Journal of Herpetology, Vol. 56, No. 4, 461–469, 2022

Preliminary Insights on the Spatial Ecology, Population Demography, and Sexual Dimorphism of the Critically Endangered Sulawesi Forest Turtle (*Leucocephalon yuwonoi*)

ANGELA SIMMS,[1,2,9] MARTIN J. WHITING,[1] J. SEAN DOODY,[3] JUSRI NILAWATI,[4] FADLY Y. TANTU,[4] ANDREW WALDE,[5] FATMAH LAUHIDO,[6] CHRISTINE LIGHT,[5] MIRZA KUSRINI,[7] AMIR HAMIDY,[8] ANDREW P. ALLEN,[1] AND SIMON CLULOW[1]

[1]*Department of Biological Sciences, Macquarie University, North Ryde, NSW, Australia 2109*
[2]*Department of Pharmacy and Biomedical Sciences, La Trobe University, Bundoora, VIC, Australia 3086*
[3]*Department of Biological Sciences, University of South Florida – St. Petersburg, St. Petersburg, Florida, 33701, USA*
[4]*Faculty of Animal Husbandry and Fishery, Tadulako University, Jl. Soekarno Hatta km. 9., Palu, Central Sulawesi, Indonesia 94148*
[5]*Turtle Survival Alliance, 1030 Jenkins Rd., Suite D, Charleston, South Carolina, 29407, USA*
[6]*Agricultural Sciences Postgraduate, Tadulako University, Jl. Soekarno Hatta km. 9., Palu, Central Sulawesi, Indonesia 94148*
[7]*Department of Forest Resources, Conservation and Ecotourism, Bogor Agricultural University, Darmaga, Bogor, Indonesia 16001*
[8]*Museum Zoologicum Bogoriense (Zoology Division), Research Center for Biology, Indonesian Institute of Sciences, Gd. Widyasatwaloka, Jl. Raya Jakarta Bogor km 46, Cibinong, Bogor, West Java, Indonesia*

ABSTRACT.—**Sulawesi Forest Turtles (*Leucocephalon yuwonoi*) are critically endangered and endemic to the island of Sulawesi. We conducted radiotelemetry and capture–mark–recapture to study their spatial ecology, habitat selection, activity patterns, and demography in February–April and June–July, 2019. The average area occupied by 14 turtles using the minimum convex polygon (MCP) method was 0.49 ± 0.42 ha (standard deviation [SD]), whereas using the fixed 50% kernel density method averaged 0.076 ± 0.061 ha (SD). Males (mean = 0.53 ± 0.40 ha, $N = 7$) occupied a larger area (MCP method) than females (mean = 0.44 ± 0.46 ha, $N = 7$) but the difference was not statistically significant. Turtles took refuge in habitat containing significantly more canopy cover, broadleaf plant cover, and more and deeper ground cover than that in random plots. Males were predominantly active at night and females were exclusively so. We caught 25 adult females, 16 adult males, and 38 unsexed juveniles in two stream sections. Estimated population size (95% confidence intervals) in the lower stream was 17 turtles (15–28) in the wet season and 10 turtles (8–21) in the dry season. The population estimate in the upper stream was 25 (24–33) and 13 (9–28) turtles in the wet and dry seasons, respectively. Our study provides important baseline ecological data that can be used to inform future conservation and recovery programs for the species.**

Human-induced habitat loss is a global phenomenon driving biodiversity loss (Zabel et al., 2019). Turtles are considered to be one of the most threatened groups of vertebrates in the world, with more than 60% of freshwater turtles and tortoises listed as threatened with extinction (Buhlmann et al., 2009; Turtle Conservation Coalition, 2018). The highest proportion of threatened turtle species is heavily skewed toward Southeast Asia where there is widespread habitat destruction and heavy harvest for human consumption, traditional medicine, and the pet trade (Böhm et al., 2013; Rhodin et al., 2018; Turtle Conservation Coalition, 2018). Although freshwater turtles have persisted for over 200 million yr, their slow growth and delayed maturity make them particularly susceptible to anthropogenic pressures (Chessman, 2011; Anthonysamy et al., 2013; Van Dyke et al., 2018a).

Sulawesi Forest Turtles (*Leucocephalon yuwonoi*) are a freshwater species endemic to Sulawesi that is listed as critically endangered by the International Union for Conservation of Nature (Asian Turtle Trade Working Group, 2000). Threats to *L. yuwonoi* that are driving population declines include poaching, overexploitation, deforestation, and habitat degradation (Ives, 2006; Riyanto, 2006; Hagen et al., 2009). Sulawesi's forests are faced with intense deforestation even within protected areas (Whitten et al., 2002). A surge in human migration into Sulawesi in the 1990s, driven by socioeconomic issues in Indonesia, resulted in further clearing of forests for agriculture (Whitten et al., 2002). An estimated 1.1% of forest in Sulawesi was lost per year during 2000–2010, with plantations and regrowth covering 80% of the island at the end of this period (Miettinen et al., 2011). The impacts of habitat loss on *L. yuwonoi* in Sulawesi are unclear and could be exacerbated by pollution and habitat degradation caused by farming practices (i.e., use of pesticides and fertilizers; Riyanto, 2006; Tothmihaly et al., 2019). Previous research has investigated the impacts of habitat clearance on reptile and amphibian biodiversity in Sulawesi (e.g., Wanger et al., 2010; Gillespie et al., 2015), but no data were provided specifically for turtles.

Our current understanding of the ecology of *L. yuwonoi* is limited to anecdotal observations and data on captive populations. For example, in captivity female *L. yuwonoi* lay one to two eggs per clutch and may lay several clutches per year (Riyanto, 2006; Ives et al., 2008; Hagen et al., 2009), but their reproductive ecology in nature remains largely unknown. *Leucocephalon yuwonoi* are sexually dimorphic in carapace length (CL; Ives et al. 2008; described in Methods), and possibly in head size. However, it has yet to be tested whether there is a significant difference between the sexes in CL or head width, which could raise questions about the species' behavioral ecology and possible sex differences in habitat needs. Harvesting of *L. yuwonoi* for exports (e.g., to China) were observed within a year after being described in 1995 (Riyanto, 2006; Ives et al., 2008). Given the current status and threats faced by *L. yuwonoi*, there is an urgent need for data on wild populations that can inform their long-term conservation and management (Naveda-Rodriguez et al., 2018). In particular, data are required on spatial ecology, habitat selection, and population demography (Greene, 1994; Alldredge and Griswold, 2006; Micheli-Campbell et al., 2017).

---

[9] Corresponding author. E-mail: alsimms93@gmail.com

DOI: 10.1670/20-113

We investigated the spatial ecology, habitat selection, activity, and demography of *L. yuwonoi* in a human-modified ecosystem in central Sulawesi. Our specific objectives were to 1) determine movement patterns and test for sex-based differences in those parameters; 2) quantify habitat selection to determine habitat requirements; 3) estimate population size and age-class structure; and 4) quantify sexual dimorphism in head width and body size. We discuss the implications of our findings for the conservation and management of this critically endangered species.

Materials and Methods

Study Area.—Our study population was in central Sulawesi within a stream system surrounded by a village with low-density housing and plantations consisting primarily of a mixture of cocoa, coconut, and palm sugar. We do not provide the specific locality here because *L. yuwonoi* is a critically endangered species that is vulnerable to poaching (Riyanto, 2006). The climate throughout central Sulawesi is classified as tropical with an annual rainfall of 1,000–3,000 mm (Whitten et al., 2002). Central Sulawesi has two seasons: the dry season, which runs from April to August, and the wet season, from September to March. The streams were shallow, clear, and consisted of runs, riffles, and pools (~1 m deep). Substrate consisted of rocks, sand, and pebbles; the banks were moderately to heavily vegetated. There were natural forest areas embedded within the plantations and our survey site in riparian zones and adjacent forested mountainsides. The forests were considered natural as they lacked plantation trees (coconut, cocoa, and clove trees). Riparian zones consisted of dense broadleaf plants and vines, and stream riparian buffer zones were typically no more than 100 m wide before giving way to plantations. Mountainsides had large trees with a dense canopy and variable understory (plantations were absent from these areas likely because of difficult, steep terrain). Local people use the stream as a resource for bathing, clothes washing, and drinking water.

Sampling.—We surveyed for turtles during two 6-wk field trips in 2019 during the end of the wet season (February–April) and the dry season (June–July). Surveys were conducted initially by walking lengths of stream during the evening between 2000 and 0200 h. We used headlamps and the assistance of an experienced local guide to locate turtles, which were then caught by hand. Once radiotelemetry surveys began, we continued surveying for turtles in the same sections of stream daily or every second day while we were radio tracking with the assistance of the same guide, although sampling was more opportunistic. When a turtle was captured, we recorded the location with a handheld global positioning system (GPS) (Garmin GPSMap 64s). Turtles were measured using calipers (CL and width, plastron length and width, and head width) to the nearest 1 mm and weighed using spring scales (Pesola®) to the nearest 1 g. We photographed each turtle and then individually marked it by notching marginal scutes with a file following Cagle (1939). We classed turtles as adults when their CL was greater than 170 mm for females and 190 mm for males (Hagen et al., 2009). Adults were sexed in the field on the basis of males having a larger and yellow or white head, a longer tail (Fig. 1), and a more concave plastron than do females (Hagen et al., 2009). Our sample contained seven animals of a size that made it difficult to determine sex. Thus, the sex of all radio-tracked individuals was independently verified by three *L. yuwonoi* experts (from Turtle Survival Alliance) upon returning from the field, on the basis of photographs of the turtles and without prior knowledge of the sex assigned in the field. According to all three experts, the sex of the turtles matched the sex assigned in the field in all cases. Recaptured yearlings and juveniles were measured and weighed each time they were captured, whereas adults were reweighed and measured only if at least 1 mo had passed since their last capture (because of their slow growth rate).

Population Demography.—We conducted capture–mark–recapture (CMR) surveys in two separate sections of the study stream approximately 200 m apart where turtle capture numbers and recapture percentages were suitable for modeling (typically 20% recapture rates or higher). The two sections of stream are connected where there is an upper stream section that is part of a tributary that branched off the lower stream section (Fig. 2). The lower stream section was ca. 700 m in length and the upper stream section was ca. 500 m. We spent the initial 2 wk conducting just CMR surveys daily until all turtles were caught to begin the radio-tracking study. Once radiotelemetry began, we continued to conduct CMR surveys during each primary survey period (wet season and dry season, 2019) along each stream section opportunistically every 2 days (i.e., secondary survey period). Our surveys were conducted simultaneously with radiotelemetry surveys; however, we excluded any radio-tracked turtles from CMR data collection because of recapture bias (four turtles from lower stream and six turtles from upper stream).

We used the program MARK (version 9.0; White and Burnham, 1999) to model and analyze CMR data. The probability of temporary emigration (γ) was forced to equal zero in all models. The best model was selected using the Akaike information criterion corrected for small sample sizes (AIC_c; Burnham and Anderson, 2002). Models were ranked from lowest to highest AIC_c and ΔAIC values were calculated by subtracting the lowest AIC_c score from that of each of the other models. Akaike weights (w) were also calculated to quantify the relative strength of evidence in support of a particular model, given the data available (Burnham and Anderson, 2002). No covariates were used within these analyses.

Radiotelemetry.—During the wet season survey, the first 20 adult turtles captured were fitted with radio transmitters (10 of each sex). Radio-tracked turtles were caught within the first 14 days and were subsequently excluded from the CMR survey because of recapture bias from radiotelemetry surveys.

Each turtle was fitted with a radio transmitter that was <5% of the turtle's total body weight (15 g per unit; RI-2B, Holohil Systems, Ontario, Canada). Transmitters were fixed to the 9th and 10th marginal scutes on the right side of the rear carapacial edge unless there was scute damage or identification (ID) notching, in which case the transmitter was then placed on the left side ($N = 3$ males). The specific positioning on the carapace reduced the chance of transmitters getting caught on vegetation and debris and avoided potential interference with mating. Transmitters were attached with epoxy (Selleys® plumbers epoxy putty). We held the turtle for ~20 min until the epoxy hardened. Turtles were then released at the point of capture.

We tracked the 20 tagged turtles at the end of the wet season one to three times per week (one daytime for every two nighttime tracking occasions), whereas tracking occasions for the remaining 14 turtles in the middle of the dry season was three to five times per week (two daytime for every three nighttime tracking occasions). Six turtles went missing during the break between tracking periods and could not be located during the dry-season tracking period. When a turtle was

FIG. 1. Photo of sexually mature male (left) and female (right).

located, we recorded its GPS coordinates. We obtained visual sightings within a few meters of the turtles in most instances and triangulated on the transmitters of turtles that were not visible to minimize potential disturbance in densely vegetated refuges or in locations of habitat we could not penetrate. We scored each turtle as either active or in a refuge. Turtles were scored as active if they were found actively basking, crawling, or swimming. Activity status was relatively easy to score because turtles rarely retreated into their shells unless they were approached closely or handled. A turtle was scored as in a refuge if we were unable to make a direct observation because of obstruction by microhabitat (e.g., turtle was under debris), or they appeared inactive with their head tucked into their shell, sometimes with limbs retracted as well.

When we found a turtle in a refuge, the following microhabitat variables were collected from a 1-m^2 plot at the point of the turtle's location: percent ground cover, estimated as the area covered by either debris or leaf litter (or both); ground cover depth at the center of the plot to the nearest 1 cm using a ruler; and canopy cover percentage, using a spherical forestry densiometer held at ~1.5 m above ground. A short description of the microhabitat was recorded and a photograph was taken over the plot. We repeated these measurements for a paired random plot located by using a random-number generator to obtain a random direction between 1 and 360° and a random distance between 1 and 10 m from the location of the turtle. When we found turtles that were active, we recorded their location with a handheld GPS and recorded their habitat and activity. Vegetation cover was analyzed using the plot photographs. Photos were scored visually using a 5 × 5 block grid overlay for percentage of leaf litter, debris, broadleaf plants, herbaceous plants/grass, and shrubs > 1 m and bare ground/rocks. We also noted if turtles were under a bank or boulder.

We used RStudio version 1.2.1335 (RStudio Team, 2018) to analyze radiotelemetry, habitat selection, and morphometric data. Location data obtained via radiotelemetry were used to determine space use using the R package adehabitatHR. We calculated area occupied by individuals using the minimum convex polygon (MCP, function mcp(); Calenge, 2006). We also calculated the area where an individual animal spends 50% of its time (Chamberlain et al., 2000) using the utilization distribution of fixed 50% kernels (KDE_{50}, function kernelUD();

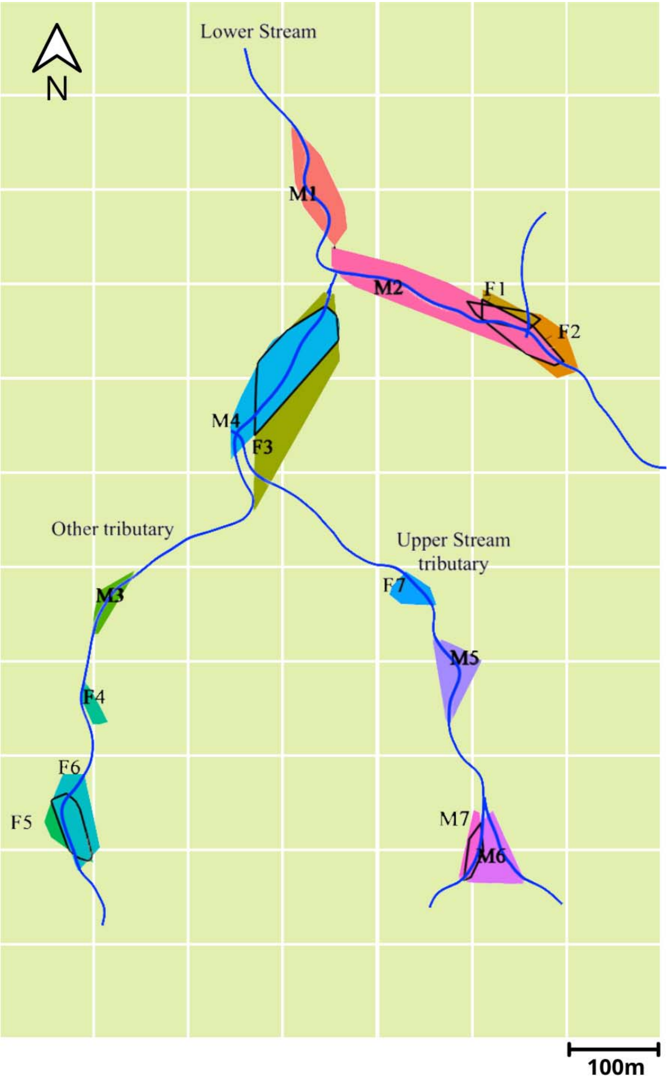

FIG. 2. Minimum convex polygons of individually numbered males (M) and females (F) from radio-tracked *Leucocephalon yuwonoi* (combined surveying periods 2019). Black outline indicates overlap in space use. Blue line represents the approximate location of the streams at the surveyed site.

Calenge, 2006). Our approach followed the methods recommended for reptiles by Row and Blouin-Demers (2006), who suggested that "LSCV" and "href" smoothing factors (*h*) are ineffective for reptiles with high site fidelity because of autocorrelation. We analyzed the degree of area overlap between individuals using the R package rgeos (function gIntersection()). We calculated daily movements by first using the R package adehabitatLT to measure the distance between each consecutive tracking point, and then dividing this distance by the number of days between fixes to get an estimate of average daily movement rate. Area occupied (MCP and KDE_{50}) and daily movement distances are reported as means ± 1 standard deviation (SD).

Microhabitat selection was assessed by comparing habitat variables for pairs of 1-m^2 plots, one centered on the turtle location and the other located randomly within a 10-m radius of the turtle. Each habitat variable was separately used as the response in a linear mixed model (LMM) or a generalized linear mixed model (GLMM) in the R package lme4, treating plot type (levels: turtle plot, random plot) as a fixed effect and turtle ID and plot pair ID as nested random effects. Depth (cm) was first $\log(x + 1)$ transformed to stabilize the variance before being used in a LMM. We also logit transformed ($\log[(x + \varepsilon)/(1 - x + \varepsilon)]$, with $\varepsilon = 0.005$) proportional-scale habitat measures with <25% zeros (i.e., canopy cover, broadleaf plant cover, ground cover) to stabilize variance while avoiding indeterminant values at 0 and 1 before conducting LMMs (Warton and Hui, 2011). Proportional-scale habitat measures with >25% zeros were submitted as the response to logit GLMM after being converted to presence/abundance data. In some instances, we reported singularities during GLMM model fitting when turtle ID and plot pair ID were submitted as nested random effects. In such instances, we dropped the random effect attributable to plot-pair ID. Turtle occupancy was generated using the best model on the basis of the lowest AIC value from model selection. The model that best explained turtle presence at plots compared with random plots used the habitat variables canopy, bare ground, leaf litter, and depth of ground cover.

We tested for sexual dimorphism using data collected from 23 females and 17 males in an analysis of covariance (ANCOVA), treating head width as the dependent variable and gender and CL as independent variables. The inclusion of CL as a covariate controlled for the effects of body size on head width. The homogeneity-of-slopes assumption was evaluated by incorporating an interaction term for gender and CL. Before analysis, a Levene's test was used to assess the assumption of homoscedasticity in our data set, which was not significant.

RESULTS

Population Demography and Size Estimates.—We captured 25 unique adult females (32%), 16 unique adult males (20%), and 38 unique unsexed juveniles (48%) across the study period. We documented a sex ratio of 1.6 females to each male but found no significant difference between the number of males and females captured ($\chi^2_{\mathrm{df}=1} = 1.98$, $P = 0.16$). Within each of the two primary survey periods (February–April, June–July) turtles displayed strong site fidelity, with numerous recaptures occurring within each stream section, but not between the stream sections. We also recorded no movement between the two sites within primary survey periods of radio-tracked animals and no mortalities or emigration away from the study area during those periods. We did, however, record the loss of 6 of 20 turtles in the radio-tracking survey between the two primary survey periods, although we do not know the cause (transmitter failure, mortality, emigration, or poaching). Thus, the data met the assumptions of relative closure during each primary survey period, but were open between each primary survey period, making them suitable for modeling with Pollock's robust design (Pollock, 1982). Pollock's robust design allows for estimates of population size (*N*) for each primary survey period, as well as temporary emigration (γ), capture (*p*), and recapture probabilities throughout (Pollock, 1982). Two primary survey periods (wet and dry season) were conducted with 20 secondary survey periods at the lower stream (p1 = 11, p2 = 9) and 16 at the upper stream (p1 = 13, p2 = 3). The best model to predict capture/recapture probability and population size estimates was similar for the upper and lower stream sections, with capture and recapture probabilities all being constant ($\{\phi(.),\gamma{=}0,p(.),c(.),\mathrm{N}(.)\}$) and only population size varying by time at the lower stream ($\{\phi(.),\gamma{=}0,p(.),c(.),\mathrm{N}(t)$}; Table 1). Capture and recapture probabilities differed from one another, with recapture probability being consistently lower than capture probability for both sites.

TABLE 1. Candidate set of models ranked by ascending Akaike information criterion corrected for small sample size ($\mathrm{AIC_c}$) used to estimate apparent capture/recapture probabilities (*p*/*c*) and population size (*N*) of *Leucocephalon yuwonoi* captured from surveys in the stream sections from wet- and dry-season surveys in 2019. The parentheses indicate the variables adopted into the model, which can vary by primary survey period = (psp), time = (*t*), or be constant = (.) in models. γ = temporary immigration/emigration parameter.

Model	AICc	$\Delta\mathrm{AIC_c}$	AICc *w*	Model likelihood	Number	Deviance
Lower stream section						
$\{\phi(.),\gamma=0,p(.),c(.),N(.)\}$	86.39	0	0.485	1	5	38.626
$\{\phi(.),\gamma=0,p= c\ (.),N(.)\}$	87.85	1.45	0.235	0.484	4	43.173
$\{\phi(.),\gamma=0,\ p\ (.),\ c\ (.),N(t)\}$	89.77	3.38	0.089	0.185	6	38.586
$\{\phi(.),\gamma=0,\ p = c\ (.),N(t)\}$	90.31	3.92	0.068	0.141	5	42.542
$\{\phi(.),\gamma=0,\ p = c\ (\mathrm{psp}),N(.)\}$	90.87	4.48	0.052	0.107	5	43.102
$\{\phi(.),\gamma=0,\ p\ (\mathrm{psp}),\ c\ (\mathrm{psp}),N(.)\}$	91.43	5.03	0.039	0.081	7	36.439
$\{\phi(.),\gamma=0,\ p = c\ (\mathrm{psp}),N(t)\}$	91.88	5.48	0.031	0.065	6	40.688
Upper stream section						
$\{\phi(.),\gamma=0,\ p\ (.),c\ (.),N(t)\}$	104.96	0	0.530	1	6	69.164
$\{\phi(.),\gamma=0,\ p\ (.),c\ (.),N(.)\}$	105.36	0.40	0.433	0.818	5	72.372
$\{\phi(.),\gamma=0,\ p = c\ (.),N(.)\}$	111.59	6.63	0.019	0.036	4	81.247
$\{\phi(.),\gamma=0,\ p = c\ (.),N(t)\}$	113.28	8.33	0.008	0.016	5	80.298
$\{\phi(.),\gamma=0,\ p = c\ (\mathrm{psp}).N(.)\}$	113.58	8.63	0.007	0.013	5	80.598
$\{\phi(.),\gamma=0,\ p = c\ (\mathrm{psp}),N(t)\}$	115.98	11.03	0.002	0.004	6	80.192

Modeled population size (95% confidence intervals [CIs]) for the lower stream was estimated to be 17 turtles (15–28) in the wet-season survey and 10 turtles (8–21) in the dry-season survey, excluding the four radio-tracked turtles. For the upper stream, population size (95% CIs) was estimated to be 25 turtles (24–33) in the wet and 13 turtles (9–28) in the dry season survey, excluding the six radio-tracked turtles. Adding radio-tracked turtles back to the population estimate means, we thus estimated population density in the lower stream to be 3.0 turtles per 100 m of stream in the wet season and 2.0 turtles per 100 m of stream in the dry season. In the upper stream, the density was estimated to be 6.2 turtles per 100 m of stream in the wet-season survey and 3.4 turtles per 100 m of stream in the dry-season survey.

Spatial Ecology.—Of the 20 turtles fitted with radio transmitters, 14 turtles were tracked for the duration of the study and therefore included in analyses. Six turtles could not be located during the dry-season surveys after a 10-wk break between tracking periods. The area occupied for both sexes combined was an average of 0.49 ± 0.42 ha ($N = 14$) for MCP and 0.08 ± 0.06 ha for $\mathrm{KDE_{50}}$ ($N = 14$, Table 2). Males had a somewhat higher MCP size than females (0.53 ± 0.40 ha vs. 0.44 ± 0.46 ha), but this did not differ significantly ($t_{12} = -0.39$, $P = 0.70$). The average $\mathrm{KDE_{50}}$ for males (0.070 ± 0.050 ha) and females (0.078 ± 0.070 ha) was also not significantly different ($t_{10} = 0.13$, $P = 0.90$). CL was not correlated with MCP ($r_s = -0.064$, $P = 0.83$) or $\mathrm{KDE_{50}}$ ($r_s = -0.011$, $P = 0.98$) of males or females.

TABLE 2. Minimum convex polygon (MCP) and 50% kernel density estimate ($\mathrm{KDE_{50}}$) results of radio-tracked *Leucocephalon yuwonoi*. CL = carapace length.

Gender	Identification	CL (cm)	MCP100 (ha)	h^a	$\mathrm{KDE_{95}}$ (ha)	$\mathrm{KDE_{50}}$ (ha)
Female	F1	20.2	0.1831	2.84	0.1826	0.0299
Female	F2	19.2	0.5473	5.49	0.5468	0.1260
Female	F3	21.1	1.4200	13.4	1.4187	0.2276
Female	F4	19.8	0.0853	2.16	0.0851	0.0127
Female	F5	19.3	0.2860	3.7	0.2859	0.0609
Female	F6	24	0.4330	4.94	0.4324	0.0694
Female	F7	20	0.1563	3.45	0.1564	0.0206
Male	M1	26.4	0.5228	5.48	0.5227	0.0619
Male	M2	19.4	1.1962	7.838	1.1967	0.1114
Male	M3	26	0.1559	2.77	0.1560	0.0221
Male	M4	26.5	0.9471	8.268	0.9472	0.1506
Male	M5	24.6	0.3564	4.52	0.3564	0.0628
Male	M6	24.7	0.4114	5.728	0.4115	0.0895
Male	M7	27.4	0.1473	3.19	0.1472	0.0182

[a] *h* represents the smoothing factor chosen for kernel estimates.

Ten of 14 radio-tagged turtles showed space use overlap, with male–male, male–female, and female–female overlap all occurring (Fig. 2). The proportion of overlap varied across interaction type. Male pairs had the lowest overlap (average proportion of overlap = 14.88% ± 20.7% SD), whereas female pairs had the highest proportion of overlap (51.0% ± 22.8% SD). Mixed pairs that had overlapping occupied areas included a male and two females with an average overlap of 41.62% ± 24.1% SD.

Activity Patterns.—Both male and female turtles were primarily nocturnal but still displayed some daytime activity. Males were significantly more active than females at night ($X^2_{\mathrm{df}=1}$= 23.7, P = 23.7, $P < 0.001$) and during the day ($X^2_{\mathrm{df}=1}$= 10.62 = 10.62, $P = 0.001$). Daytime activity for males doubled during the dry season compared with the wet season. Average daily distance moved was greater in males (14.4 ± 7.2 m SD straight-line distance) than in females (8.4 ± 2.7 m SD straight-line distance), but the difference was not statistically significant ($t_8 = -2.08$, $P = 0.072$).

Habitat Selection.—Turtles used refuges with significantly greater canopy cover, broadleaf plant cover, ground cover, and deeper ground cover than random plots (Table 3). GLMMs indicated that the presence of debris was higher in plots containing turtles than adjacent random plots, but random plots were significantly more likely to have leaf litter, bare ground, and herbaceous plants.

We found a significant positive response of turtle presence (plot) with an increase in canopy cover and depth of ground cover, whereas higher cover in bare ground, leaf litter, and herbaceous plants reduced the occurrence of turtles (random plot). Plots used by females had significantly more herbaceous plants and grass than those used by males.

Sexual Dimorphism.—CL was significantly ($t_{38} = -9.29$, $P < 0.001$) larger in males than in females (males: mean = 24 ± 1.9 cm SD; females: mean = 19.8 ± 1.2 cm SD). On average, males had significantly wider heads (41 ± 3.1 mm SD) than females (32 ± 2.0 mm SD), including when controlling for CL length (ANCOVA, CL: $F_{1,36} = 491.3$, $P < 0.001$; sex: $F_{1,36} = 122.7$, $P < 0.001$; CL × gender interaction: $F_{36,37} = 0.166$, $P = 0.69$).

TABLE 3. Results of linear mixed model (LMM) analysis comparing habitat characteristics of plots with turtles present with adjacent randomly selected plots. Significance was assessed by separately running each habitat variable as the response variable in a LMM, treating plot type (levels: turtle plot, random plot) as the fixed effect. Bold type indicates that the fixed effect is significant ($P < 0.05$, Satterthwaite's method), with negative estimates indicating higher values for turtle plots than random plots.

Variable[a]	Estimate	Standard error	df	t	P-value
Canopy	−0.429	0.161	247.0	−2.663	**0.008**
Broadleaf plants	−0.884	0.233	247.0	−3.794	$\mathbf{1.87 \times 10^{-4}}$
Ground cover	−1.652	0.261	247.0	−6.38	$\mathbf{1.09 \times 10^{-9}}$
Depth of ground cover	−0.701	0.089	244.7	−7.869	$\mathbf{1.15 \times 10^{-13}}$

[a] Percentage of cover variables (canopy, broadleaf plants, ground cover) logit-transformed before analysis using $y=\log[(x+\varepsilon)/(100-x+\varepsilon)]$, with $\varepsilon=0.5\{\%$, to stabilize variances while avoiding indeterminant values at 0 and 100%. Depth (in cm) was $\log(x+1)$-transformed.

DISCUSSION

The lack of ecological and behavioral data for *L. yuwonoi* hinders its conservation and management (Hagen et al., 2009), especially in light of the Asian turtle crisis (Rhodin et al., 2018). Our study provides the first quantitative understanding of the demography, spatial ecology, habitat selection, and activity of *L. yuwonoi* in nature.

Population Demography.—The relatively high capture rate of juveniles indicates that recruitment was likely occurring, although repeated CMR surveys are needed to establish population viability over the longer term (Van Dyke et al., 2018b). As *L. yuwonoi* are known to lay one to two large eggs, females may invest more reproductive effort into hatchling size than quantity, increasing the probability of hatchling survival (Jonsson and Ebenman, 2001; Janzen and Warner, 2009). However, the high proportion of juveniles compared with adults may also indicate that our study population has potentially been affected by some level of harvesting. Sung et al. (2013) found that Big-Headed Turtles (*Platysternon megacephalum*) had high proportions of juveniles at harvested sites (61.5–87.5%) compared with unharvested sites (31.8%). Unharvested sites also had larger adult turtles (>110-mm plastron length) than the harvested sites (Sung et al., 2013). Seateun et al. (2019) found a skewed size-class population for Oldham's Leaf Turtle (*Cyclemys oldhamii*) in Thailand because of harvesting, with a higher proportion of small subadults (51%) at constructed ponds where illegal collection occurred compared with a protected stream (Seateun et al., 2019). It therefore seems possible that illegal collection of turtles has affected the demography of *L. yuwonoi* at our study site because almost half the captures were juveniles.

The small population estimates, skewed age-class structure, and a 30% loss of turtles from our radiotelemetry study also raise concerns surrounding harvesting. It is possible that some or all of our missing radio-tagged turtles were collected during the clove-harvesting season in central Sulawesi, where people from other villages visited our survey site starting at the beginning of May until the end of August. We were not tracking our turtles for a 10-wk period at that time. Additionally, radio-tagged turtles were lost from the two tributaries branching off the lower stream (Fig. 2). Both tributaries were narrow (∼1–3 m wide) and lined by clove orchards a short distance from the stream. However, no turtles were lost from the lower connecting stream, which was much wider and more open (∼5–10 m wide) and was not within sight of any clove orchards. On the basis of our observations, we never encountered anyone looking for turtles at our site, and conversations with our guide and local villagers indicated that their community does not tend to harvest turtles in the study area. However, local people informed us that nonlocal people harvest wildlife, including turtles, especially during the clove-harvesting season. The propensity to harvest wildlife varies across villages and ethnicities, with at least some groups known to harvest turtles. We conducted expanded searches for the missing turtles during our study (including radiotelemetry and visual searches). Considering the strong site fidelity observed from our study and the high recapture rate of turtles in the study area, transmitter failure seems unlikely because we probably would have captured at least some of the missing turtles by chance. We had two transmitters fall off turtles during the study, but they were retrieved again later because of the nature of the stream environment (mostly shallow rocky streams). Shed transmitters were found tangled in debris not far downstream. We therefore believe it was unlikely for the transmitters of the missing turtles to have fallen off and been lost completely.

Spatial Ecology.—The area occupied using the MCP method was ∼17% larger in males than in females. The lack of statistical significance for this difference was likely because of low sample size (power). Because KDE_{50} was similar between the sexes, the larger MCP in males may have reflected mate searching. Because of the short duration of our study, we have avoided the use of the term "home range" despite reaching an asymptote for the MCP (∼27 tracking fixes) during our study. Further radio tracking is required to determine a precise home-range size for *L. yuwonoi*. However, we still compared the size of the area occupied by *L. yuwonoi* with the home-range size from other species within the family Geoemydidae (Table 4) and found that *L. yuwonoi* may occupy the smallest area. However, the MCP method is sensitive to sample size and extreme outliers (Börger et al., 2006; Harless et al., 2010), so caution should be exercised in this comparison. Regardless, we provided evidence for strong site fidelity from the KDE_{50} method for *L. yuwonoi* where an asymptote was reached at around 27 tracking fixes during surveys. Kernel density estimates may be better for comparisons, where we find *L. yuwonoi* to be more similar to *C. oldhamii* in their KDE_{50} (Table 4; Durkin, 2012), despite MCP being vastly different.

Activity Patterns.—*Leucocephalon yuwonoi* were primarily nocturnal during the survey period, with males being more active than females. Males also displayed some diurnal activity (females did not), which increased during the dry season. There may be seasonal patterns in diurnal activity for these turtles that are not currently understood and would require further investigation.

Habitat Selection.—The turtles we radio tracked were often found on land or in shallow water (not deep enough to swim), rarely in deeper pools. Turtles favored habitat with structure composed of debris, generous ground cover, and broadleaf plants and canopy for refuge. Our results are similar to other studies on forest-dwelling species (e.g., *Rhinoclemmys rubida*, *Terrapene ornata ornata*) where turtles nonrandomly selected structural microhabitat variables (e.g., increase in debris and canopy cover; Butterfield et al., 2018; Ursek and Higa, 2019). A potential reason for the selection of relatively dense cover by *L. yuwonoi* may be to avoid the heat in Central Sulawesi where maximum day temperatures were recorded at 33°C during surveys. *Leucocephalon yuwonoi* selected for particular habitats within more natural sites and plantations. For example, one female turtle was consistently found in a refuge of fallen palms under dense canopy in a salak

TABLE 4. Review of home range sizes (MCP and KDE_{50}) from turtle species in the family Geoemydidae.

Species			Home range ± SD (ha)		
Family: Geoemydidae	Habitat use	*N*	MCP	KDE_{50}	Cited in:
Leucocephalon yuwonoi	Semiaquatic	14	0.49 ± 0.42	0.07 ± 0.06	Present study
Cuora flavomarginata	Semiaquatic	17	1.06 ± 1.62	NA[a]	Lue and Chen, 1999
Cyclemys oldhamii	Semiaquatic	13	13.9 ± 15.76	0.06 ± 0.05	Durkin, 2012
Mauremys leprosa	Aquatic	6	3.27 ± 0.76	NA	Pérez-Santigosa et al., 2013
Melanochelys tricarinata	Terrestrial	[b]	1.15 ± unknown	NA	Mondal et al., 2016
Rhinoclemmys rubida perixantha	Terrestrial	12	0.92 ± 0.41	NA	Butterfield et al., 2018
Vijayachelys sylvatica	Terrestrial	11	7.2 ± 4.77	NA	Vasudevan et al., 2010

[a] NA = not applicable.

[b] Sample size could not be determined from article.

(*Salacca zalacca*) plantation. In addition, we observed turtles to take refuge in holes in banks and gaps under boulders. Although our study was in a human-modified environment, there was apparently enough heterogeneity in vegetation from cultivated fruit trees and plants, including some remnant vegetation, to allow *L. yuwonoi* to persist. Only a single major difference in habitat selection occurred between the sexes, where female refuges had significantly more herbaceous plants and grass cover than did those used by males. Further investigation is required to explain the observed differences in habitat selection between the sexes.

Sexual Dimorphism.—Males were larger in size (CL) and had wider heads than did females, a finding that is unusual within the Geoemydidae, where females are typically larger than males (Cox et al., 2007). The larger head size in *L. yuwonoi* males could be a result of ecological pressures for resource partitioning (e.g., diet or male–male combat; Slatkin, 1984; Shine, 1989; Fairbairn, 1997). Sexual size dimorphism in *L. yuwonoi* appears to support the hypothesis that habitat type correlates with sexual size dimorphism, whereby larger males are more common in semiaquatic turtles (Berry and Shine, 1980; Ceballos et al., 2013). Observations of male *L. yuwonoi* in captivity support the notion that forced insemination of females is often linked with male-biased sexual size dimorphism (Berry and Shine, 1980; Hagen et al., 2009). Female choice is an unlikely factor if sexual selection is being driven by forced insemination. The male-biased sexual size dimorphism we found may be explained by male–male combat. Although male–male combat has not been observed in the wild, it has been observed in captivity (C. Hagen, pers. comm.). Finally, conspicuous ornamentation is suggested to occur mainly in species with female-biased sexual size dimorphism (Brejcha and Kleisner, 2016); this is not the case for *L. yuwonoi*, which exhibits male-biased sexual size dimorphism.

Conservation Implications.—Habitat for *L. yuwonoi* is thought to be diminishing because of land clearing for agriculture (Riyanto, 2006; Tothmihaly et al., 2019). Protecting viable habitat by preventing further habitat clearing or management of farming practices for the remaining turtle populations is particularly important given their life-history traits (slow growth rate, delayed maturity; Ives, 2006; Enneson and Litzgus, 2008). Understanding habitat use and requirements, such as what we report here, is crucial for effective management of habitat protection and species conservation (Rasmussen and Litzgus, 2010). The turtles in our study appear to be able to persist in human-altered habitat that is dominated by nearby coconut and cocoa plantations, although we are unable to comment on longer-term population viability in these landscapes. Ives et al. (2008) also noted that *L. yuwonoi* did not appear to be dependent on undisturbed primary forest, perhaps partly because turtles do not venture far from the stream, where riparian vegetation contains more natural forest and is complex, offering microhabitats in which they can take refuge. The riparian vegetation might thus be acting as an important buffer zone for *L. yuwonoi*, supporting recommendations that conservation strategies implement buffer zones of at least 123 m to 289 m from wetland and stream habitat for turtles (Semlitsch and Bodie, 2003). It is difficult, however, to determine to what extent habitat loss and degradation have affected turtles in our study population, as we lack before-and-after data.

Findings from our study provide important baseline ecologic data for *L. yuwonoi*. We recommend implementing a long-term monitoring program for further conservation management of *L. yuwonoi*, while also documenting the impacts of human activity (e.g., population size, hunting practices, source of income, etc.) and farming practices (e.g., crop types, fertilizer/pesticide/herbicide use and frequency, etc.) on the species. Conservation management efforts should include continuing CMR surveys to provide ongoing population information that can be compared with our baseline data to assess any future management actions.

Despite export restrictions being in place (CITES Appendix II, 2021; Shepherd and Nijman, 2007), lack of on-ground protection and education for collecting and trade of turtles within Sulawesi is likely a threatening process (Riyanto, 2006). Removal of adult turtles can have heightened detrimental effects for populations because of particular life-history traits that include delayed sexual maturity and small clutch sizes (Turtle Conservation Coalition, 2018), thus making them more vulnerable to overexploitation. For turtles with low fecundity, it has been suggested that conservation should prioritize the survival and persistence of adults to stabilize declining populations and maintain recruitment (Heppell, 1998; Enneson and Litzgus, 2008; Tutterow et al., 2017). We recommend the implementation of this strategy for *L. yuwonoi*, which has low fecundity. Different communities vary in hunting practices and their intensity, often associated with ethnicity and religion (Luskin et al., 2014). In an effort to mitigate overexploitation, identifying where *L. yuwonoi* are more likely to be hunted on the basis of community practice may be a valuable conservation tool. Furthermore, areas supporting those communities that are likely to hunt turtles should be avoided when captive animals are released after any potential head-start programs. We hope that the fundamental ecologic data we collected during telemetry and stream surveys will help in ongoing efforts to better understand and conserve this unique but critically endangered turtle.

Acknowledgments.—Generous support and funding for this project came from the following organizations: Turtle Survival Alliance, Macquarie University, Wildlife Reserves Singapore, Mohamed bin Zayed Species Conservation Fund, Turtle Conservation Fund, Holohil Systems Ltd., Riverbanks Zoo & Garden, Columbus Zoo and Aquarium, Oklahoma City Zoo, and Global Wildlife Conservation. This research was conducted with permission and approval of the Indonesian research authority, Ristek (permit no: 303/SIP/FRP/E5/Dit.KI/X/2018) and approved by the Macquarie University Animal Ethics committee (AEC Ref. no: 2019/004). We thank our local guide W. Wati for his assistance with daily fieldwork and his family and other community members for providing warm hospitality. We also thank J. Lawson for his assistance with R and our analyses.

Literature Cited

Alldredge, J. R., and J. Griswold. 2006. Design and analysis of resource selection studies for categorical resource variables. Journal of Wildlife Management 70:337–346.

Anthonysamy, W. J. B., M. J. Dreslik, and C. A. Phillips. 2013. Disruptive influences of drought on the activity of a freshwater turtle. American Midland Naturalist 169:322–335.

Asian Turtle Trade Working Group. 2000. *Leucocephalon yuwonoi*. The IUCN Red List of Threatened Species 2000: e.T40761A97369570.

Berry, J. F., and R. Shine. 1980. Sexual size dimorphism and sexual selection in turtles (Order Testudines). Oecologia 44:185–191.

Böhm, M., B. Collen, J. E. M. Baillie, P. Bowles, J. Chanson, N. Cox, G. Hammerson, M. Hoffmann, S. R. Livingstone, M. Ram, et al. 2013. The conservation status of the world's reptiles. Biological Conservation 157:372–385.

Börger, L., N. Franconi, G. De Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari, and T. Coulson. 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75:1393–1405.

Brejcha, J., and K. Kleisner. 2016. Turtles are not just walking stones: conspicuous coloration and sexual selection in freshwater turtles. Biosemiotics 9:247–266.

Buhlmann, K. A., T. S. B. Akre, J. B. Iverson, D. Karapatakis, R. A. Mittermeier, A. Georges, A. G. J. Rhodin, P. P. van Dijk, and J. W. Gibbons. 2009. A global analysis of tortoise and freshwater turtle distribution with identification of priority conservation areas. Chelonian Conservation and Biology 8:116–149.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach. Springer, United States.

Butterfield, T. G., A. Scoville, A. García, and D. D. Beck. 2018. Habitat use and activity patterns of a terrestrial turtle (*Rhinoclemmys rubida perixantha*) in a seasonally dry tropical forest. Herpetologica 74:226–235.

Cagle, F. R. 1939. A system of marking turtles for future identification. Copeia 3:170–173.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Ceballos, C. P., D. C. Adams, J. B. Iverson, and N. Valenzuela. 2013. Phylogenetic patterns of sexual size dimorphism in turtles and their implications for Rensch's rule. Evolutionary Biology 40:194–208.

Chamberlain, M. J., C. D. Lovell, and B. D. Leopold. 2000. Spatial-use patterns, movements, and interactions among adult coyotes in central Mississippi. Canadian Journal of Zoology 78:2087–2095.

Chessman, B. C. 2011. Declines of freshwater turtles associated with climatic drying in Australia's Murray–Darling Basin. Wildlife Research 38:664–671.

CITES. 2021. Convention on International Trade in Endangered Species of Wild Fauna and Flora. Appendices I, II and III. Valid from 22 June 2021. https://cites.org/sites/default/files/eng/app/2021/E-Appendices-2021-06-22.pdf

Cox, R. M., M. A. Butler, and H. B. John-Alder. 2007. The evolution of sexual size dimorphism in reptiles. Pp. 38–49 in D. J. Fairbairn, W. U. Blanckenhorn, and T. Székely (eds.), Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford University Press, U.K.

Durkin, L. 2012. The spatial ecology of the Southeast Asian leaf turtle (*Cyclemys oldhamii*) in Phnom Kulen national park. Honours Thesis, La Trobe University, Melbourne, Australia.

Enneson, J. J., and J. D. Litzgus. 2008. Using long-term data and a stage classified matrix to assess conservation strategies for an endangered turtle (*Clemmys guttata*). Biological Conservation 141:1560–1568.

Fairbairn, D. J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. Annual Review of Ecology and Systematics 28:659–687.

Gillespie, G. R., S. Howard, J. T. Stroud, A. Ul-Hassanah, M. Campling, B. Lardner, M. P. Scroggie, and M. Kusrini. 2015. Responses of tropical forest herpetofauna to moderate anthropogenic disturbance and effects of natural habitat variation in Sulawesi, Indonesia. Biological Conservation 192:161–173.

Greene, H. W. 1994. Systematics and natural history, foundations for understanding and conserving biodiversity. American Zoologist 34: 48–56.

Hagen, C., S. G. Platt, and C. J. Innis. 2009. *Leucocephalon yuwonoi* (McCord, Iverson, and Boeadi 1995)—Sulawesi forest turtle, kura-kura Sulawesi. In A. G. J. Rhodin, P. C. H. Pritchard, P. P. van Dijk, R. A. Saumure, K. A. Buhlmann, J. B. Iverson, and R. A. Mittermeier (eds.), Conservation Biology of Freshwater Turtles and Tortoises 5: 039.1–039.7. doi:10.3854/crm.5.039.yuwonoi.v1.2009.

Harless, M. L., A. D. Walde, D. K. Delaney, L. L. Pater, and W. K. Hays. 2010. Sampling considerations for improving home range estimates of Desert Tortoises: effects of estimator, sampling regime, and sex. Herpetological Conservation and Biology 5:374–387.

Heppell, S. S. 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia 1998:267–275.

Ives, I. 2006. Conservation of Sulawesi's Two Endemic Chelonians, *Leucocephalon yuwonoi* and *Indotestudo forstenii*: an investigation into in-situ conservation concerns. M.S. Thesis, Antioch University New England, New Hampshire.

Ives, I. E., S. G. Platt, J. S. Tasirin, I. Huwowu, S. Siwu, and T. R. Rainwater. 2008. Field surveys, natural history observations, and comments on the exploitation and conservation of *Indotestudo forstenii*, *Leucocephalon yuwonoi*, and *Cuora amboinensis* in Sulawesi, Indonesia. Chelonian Conservation and Biology 7:240–248.

Janzen, F. J., and D. A. Warner. 2009. Parent–offspring conflict and selection on egg size in turtles. Journal of Evolutionary Biology 22: 2222–2230.

Jonsson, A., and B. Ebenman. 2001. Are certain life histories particularly prone to local extinction? Journal of Theoretical Biology 209:455–463.

Lue, K.-Y., and T.-H. Chen. 1999. Activity, movement patterns, and home range of the yellow-margined box turtle (*Cuora flavomarginata*) in Northern Taiwan. Journal of Herpetology 33:590–600.

Luskin, M. S., E. D. Christina, L. C. Kelley, and M. D. Potts. 2014. Modern hunting practices and wild meat trade in the oil palm plantation-dominated landscapes of Sumatra, Indonesia. Human Ecology 42:35–45.

Micheli-Campbell, M. A., M. J. Connell, R. G. Dwyer, C. E. Franklin, B. Fry, M. J. Kennard, J. Tao, and H. A. Campbell. 2017. Identifying critical habitat for freshwater turtles: integrating long-term monitoring tools to enhance conservation and management. Biodiversity and Conservation 26:1675–1688.

Miettinen, J., C. Shi, and S. C. Liew. 2011. Deforestation rates in insular Southeast Asia between 2000 and 2010. Global Change Biology 17: 2261–2270.

Mondal, I., R. S. Kumar, B. Habib, and G. Talukdar. 2016. Modelling fine scale movement corridors for the tricarinate hill turtle. International Archives of Photogrammetry, Remote Sensing and Spatial Information Sciences 41:719–725.

Naveda-Rodriguez, A., R. Cueva, and G. Zapata-Rios. 2018. Space use of yellow-spotted river turtles (*Podocnemis unifilis*) in Yasuni national park, Ecuador. Chelonian Conservation and Biology 17:37–43.

Pérez-Santigosa, N., J. Hidalgo-Vila, and C. Díaz-Paniagua. 2013. Comparing activity patterns and aquatic home range areas among exotic and native turtles in southern Spain. Chelonian Conservation and Biology 12:313–319.

Pollock, K. H. 1982. A capture–recapture design robust to unequal probability of capture. Journal of Wildlife Management 46:752–757.

Rasmussen, M. L., and J. D. Litzgus. 2010. Habitat selection and movement patterns of spotted turtles (*Clemmys guttata*): effects of spatial and temporal scales of analysis. Copeia 2010:86–96.

Rhodin, A. G. J., C. B. Stanford, P. P. van Dijk, C. Eisemberg, L. Luiselli, R. A. Mittermeier, R. Hudson, B. D. Horne, E. V. Goode, G. Kuchling, et al. 2018. Global conservation status of turtles and tortoises (Order Testudines). Chelonian Conservation and Biology 17:135–161.

Riyanto, A. 2006. Notes on exploitation, population status, distribution, and natural history of the Sulawesi forest turtle (*Leucocephalon yuwonoi*) in North Central Sulawesi, Indonesia. Chelonian Conservation and Biology 5:320–323.

Row, J. R., and G. Blouin-Demers. 2006. Kernels are not accurate estimators of home-range size for herpetofauna. Copeia 2006:797–802.

RStudio Team. 2018. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA. http://www.rstudio.com/.

Seateun, S., N. E. Karraker, B. L. Stuart, and A. Aowphol. 2019. Population demography of Oldham's leaf turtle (*Cyclemys oldhamii*) in protected and disturbed habitats in Thailand. PeerJ 7:e7196.

Semlitsch, R. D., and J. R. Bodie. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology 17:1219–1228.

Shepherd, C. R., and V. Nijman. 2007. An overview of the regulation of the freshwater turtle and tortoise pet trade in Jakarta, Indonesia. TRAFFIC Southeast Asia, Malaysia.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Quarterly Review of Biology 64:419–461.

Slatkin, M. 1984. Ecological causes of sexual dimorphism. Evolution 38: 622–630.

Sung, Y-. H., N. F. Karraker, and B. C. H. Hau. 2013. Demographic evidence of illegal harvesting of an endangered Asian turtle. Conservation Biology 27:1421–1428.

Tothmihaly, A., V. Ingram, and S. von Cramon-Taubadel. 2019. How can the environmental efficiency of Indonesian cocoa farms be increased? Ecological Economics 158:134–145.

Turtle Conservation Coalition. 2018. Turtles in trouble: the world's 25+ most endangered tortoises and freshwater turtles—2018. C. B. Stanford, A. G. J. Rhodin, P. P. van Dijk, B. D. Horne, T. Blanck, E. V. Goode, R. Hudson, R. A. Mittermeier, A. Currylow, C. Eisemberg, et al. (eds.).

Tutterow, A. M., G. J. Graeter, and S. E. Pittman. 2017. Bog turtle demographics within the southern population. Copeia 105:293–300.

Ursek, D. W., and A. Higa. 2019. Habitat characteristics and selection by ornate box turtles in the Sandhills of South Dakota. Western North American Naturalist 79:56–62.

Van Dyke, J., B. O. Ferronato, and R.-J. Spencer. 2018a. Current conservation status of Australian freshwater turtles. Australian Journal of Zoology 66:1–3.

Van Dyke, J., R.-J. Spencer, M. B. Thompson, B. Chessman, K. Howard, and A. Georges. 2018b. Conservation implications of turtle declines in Australia's Murray River system. Nature 9:1–12.

Vasudevan, K., B. Pandav, and V. Deepak. 2010. Ecology of two endemic turtles in Western Ghats. Final Technical Report, Wildlife Institute of India. https://wii.gov.in/images/publications/researchreports/2010/ecology_endemic_turtle_2010.pdf

Wanger, T. C., D. T. Iskandar, I. Motzke, B. W. Brook, N. S. Sodhi, Y. Clough, and T. Tscharntke. 2010. Effects of land-use change on community composition of tropical amphibians and reptiles in Sulawesi, Indonesia. Conservation Biology 24:795–802.

Warton, D. I., and F. K. C. Hui. 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology 92:3–10.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimations from populations of marked animals. Bird Study 46: S120–S139.

Whitten, T., G. S. Henderson, and M. Mustafa. 2002. The Ecology of Sulawesi. 6th ed. Gadjah Mada University Press, Indonesia.

Zabel, F., R. Delzeit, J. M. Schneider, R. Seppelt, W. Mauser, and T. Václavík. 2019. Global impacts of future cropland expansion and intensification on agricultural markets and biodiversity. Nature Communications 10:1–10.

Accepted: 28 January 2022.