river from the planned dam reservoir to a remote reach above a large, tiered waterfall inside the national park, near the river's headwaters (Fig. 1). We also aimed to survey two streams (one inside the park and one outside) that we searched previously, including the irrigated stream noted above, where villagers have reported seeing turtles.

We set traps along transects using a spatially stratified approach that aimed to maximize sampling area and units (traps) and limit potential bias in trap placement. We set traps in pools, the preferred habitat type of big-headed turtles (Sung et al. 2015a). In two separate studies in China, the observed daily and weekly displacement distances of radio-marked *P. m. megacephalum* averaged 7.5 m (range: 0–33.6; Shen et al. 2010) and 9.5 m (range: 0–140.0; Sung et al. 2015a), respectively. Thus, we considered 20-m spacing between traps to be a sensible compromise between the need to increase the overall sampling area and opportunities for encountering potentially rare turtles over short two-night sampling periods (see below) on the one hand, and the need to efficiently deploy heavy sets of traps over difficult terrain on the other hand (Thompson

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2004, MacKenzie and Royle 2005). We separated neighboring transects by 100 m to further increase the overall sampling area. In three cases, we separated neighboring transects by ~400–700 m to bypass the tiered waterfall in the river and extremely steep sections of streams. Moreover, another tiered waterfall forced us to limit the uppermost river transect to only four traps.

We selected trap sites by iteratively measuring 20-m segments along a given transect and setting one trap in a pool located within each segment, prioritizing pools with maximum water depth > 25 cm (Sung et al. 2015a) and nearest to the end point of the corresponding measurement. In four cases where a single large pool overlapped two adjacent segments and no other pools existed in either segment, we accepted a small amount of pseudo-replication and set two traps spaced > 10 m apart in each pool.

We used two trap types for two reasons. The first was to increase flexibility in trap placement; one trap type is more stable on flat surfaces, whereas the other type is more stable on uneven surfaces. The second was to avoid potential sampling bias in turtle age or sex, which can result from using a single trap type (Tesche and Hodges 2015). We balanced this introduction of heterogeneity into the data by using equal numbers of each trap type on each transect. We also checked for potential effects of trap type on apparent species occurrence and observed body size during data analyses.

We trapped different reaches of the river during two consecutive dry seasons (24 March–6 April 2024 and 9–19 March 2025), and both streams during the start of the intervening winter (17–25 November 2024). This timing protected the field crew from high water levels and flash floods in the river during rainy and winter seasons, while ensuring that the crew surveyed streams before water levels receded during hot dry seasons, when some turtles may disperse or temporarily emigrate (Pipatsawasdikul 2009: p. 6). Consequently, season and reach type (river or stream) were

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confounded, which precluded assessment of potential seasonal changes in species occurrence or habitat associations (discussed below).

We aimed to trap each site for two consecutive nights to increase detection probability and allow for potential modelling of site occupancy corrected for imperfect detection (MacKenzie and Royle 2005). However, we could only trap the two uppermost river transects (14 total traps) for one night due to a storm. In total, we surveyed 254 trap sites (194 in the river and 60 in streams) distributed across 250 pools (190 in the river, 60 in streams) and 26 transects (20 in the river, six in streams), including four transects (40 trap sites/pools) inside the planned dam reservoir.

We baited traps during the two hours before and one hour after sunset and checked traps the following morning after sunrise. We measured basic morphometrics of captured turtles, including straight-line carapace length (SCL) using vernier calipers, and body weight using a spring scale. We could determine the sex of individuals with SCL > 128 mm based on secondary sexual characteristics, namely precloacal tail length and thickness. Thus, we regarded turtles with SCL < 105 mm as juveniles (Sung et al. 2015b), and turtles with SCL of 105–128 mm as subadults. We photographed all turtles and distinguished individuals by size, plastron coloration, and pre-existing scars. We never moved turtles away from capture locations and released all turtles unharmed within about 10 minutes of retrieving them from traps. All field work was approved beforehand by relevant government agencies and an animal ethics committee (see Acknowledgements).

We recorded nine pool features we considered a priori to be potentially important determinants of big-headed turtle occurrence (Table S1). We measured maximum pool (1) depth and (2) width, dimensions of pool size that could influence space use and habitat selection by turtles (Shen et al. 2010, Sung et al. 2015a). Two observers jointly visually estimated the percent area of submerged pool substrate comprising (3) boulders (rocks > 26 cm in length; Jowett 1993)

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or bedrock and (4) leaf litter, each of which could provide refuge (Pipatsawasdikul et al. 2010, Shen et al. 2010, Sung et al. 2015a). We measured water (5) temperature and (6) pH using a handheld tester (model 98107, Hanna Instruments Ltd., Bangkok, Thailand). Environmental temperature constrains the physiological capacities and fitness of animals, particularly ectotherms, which respond behaviorally by selecting thermally suitable habitats or microhabitats (Huey 1991, Kidman et al. 2023). Water pH also influences animal physiology, and highly acidic conditions can indicate degradation from agricultural runoff or other nutrient inputs (Doupé et al. 2009, Soo et al. 2021). One observer measured (7) percent forest canopy closure above traps using a spherical densiometer (model A, James C. Doster Forest Densiometers, Marianna, Florida, United States). Forest canopy closure and low hanging vegetation could provide turtles with real or perceived protection from predators and/or favorable conditions for nesting beside river or stream edges (Sung et al. 2014, Guimarães et al. 2023). We estimated (8) elevation by overlaying trap coordinates obtained from a handheld GPS with 90-m Shuttle Radar Topography Mission digital elevation data available online (www.viewfinderpanoramas.org, accessed 8 July 2025) in QGIS version 3.40.5 (QGIS Development Team 2025). Although big-headed turtles have been recorded over an extensive elevational gradient in Thailand, species occurrence and population density could vary with elevation along this gradient if elevation affects habitat or food availability. Last, we recorded (9) reach type (river or stream), which could determine water flow or other conditions (e.g. nest site availability) that are important to big-headed turtle demography but not well represented by the other features we recorded.

Data analyses

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Limited detections of turtles during multiple trapping nights at individual sites (see Results) precluded occupancy modelling. Thus, we collapsed the capture data by classifying sites with ≥ 1 detection as 'occupied' and all other sites 'unoccupied' and modelled species occurrence using binomial generalized linear mixed effect models (GLMMs) (Bolker et al. 2009). Importantly, the resulting estimates of species occurrence are products of true occurrence and detection probability, and thus undoubtedly underestimates of true occurrence (discussed below). Nevertheless, this study aimed to assess how species occurrence varies with different pool features, and we did not expect detection probability to vary systematically with these features.

Given our small sample size (see Results), we limited our analysis of species occurrence to single-factor (fixed effect) GLMMs to avoid overfitting models (Bolker et al. 2009, Burnham et al. 2010). We assessed the relative importance of all 10 candidate predictor variables for explaining variation in species occurrence against each other and an intercept-only (null) model. We standardized all continuous predictors to facilitate direct comparison of effect sizes (slope estimates, $\hat{\beta}$). We included a random effect of transect in all models to account for spatial non-independence among traps. We compared model fits using corrected Akaike information criterion (AICc) and model weights (w_i), regarding models with ΔAICc > 4 and 85% confidence intervals (CIs) of $\hat{\beta}$ overlapping zero as non-competitive (Burhnam et al. 2010, Sutherland et al. 2023). For competitive models, we calculated the proportion of the response variance explained by fixed effects (marginal R^2) and spatial grouping (random effect of transect, equal to the difference between conditional R^2 and marginal R^2) as additional measures of fit (Nakagawa et al. 2017). We fit and assessed models using the packages 'lme4' (Bates et al. 2026) and 'MuMIn' (Bartoń 2025) in R (R Core Team 2025). We validated GLMMs by confirming that variances were not over-dispersed using X^2 tests (Bolker et al. 2009) in the package 'aods3' (Lesnoff et al. 2026). We also

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confirmed that residuals were not spatially autocorrelated using spline correlograms (Fig. S2) in the package 'ncf' (Bjørnstad and Cai 2026).

We modelled SCL, a common index of turtle body size (TTWG 2025), using linear mixed effect models (LMMs). We fit and compared LMMs following the same approach described above for GLMMs, except that we validated LMMs by visually confirming that residuals were approximately independent of fitted values (Bolker et al. 2009). We also compared the SCL distribution of *P. m. peguense* individuals we captured to those of *P. m. megacephalum* individuals captured in four hunted streams (n = 105 turtles) and one protected stream (n = 62 turtles) in Hong Kong, Special Administrative Region of China, as part of a separate study (Sung et al. 2013). Hunted populations in Hong Kong were characterized by absences of large adults and disproportionately large numbers of juveniles, whereas the protected population exhibited opposite demographic patterns (Sung et al. 2013). Thus, using the Hong Kong populations as references, we assessed the focal population for possible evidence of targeted exploitation or lack thereof.

RESULTS

We trapped at 240 of 254 (94%) sites for two consecutive nights each and the rest for only one night each, resulting in 494 total trap-nights (354 trap-nights in the river and 140 trap-nights in streams). We detected 24 individual big-headed turtles (17 in the river, seven in streams) in 22 of 254 (9%) trap sites and 22 of 250 (9%) pools (16 in the river, six in streams) distributed across 12 of 26 (46%) transects, including parts of the river, both study streams, and most (84%) of the elevational gradient we surveyed (716–1206 MASL; Table S1). We found 13 adults (seven females and six males), four subadults, and seven juveniles. Juveniles comprised more of the turtles we found in streams (4 of 7, 57%) than in the river (3 of 17, 18%). Moreover, the three smallest

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juveniles we found (SCL ≤ 54.0 mm) were all in the irrigated study stream (Fig. 2). We did not detect any turtles inside the planned dam reservoir area but did detect three turtles in a cluster of three closely-spaced pools ~400–500 m upriver.

We detected only one turtle on more than one occasion; this turtle was a small juvenile we captured incidentally in an un-baited trap in the irrigated stream during the daytime following the first trapping night and then recaptured in the same (baited) trap on the second trapping night. We also detected two other small juveniles incidentally in one other study pool in the same stream; we captured one in an un-baited trap following the first trapping night and the other by hand outside the same trap following the second trapping night. Although we never captured either of these two turtles in any baited trap, we included them in our data analyses because they both occurred in a study pool, and the odds of encountering turtles incidentally was similar across all study pools. We never encountered any turtles outside of study pools.

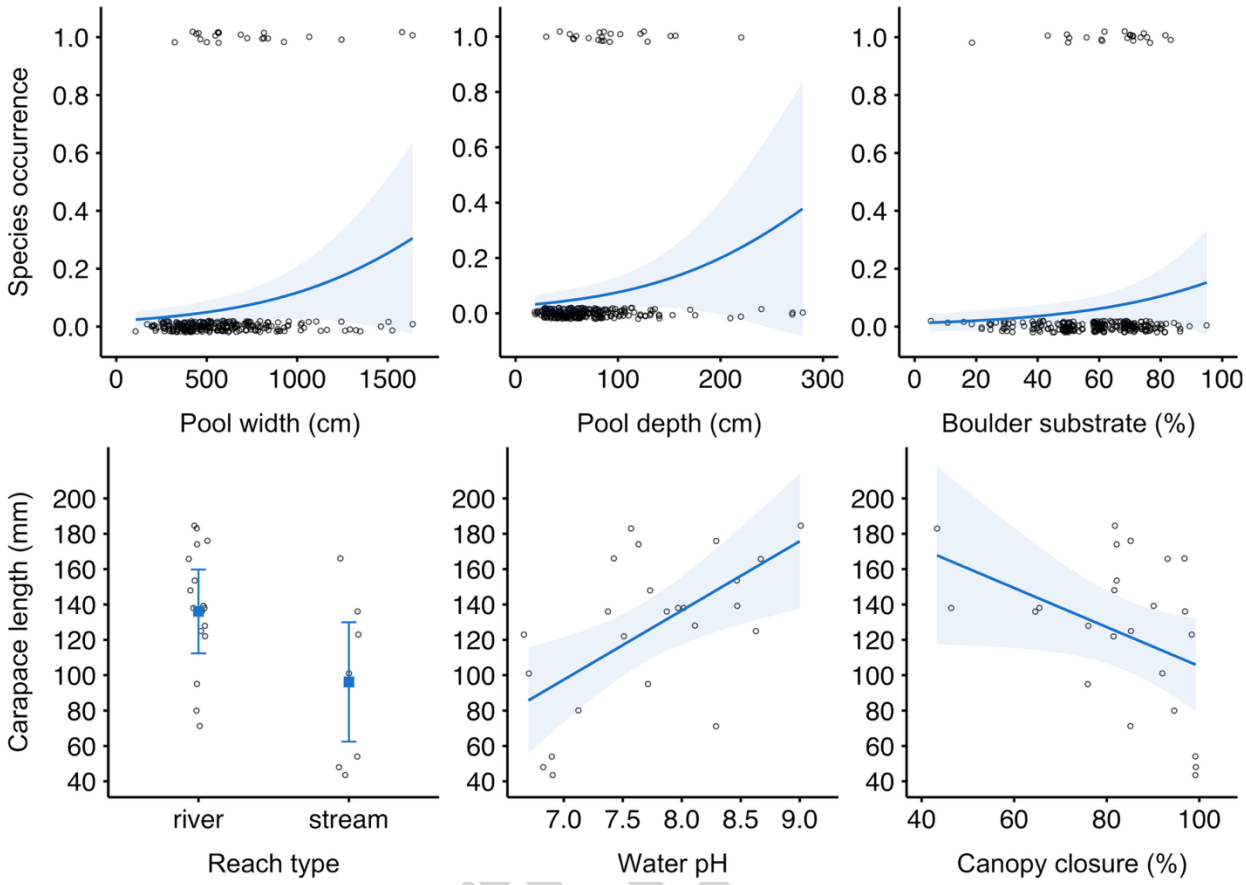
Species occurrence increased with pool width ($\hat{\beta}$ = 0.53; 95% CI: 0.118, 0.940) and depth ($\hat{\beta}$ = 0.48; 95% CI: 0.061, 0.888) and percent substrate comprising boulders ($\hat{\beta}$ = 0.46; 95% CI: −0.111, 1.031) (Fig. 3, Tables S2, S3). Pool width explained the most variation in species occurrence (w_i = 0.42, marginal R^2 = 0.064), followed by pool depth (ΔAICc = 1.27, w_i = 0.22, marginal R^2 = 0.051) and percent boulders (ΔAICc = 3.39, w_i = 0.08, marginal R^2 = 0.049) (Table S2). Pool width and depth were moderately correlated (r = 0.66), whereas correlations among the other important predictors were low ($r \leq 0.21$). No other candidate predictors of species occurrence were supported during model selection (Tables S2, S3). After accounting for variance in species occurrence explained by the individual pool features listed above, the proportion of additional variance explained by spatial grouping ranged from 0.181 to 0.205.

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Overall, mean SCL was 126.2 mm (median = 136.0, SD = 42.4, range: 43.5–184.6) and mean weight was 501.7 g (median = 475.0, SD = 368.2, range: 20–1150). SCL was lower in streams than in the river ($\hat{\beta}$ = −39.9; 95% CI: −81.143, 1.356), increased with water pH ($\hat{\beta}$ = 26.5; 95% CI: 9.187, 43.755), and decreased with forest canopy closure ($\hat{\beta}$ = −17.0; 95% CI: −34.468, 0.389) (Fig. 3, Tables S2, S3). Water pH explained the most variation in SCL (w_i = 0.554, marginal R^2 = 0.352), followed by reach type (ΔAICc = 2.37, w_i = 0.170, marginal R^2 = 0.177) and canopy closure (ΔAICc = 3.83, w_i = 0.082, marginal R^2 0.151) (Table S2). Water pH and reach type were strongly correlated (r = 0.75), whereas reach type and canopy closure (r = 0.61) and water pH and canopy closure (r = 0.34) were moderately correlated. No other candidate predictors were supported during model selection (Tables S2, S3). In competitive LMMs, the proportion of SCL variance explained by spatial grouping ranged from 0.202 to 0.364.

The SCL distribution of turtles we captured was characterized by small proportions of juveniles and subadults and a majority proportion of adults, including large adults, consistent with the protected reference population in Hong Kong (Fig. 4). Moreover, the largest adults we found were larger than those found in Hong Kong (Fig. 4).

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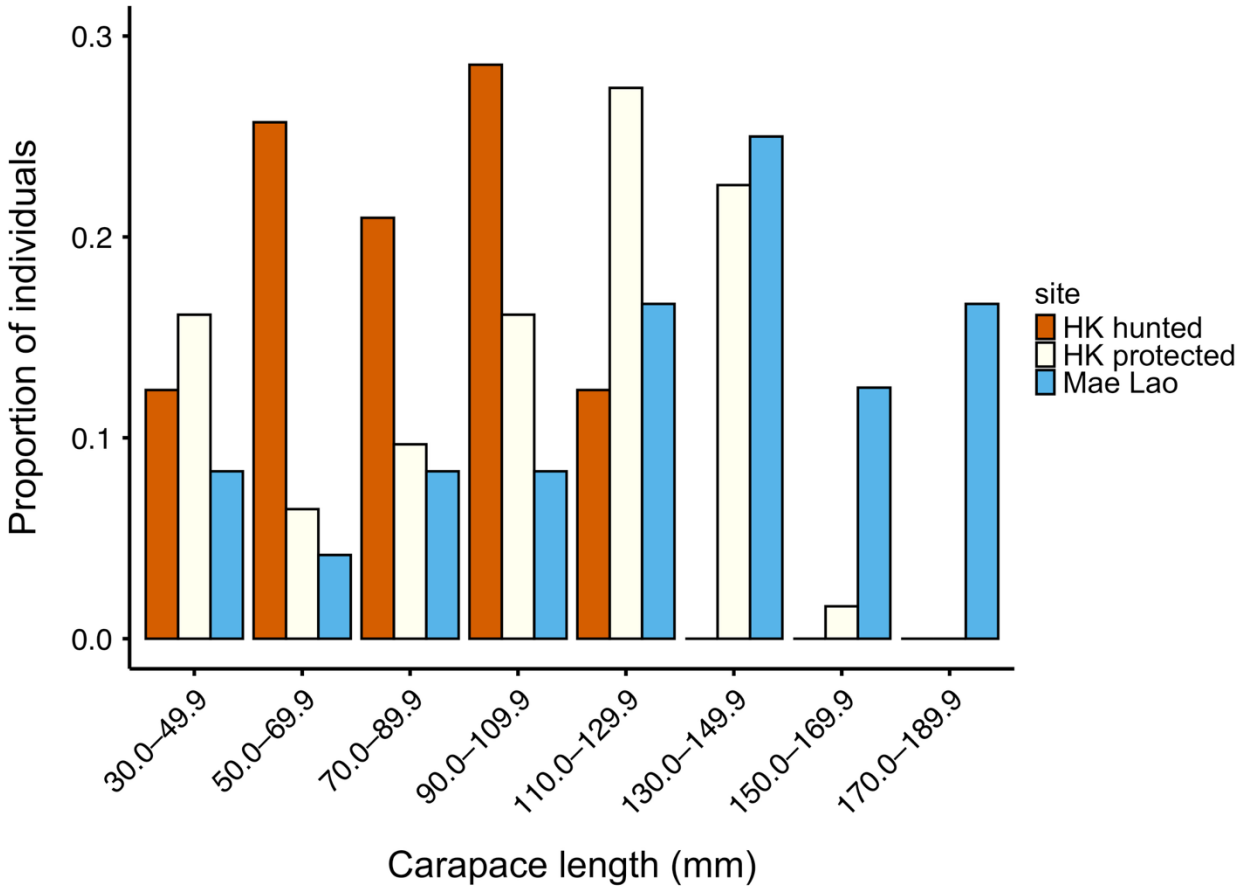
398 **Figure 3**. Estimates (blue lines and square points) and 95% confidence limits (blue ribbons and

399 error bars) of the effects of different habitat features on the occurrence (top row) and observed

400 body size (bottom row) of big-headed turtles. Hollow grey circles are raw data, offset slightly to

401 make them more visible.

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402

403 **Figure 4**. Body size-class distributions of big-headed turtles we found in the Mae Lao River
404 watershed (n = 24 turtles) in Thailand versus turtles found previously in four hunted streams (n =
405 105 turtles) and one protected stream (n = 62 turtles) in Hong Kong (HK).

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DISCUSSION

In a mountainous watershed overlapping an ambiguous national park boundary in Thailand, we documented a widely distributed and potentially viable big-headed turtle population just above a state-planned large dam site. Turtles were associated with medium- and large-sized river and stream pools containing boulders (Figs. 2, 3), which could be explained by species-level space-use requirements and dependence on submerged refugia (Sung et al. 2015a). Moreover, observed body size was smaller in streams than in the river, increased with water pH, and decreased with forest canopy closure (Fig. 3), possibly reflecting favorable conditions for nesting and/or juvenile survival in streams. For example, sheltered streams may provide thermal advantages for nesting near water (Sung et al. 2014) and/or protection from predators or flooding (Guimarães et al. 2023).

Crucially, occurrences of juvenile, subadult, and adult turtles indicated a relatively intact breeding population. Researchers in Hong Kong found that hunted populations of big-headed turtles comprised mostly juveniles and no large adults, whereas a protected population comprised mostly adults, including large individuals (Sung et al. 2013). The body size-class distribution of turtles we found was markedly similar to that of the protected population in Hong Kong (Fig. 4), which suggests that the focal population has faced little or no targeted exploitation in recent years, consistent with claims of local villagers. Moreover, despite our smaller sample size, we found larger adults in the Mae Lao River than researchers found in Hong Kong (Fig. 4). These differences in maximum observed body size could be due to a longer-term absence of targeted hunting in our study area, or morphological differences between *P. m. peguense* and *P. m. megacephalum*, or both.

Population threats and management implications

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The results of our study raise immediate concerns about three main threats to big-headed turtles. First, the Mae Lao Reservoir project could directly impact the focal turtle population by inundating swathes of the river and parts of several streams (Figs. 1, 2). Although we did not detect any turtles in any of the 40 pools we surveyed inside the planned dam reservoir (the area that would be permanently flooded by the dam), we found three turtles in three closely-spaced pools ~400–500 m upriver. The mean linear home range size of nine radio-marked big-headed turtles in Chiang Mai Province was 619 m (range: 96–1233; Pipatsawasdikul 2009: p. 49). Thus, assuming turtles in our study area exhibit similar patterns of annual space use as those observed in Chiang Mai, dam construction could flood parts of the home ranges of some of the turtles we found.

Importantly, our sampling occurred over short periods at only a subset of available pools, and we observed potentially suitable pools (Table S1) inside the planned reservoir (Fig. 2). Thus, we cannot rule out the possibility that dam construction could also inundate habitats of additional turtles, which we may have failed to detect.

Moreover, dam construction could block turtle dispersal between upper and lower reaches of the Mae Lao River and other watersheds (Thirakhupt and van Dijk 1994, Moll and Moll 2004), thereby reducing gene flow and long-term population viability (Bárcenas-García et al. 2022). Likewise, the dam could indirectly impact turtles by altering flow regimes and food web structures in ways that reduce food availability and habitat quality. For instance, the dam could block migratory fish and invertebrates from accessing free-flowing river and stream reaches far above the dam site (Bunn and Arthington 2002, Greathouse et al. 2006, Sor et al. 2023, Huang and Li 2024). Besides eliminating potential food sources for turtles, loss of native consumers could degrade ecosystem functioning (e.g. organic material processing) and integrity by removing

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important top-down effects of consumers on basal food resources and co-occurring species (Bunn and Arthington 2002, Greathouse et al. 2006).

Second, hazardous irrigation practices could reduce turtle survivorship and/or habitat suitability. For instance, at least one juvenile big-headed turtle has recently become lodged in Ban Khanaeng's main PVC irrigation line inside Tham Sakoen National Park. This turtle was dislodged and reportedly released alive by an inspecting villager (Living River Association 2023: p. 12). However, other turtles could have become trapped in PVC tubes and gone undiscovered or unreported. Importantly, the three youngest turtles (SCL ≤ 54 mm, i.e. ≤ 3 years since hatching; Sung et al. 2015b) we found were in the same reach as the main 3-inch (76.2 mm) diameter intake tube (Fig. 2). Thus, the intake is likely located near a turtle nesting area and could pose a mortality risk for juveniles. We informed residents of this risk, and they subsequently blocked the intake using nylon mesh (Fig. 2). However, this mesh could degrade or wash away periodically. Moreover, other open PVC tubes have been installed in the river and some streams by individual farmers. Such irrigation systems are common across the hills and mountains of northern Thailand (Badenoch 2009), so deploying durable exclusion devices (e.g. metal leaf filters) that prevent young turtles and other small aquatic vertebrates from entering PVC tubes could be an important and feasible aim for future conservation work.

Local irrigation could also impact turtles by diminishing freshwater. Although water runs in the Mae Lao River and parts of spring-fed streams year-round, excess irrigation during particularly hot dry seasons could reduce water flows to critically low levels such that they eliminate key refuges and/or reduce habitat connectivity for turtles. In recent dry seasons, water levels in the irrigated study stream have been markedly lower downstream of the water diversion site than those upstream (M.R. Herse, N. Khuntong, 2024–2026, personal observation), which

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could prevent turtles in the upper stream from accessing the river and vice versa. Moreover, use of stream water for agriculture appears set to increase. For instance, a large water retention tank was recently constructed and linked to the irrigated study steam for supplying a new durian plantation along the immediate edge of the park (Fig. 2). Several residents have independently stressed that the lessee of this new plantation (a non-resident) has not been subjected to the typically stringent building regulations associated with forest reserve lands and expressed concerns about possible water shortages that could follow (anonymous residents, M.R. Herse, N. Khuntong, March 2026, personal communication). The potential impacts of such irrigation on river turtles in our study area and elsewhere will likely increase as climate change generates more extreme droughts and heatwaves (Chaiwino et al. 2025, Chen et al. 2025).

Third, certain fishing practices could pose another mortality risk for turtles. For example, one risky fishing practice involves setting baited traps entirely underwater overnight, which could drown turtles captured incidentally. Moreover, on multiple occasions the field crew encountered people using electricity or small explosives for fishing (Fig. 2), which could kill, injure, or disturb turtles and prey species. Our study was not designed to assess potential effects of fishing on turtles. However, disturbances linked to relatively high fishing activity nearer to the village and planned dam site could explain some of the apparent absences of turtles that we observed in that area.

During a consultation between researchers and 12 residents of Ban Khanaeng (e.g. village council members, farmers, schoolteachers, fisher-hunters) in January 2025, the village head recognized our concerns and stressed that illegal use of electricity and explosives is uncommon and discouraged within the village, including during periodic loudspeaker announcements. However, he also stressed that local leaders have limited abilities to control all fishing activities, including some by non-residents, and suggested that posting signs outlining fishing regulations

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and the protected status of big-headed turtles at some river and stream access points could help to reduce disturbances and potential consumption of turtles. Indeed, following this consultation, a hired laborer working on the water retention tank noted above reportedly harvested a big-headed turtle they found while fishing in the irrigated stream before returning home to another province, ignoring a resident's suggestion to return the turtle to the stream (anonymous resident, M.R. Herse, N. Khuntong, March 2026, personal communication). Other workers (also non-residents) at the site subsequently told researchers they were unaware of the species' protected status.

The village head also encouraged researchers to offer residents information booklets about the ecology and status of big-headed turtles, and potential impacts of irrigation and fishing practices, as part of a separate project. Likewise, a schoolteacher invited researchers to develop engaging lessons for youth as a part of a new local environmental education program. Such community-based education efforts could help to raise public awareness and promote conservation within local watershed management (van der Ploeg et al. 2011, Ismail et al. 2021, Punya 2022).

Study limitations

Our study has three main limitations. First, lack of turtle detections during multiple trapping nights at individual pools precluded modelling site occupancy corrected for imperfect detection, which undoubtedly led to underestimates of true species occurrence and could have biased our estimates of habitat effects (Gu and Swihart 2004). We prioritized increasing sampling area (number of pools trapped) over sampling intensity (number of trapping nights per pool) to increase our odds of encountering turtles. Although this strategy was effective for detecting turtles over an extensive area, our results indicate that trapping for more than two consecutive nights is necessary to limit false absences and ensure some repeat detections (a precondition for occupancy modelling).

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519 Nevertheless, our finding that species occurrence was influenced by pool size and substrate is
520 plausible and consistent with separate research noted above, indicating that potential bias in our
521 estimates of habitat effects on species occurrence is likely negligible. However, we stress that
522 apparent absences of turtles in some parts of our study area could be due to imperfect detection.
523 Likewise, the relatively small number of juveniles that we observed could be at least partly due to
524 relatively low detectability of turtles during early life stages (McKnight et al. 2025).

525 Second, our survey design confounded season and reach type (river or stream). Surveying
526 individual pools and reaches during both winter and dry seasons could have allowed us to compare
527 seasonal habitat associations in river versus stream habitats. In Thailand, some big-headed turtles
528 may disperse or temporarily emigrate from streams as they retract during hot dry seasons. Even in
529 areas that do not dry up entirely, species occurrence and habitat use could shift seasonally in
530 response to fluctuations in local population density and intraspecific competition for shelter and/or
531 food. Thus, species occurrence and habitat associations could vary by season, or reach type, or
532 both. However, sampling individual pools during both seasons would have required allocating
533 substantial amounts of time to revisiting previously sampled areas (including some that lacked
534 water during the dry season) instead of sampling new areas, which could have resulted in fewer
535 total detections. More research is clearly needed to understand the annual population ecology of
536 big-headed turtles. Meanwhile, we stress that the results of this study pertain to stream pools during
537 early winter and river pools during the hot dry season and should be interpreted as such.

538 Third, notwithstanding our extensive survey effort, small sample size precluded reliable
539 assessments of potential additive, interactive, and nonlinear habitat effects. For instance, the
540 magnitude of the effect of boulder substrate on species occurrence may depend on pool size (a
541 potential interactive effect), such that large pools containing many boulders are occupied

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frequently, whereas small pools that do not meet the minimum space-use requirements of big-headed turtles are occupied infrequently regardless of boulder substrate. Identifying potential interactive or nonlinear habitat effects could reveal thresholds in habitat suitability but requires more data to support more complex modelling (Ficetola and Denoël 2009).

Despite these limitations, our trapping study provides important insights into the population ecology and status of big-headed turtles that cannot be inferred from visual search techniques, which do not reliably detect turtles, or modern environmental DNA survey techniques, which produce limited and sometimes misleading information (Lam et al. 2022).

Conservation, development, and people in between

Local opposition to the Mae Lao Reservoir is positioned at an ambiguous and complex intersection of national forest reserve and national park lands (Sato 2003, Woods et al. 2011; Fig. S1-2), and different state agencies (e.g. RID, RFD, DNP, DOF) with different mandates and jurisdictions. The dam project was planned by RID (Fig. S1), which is tasked with managing and developing inland water resources for household use and agricultural, energy, and industrial production (RID 2019). Despite the potential impacts of the project on big-headed turtles and riverine habitats, DNP may have limited ability to control the outcome of the project because DNP is not mandated to manage biodiversity or habitats outside of protected areas. Likewise, RFD responsibilities for forest reserve lands focus on overseeing registered community forests, smallholder farms, and commercial plantations (Open Development Thailand 2020). Moreover, although DOF is responsible for protecting "rare aquatic animals" and managing "threats to ... aquatic animals' migration [and] ... habitats" outside of protected areas, this occurs primarily through regulation of fishing activities (Sections 65, 66, Royal Ordinance on Fisheries A.D. 2015 and Royal Ordinance on Fisheries [No.

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2] A.D. 2017), if at all. Leaving aside issues of limited resourcing, competition, and corruption associated with some agencies (Kijtewachakul 2010, Sopera 2022, Thai PBS World 2025), this compartmentalization of environmental management clearly creates blind spots for conservation. In this case, big-headed turtles use both aquatic and terrestrial habitats inside and outside of protected areas, where they may face certain threats such as dam construction that fall outside the jurisdiction of concerned officials. Grassroots opposition to such threats is therefore important for conservation in the context of highly compartmentalized administrative responsibilities, which is characteristic of many contemporary environmental management and governance arrangements (Herse et al. 2020, Wong 2025, Yuthavong et al. 2025).

Opposition to the dam project is also positioned at a critical convergence point between contradictory policies for biodiversity conservation on the one hand and perpetual economic growth on the other (Sato 2000, Otero et al. 2020). In Thailand, state policies for addressing biodiversity declines since the mid-twentieth century have focused on establishing and expanding protected areas, regulating human consumption of wild species, and financializing conservation programs and biodiversity itself under the guidance of various international agencies and conventions (Laungaramsri 2001, Herse et al. 2024, ONEP 2025). Meanwhile, the very processes of economic growth and ensuing environmental degradation that first sparked widespread biodiversity declines in Southeast Asia have continued (Rigg 1995, Herse et al. 2024). Indeed, construction of destructive diversion and hydropower dams have surged across Southeast Asia in recent decades, spurred by the ever-increasing water and electricity demands of perpetual economic growth and private capital investments (Aylward and Tognetti 2003, Hirsch et al. 2022, Ang et al. 2024). In the absence of effective policies for addressing currently unsustainable trends in land-use intensification, infrastructure development, and environmental exploitation, grassroots

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initiatives to prevent undesirable development projects and improve environmental management have crucial roles in protecting threatened species. Such initiatives could also serve as key levers for establishing wider community-based ecosystem conservation and restoration programs.

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Author contributions

M.R.H. led all aspects of the research and writing. M.R.H., W.C., and G.A.G. secured project funding. N.K. and W.C. assisted in data collection and facilitated communication with local community members. Y.-H.S. provided previously unpublished demographic data collected as part of a separate study. All authors contributed to the study design and reviewed the manuscript. All

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authors are originally from and/or based in Asia. Two authors are from Thailand, where the study took place. Regular engagement with local community members at the study site was central to our research. We have shared personal communications with informants with their verbal permission, while keeping the names of informants anonymous to protect personal privacy. We always compensated community members for field assistance and accommodations.

Conflict of Interest

The authors have no conflicts of interest to report.

Data Accessibility Statement

All data corresponding to this study (excluding coordinates of trap site and turtle capture locations) will be archived at Dryad (https://datadryad.org/) upon acceptance of the manuscript.

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Supporting Information for:

Herse M.R., Chutipong W., Khunton N., Sung Y.-H., Gale G.A. Assessing habitat associations of critically endangered big-headed turtles to support grassroots river conservation.

Preliminary searches

Two or three observers searched for big-headed turtles in 23, 100-meter reaches of the upper Mae Lao River (6 reaches) and six stream tributaries (17 reaches) during October–November 2023 and January 2024. Observers searched each these 23 reaches during daytime, and 21 during nighttime on the same day using spotlights (44 total search occasions). Observers could not search two stream reaches during nighttime due to storms. Overall, observers spent 47 hours searching for turtles (32 hours during daytime, 15 hours during nighttime). During searches, observers aimed to search all potential turtle habitats within each reach, including pools, runs, riffles, and river or stream banks (Sung et al. 2015). However, observers were frequently limited in their ability to search deep pools and crevices due to limited visibility.

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Table S1. Means ($\overline{x}$), standard deviations (SD), and ranges of pool features corresponding to all study pools where we set traps and pools where we captured big-headed turtles.

River and stream pools		
	all study pools (n = 250)	capture pools (n = 22)
variable	$\overline{x}$ (SD, range)	$\overline{x}$ (SD, range)
pool depth (cm)	70.7 (42.8, 19–280)	93.7 (43.4, 30–220)
pool width (cm)	580.4 (282.3, 107–1638)	752.7 (356.7, 323–1638)
boulder (%)	58.0 (16.1, 5–95)	63.9 (14.6, 20–85)
leaf litter (%)	10.2 (13.1, 0–75)	8.0 (8.3, 0–30)
canopy (%)	76.7 (20.9, 10.3–100)	82.3 (15.7, 43.3–99.2)
temperature (ºC)	21.8 (2.1, 18.1–24.9)	21.4 (2.1, 18.1–24.6)
pH	7.6 (0.6, 6.0–9.0)	7.8 (0.7, 6.7–9.0)
elevation (MASL)	882.6 (176.1, 631–1216)	937.1 (162.2, 716–1206)

River pools (hot dry season)		
	all study pools (n = 190)	capture pools (n = 16)
variable	$\overline{x}$ (SD, range)	$\overline{x}$ (SD, range)
pool depth (cm)	75.7 (46.6, 19–280)	104.4 (45.9, 30–220)
pool width (cm)	624.2 (294.7, 170–1638)	863.1 (358.3, 422–1638)
boulder (%)	58.2 (15.7, 15–95)	63.1 (16.3, 20–85)
leaf litter (%)	10.6 (13.4, 0–75)	9.1 (9.2, 0–30)
canopy (%)	70.0 (20.7, 10.3–100)	76.8 (14.9, 43.3–94.5)
temperature (ºC)	22.7 (1.6, 19.2–24.9)	22.2 (1.7, 19.4–24.6)
pH	7.9 (0.5, 6.7–9.0)	8.1 (0.5, 7.1–9.0)
elevation (MASL)	805.0 (128.7, 631–1092)	873.1 (124.6, 716–1054)

Stream pools (early winter)		
	all study pools (n = 60)	capture pools (n = 6)
variable	$\overline{x}$ (SD, range)	$\overline{x}$ (SD, range)
pool depth (cm)	57.4 (26.8, 19–175)	65.2 (16.2, 43–84)
pool width (cm)	465.0 (207.6, 107–1106)	458.3 (79.7, 323–565)
boulder (%)	57.4 (17.0, 5–90)	65.8 (9.2, 50–75)
leaf litter (%)	9.4 (12.3, 0–70)	5.6 (4.4, 1–10)
canopy (%)	94.7 (4.6, 80.0–99.5)	97.1 (2.7, 91.9–99.2)
temperature (C)	19.4 (1.1, 18.1–21.6)	19.3 (1.3, 18.1–21.1)
pH	7.0 (0.5, 6.0–8.0)	7.0 (0.3, 6.7–7.4)
elevation (MASL)	1087.0 (107.2, 905–1216)	1108.0 (125.5, 922–1206)

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Table S2. Results of model selection (K: number of parameters; LL: log-likelihood; AICc: Akaike information criterion corrected for small sample size; w_i: Akaike weight) evaluating the effects of pool features and trap type on (a) the occurrence and (b) observed body size of big-headed turtles. All models include a random effect of transect.

(a) Species occurrence						
model	variable	K	LL	AICc	ΔAICc	w_i
m3	width	3	–69.817	145.7	0.00	0.422
m2	depth	3	–70.452	147.0	1.27	0.224
m4	boulder	3	–71.512	149.1	3.39	0.077
m1	null (intercept only)	2	–72.842	149.7	4.00	0.057
m9	elevation	3	–72.045	150.2	4.46	0.045
m6	forest canopy	3	–72.118	150.3	4.60	0.042
m11	trap type	3	–72.438	151.0	5.24	0.031
m5	litter	3	–72.480	151.1	5.33	0.029
m8	pH	3	–72.581	151.3	5.53	0.027
m7	temperature	3	–72.618	151.3	5.60	0.026
m10	reach type	3	–72.836	151.8	6.04	0.021
(b) Observed body size						
model	variable	K	LL	AICc	ΔAICc	w_i
m8	pH	4	–112.010	234.1	0.00	0.554
m10	reach type	4	–113.192	236.5	2.37	0.170
m6	forest canopy	4	–113.927	238.0	3.83	0.082
m9	elevation	4	–114.381	238.9	4.74	0.052
m7	temperature	4	–114.803	239.7	5.59	0.034
m11	trap type	4	–114.821	239.7	5.62	0.033
m2	depth	4	–115.131	240.4	6.24	0.024
m3	width	4	–115.372	240.8	6.72	0.019
m4	boulder	4	–115.637	241.4	7.26	0.015
m5	litter	4	–115.683	241.5	7.35	0.014
m1	null (intercept only)	3	–118.749	244.7	10.57	0.003

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967 **Table S3**. Effect sizes (slope estimates, $\hat{\beta}$) and corresponding standard errors (SE), 95% and 85%
968 confidence intervals (CI), and p-values for single-factor (a) generalized linear mixed effect models
969 of big-headed turtle occurrence and (b) linear mixed effect models of observed body size. All
970 models include a random effect of transect. Asterisks indicate significance (* if $p < 0.05$, § if 0.05
971 $< p < 0.157$; see Sutherland et al. 2023).
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(a) Species occurrence						
model	variable	$\hat{\beta}$	SE	95% CI	85% CI	*p*-value
m3	width	0.529	0.210	0.118, 0.940	0.227, 0.831	*0.012
m2	depth	0.475	0.211	0.061, 0.888	0.171, 0.778	*0.024
m4	boulder	0.460	0.291	–0.111, 1.031	0.040, 0.879	§0.115
m11	trap type	–0.420	0.471	–1.343, 0.503	–1.098, 0.258	0.373
m9	elevation	0.396	0.318	–0.228, 1.019	–0.063, 0.854	0.214
m6	canopy	0.380	0.333	–0.272, 1.032	–0.099, 0.859	0.253
m5	litter	–0.267	0.339	–0.931, 0.398	–0.755, 0.222	0.432
m8	pH	0.219	0.298	–0.365, 0.804	–0.210, 0.649	0.462
m7	temperature	–0.212	0.317	–0.833, 0.410	–0.668, 0.245	0.505
m10	reach type	0.081	0.712	–1.315, 1.477	–0.945, 1.107	0.910
(b) Observed body size						
model	variable	$\hat{\beta}$	SE	95% CI	85% CL	*p*-value
m10	reach type	–39.893	21.046	–81.143, 1.356	–70.199, –9.587	§0.091
m8	pH	26.471	8.818	9.187, 43.755	13.773, 39.170	*0.013
m6	canopy	–17.040	8.892	–34.468, 0.389	–29.844, –4.235	§0.069
m9	elevation	–15.837	12.263	–39.872, 8.198	–33.496, 1.822	0.157
m7	temperature	12.413	10.801	–8.758, 33.583	–3.141, 27.967	0.279
m11	trap type	–11.381	15.540	–41.839, 19.078	–33.758, 10.997	0.473
m2	depth	8.890	7.626	–6.057, 23.836	–2.092, 19.871	0.259
m3	width	6.791	8.518	–9.904, 23.485	–5.475, 19.056	0.434
m4	boulder	1.167	8.984	–16.442, 18.775	–11.770, 14.103	0.898
m5	litter	0.369	8.646	–16.576, 17.314	–12.081, 12.818	0.966

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Figure S1-1. The first page of a two-page infographic (www.pdc-consultant.com, accessed January 2025) about the Thai state-planned "Mae Lao Reservoir" project in Mae Lao Subdistrict, Phayao Province, northern Thailand. The infographic was prepared by Pre-Development Consultant Co. Ltd. (Bangkok, Thailand) and Inter Tech Consultant Co. Ltd. (Nanthaburi, Thailand) under contract with Thailand's Royal Irrigation Department. The page outlines the initial contract duration (23 November 2020 to 19 August 2021), expected timelines for conducting impact assessments and organizing engagements with the public and media, and contact information for contracting parties. The right image is a rendering of the planned dam and reservoir. The lower left image shows a downstream area of the river during a high-water event.

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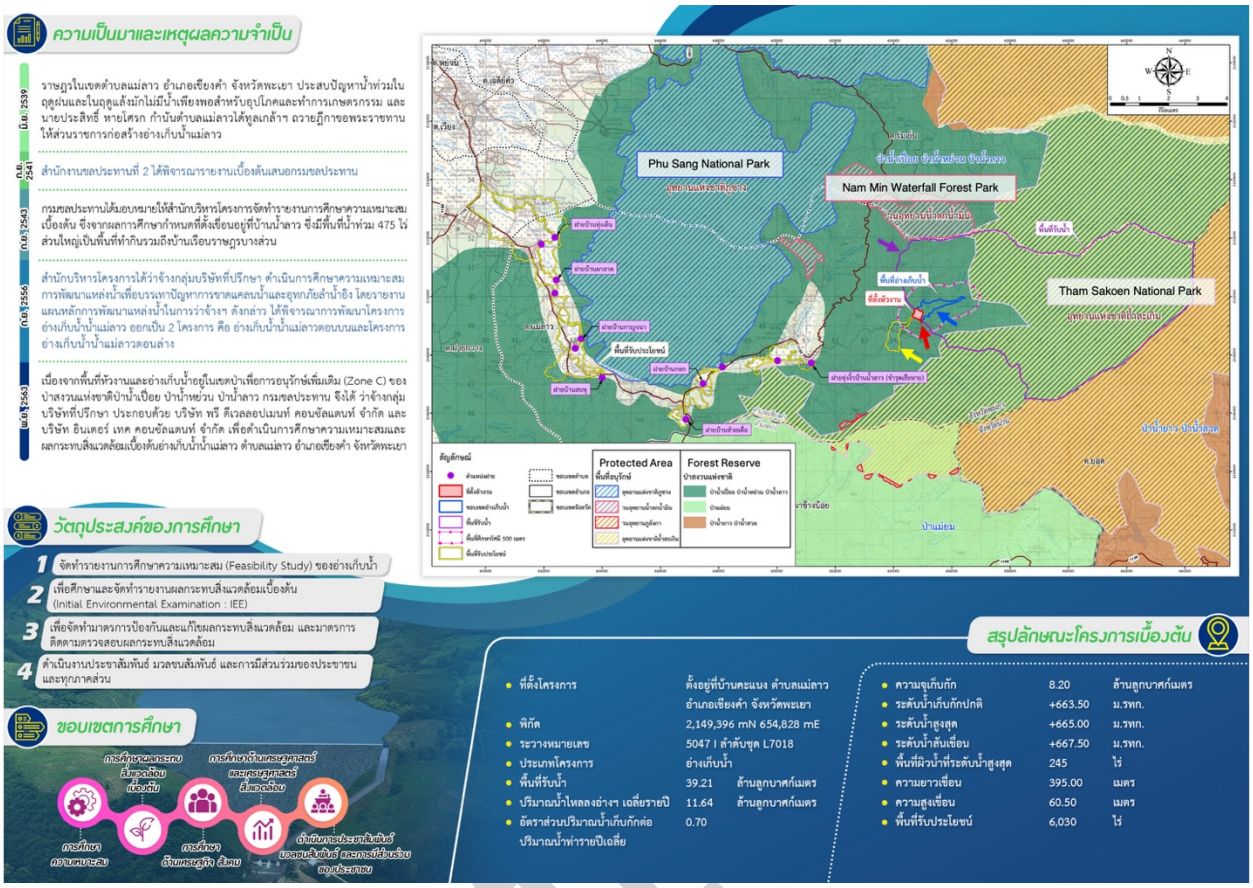
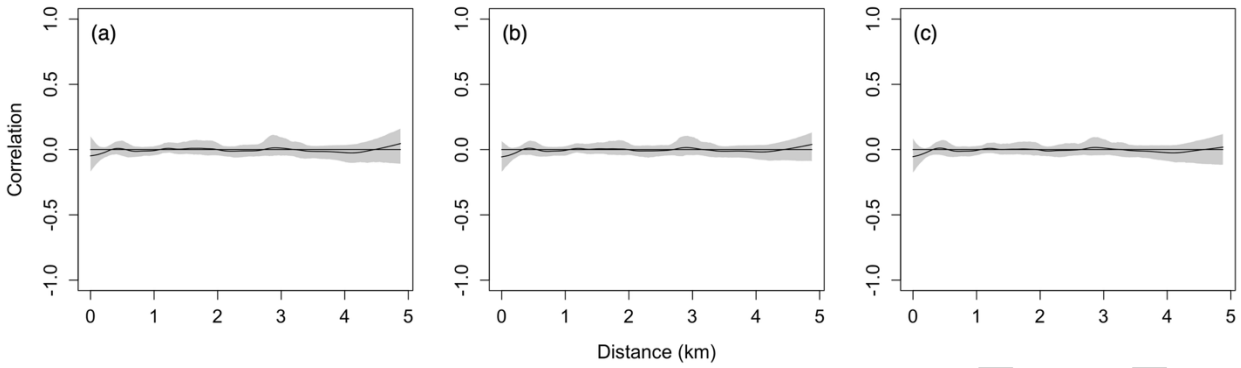


Figure S1-2. The second page of a two-page infographic (www.pdc-consultant.com, accessed January 2025) about the Thai state-planned "Mae Lao Reservoir" project in Mae Lao Subdistrict, Phayao Province, northern Thailand. The map shows different land classifications, including national forest reserve (dark green) and protected areas (hatched diagonal lines, labelled in English by the authors of the present paper), and other features, including the planned dam site (shaded red polygon) and reservoir area (empty blue polygon), reservoir catchment area (empty purple polygon), and downstream irrigation benefit area (empty yellow polygon), each indicated by correspondingly colored arrows we added. The page also describes the rationale for the project (water retention and flood control) and technical specifications of the planned dam and reservoir.

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998 **Figure S2**. Spline correlograms showing estimated spatial autocorrelation (solid black line) and
999 95% confidence limits (grey ribbons) of standardized residuals from competitive generalized linear
1000 mixed effect models of big-headed turtle occurrence fit as functions of pool (a) width, (b) depth,
1001 and (c) and boulder substrate. All models include a random effect of transect. Confidence limits
1002 overlapping zero in all cases indicate no evidence of significant spatial autocorrelation.

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