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SPATIAL ECOLOGY AND CONSERVATION OF THE CENTRAL AMERICAN RIVER
TURTLE (*DERMATEMYS MAWII*)

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SPATIAL ECOLOGY AND CONSERVATION OF THE CENTRAL AMERICAN RIVER
TURTLE (DERMATEMYS MAWII)

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ABSTRACT

Overexploitation of species is one of the primary causes of severe population declines. Conservation initiatives employ various strategies, such as protected land and captive breeding programs, to mitigate the effects of overexploitation. However, detailed knowledge of species' spatial ecology is a vital component of these successful conservation initiatives. We address the underlying need to elucidate spatial information for the Central American river turtle (*Dermatemys mawii*) — a wholly aquatic species that is suffering the effects of overharvesting to the point of endangerment— using two separate studies focusing on spatial ecology at broad and fine scales.

For the first study, we created a species distribution model to predict the extent of habitat suitability in Central America and quantify relevant factors that help define the ecological niche of *D. mawii* on a broader, regional scale. We examined overlap of highly suitable habitat and regions of increased hunting pressure represented by human settlements to better understand the optimal habitat with respect to environmental and anthropogenic factors. We expanded the potential range of *D. mawii* in Belize, Guatemala, and southern Mexico and found that areas of predicted suitable habitat were correlated with low elevation and moderate amounts of rain and precipitation seasonality. Although much of this area is fragmented, nearly one-half of this suitable habitat is outside zones of human settlement and may either represent previously unknown populations or be suitable for future attempts to bolster populations through translocations.

For the second study, we used radio telemetry to gain a better insight into the spatial requirements of *D. mawii* at a finer scale. We investigated juvenile home ranges at two separate sites on a single river in Belize. We calculated home range sizes using 95% and 100% minimum

convex polygons and found the mean home range size (95% mcp) to be 3.53 ha. We determined that juveniles largely maintain a small home range, from which they occasionally travel, suggesting that protection areas may be sufficient to protect individuals.

Together, these two studies add to our understanding of the distribution and habitat requirements of this rare species. This information can serve to inform policy, conservation programs, and wildlife management practices.

1 **Chapter 1: A Species Distribution Model for Conservation of the Central**
2 **American River Turtle (*Dermatemys mawii*)**

3 **ABSTRACT**

4 The Critically Endangered Central American river turtle (*Dermatemys mawii*) is endemic to
5 Belize, Guatemala, and the Yucatan peninsula region of Mexico. Although this turtle is culturally
6 important, the exact range of this species is unknown. Defining the exact range is hampered by
7 the rarity and fully aquatic nature of this species. Here, we used species distribution modelling in
8 MaxEnt to extrapolate habitat suitability on a regional scale and estimate the importance of
9 several environmental predictors on the species' range. Our results show a limited area of high
10 habitat suitability in this region with approximately 50% of that habitat falling within areas of
11 high-risk human impact, including hunting. Improved range and habitat suitability information
12 from this species distribution model is crucial to targeted conservation programs to protect
13 critical habitat areas and implement policy improvements.

14 **INTRODUCTION**

15 The Central American river turtle (*Dermatemys mawii*), the sole extant member of its family, is
16 found in lowland rivers and lagoons in the Yucatan peninsula region of Central America (Fig. 1)
17 (Iverson and Mittermeier, 1980; Vogt et al., 2011; Legler et al., 2013; Briggs-Gonzalez et al.,
18 2019). *Dermatemys mawii* has historically been hunted for sustenance and remains culturally
19 important and highly sought after in this region (Moll 1986). Within the last 50 years, mass
20 harvesting practices and commercialization have caused extirpations and fragmented populations
21 within its range (del Toro et al., 1979; Iverson and Mittermeier, 1980) leading to the IUCN
22 classification of Critically Endangered (Vogt et al., 2006). Beyond extirpation, direct effects

23 have not been documented in this species. Studies of other turtles and aquatic vertebrates show
24 that overexploitation by removing too many individuals from breeding populations cause further
25 population declines by decreasing clutch sizes (Daza and Páez, 2007; Eiseberg et al., 2017),
26 reducing recruitment (Walsh et al., 2006), and restricting genetic variability (Ratner and Lande,
27 2001; Walsh et al., 2006; Allendorf et al., 2008). *Dermatemys mawii* populations are particularly
28 vulnerable to overexploitation by having long generation times characterized by low offspring
29 survivorship and long maturation times.

30 As *D. mawii* populations decline, conservation organizations are becoming increasingly
31 involved in programs to protect this endangered species by mitigating anthropogenic threats
32 while individuals grow and reproduce. Unfortunately, for many freshwater turtle species, merely
33 allocating protected areas are inadequate to preserve endangered species populations (Norris et
34 al., 2019; Fagundes et al., 2016). However, populations in protected habitats can succeed when
35 combined with community involvement (Freitas et al., 2019), informed legislation (Karunaratna
36 et al., 2017), and captive breeding programs (Norris et al., 2019). Many such conservation
37 strategies are dependent on identifying where a species is likely to occur.

38 To counter the serious threat *D. mawii* is facing and guide future field research, a more
39 thorough understanding of this species' distribution and the environmental variables that shape
40 its distribution is necessary (Sinclair et al., 2010). The limited knowledge of *D. mawii*'s range
41 and ecological niche are based on locality data collected during diet studies (Legler and Vogt,
42 2013), population genetics studies (González-Porter et al., 2011, 2013), and habitat preference
43 observations (Legler and Vogt, 2013), with few surveys focused on understanding the full extent
44 of its distribution or fundamental niche (Vogt et al., 2011, Rainwater et al., 2012). A greater
45 ecological understanding of this species, improved planning for reintroduction sites, and

46 programs for habitat protection and conservation can be achieved by integrating habitat
47 suitability information from species distribution models (Bombi et al., 2011; Guisan et al., 2013).

48 Species distribution models (SDMs) provide information on the fundamental niche of species
49 by combining specific environmental factors (Grinnell, 1917; James et al., 1984) and the
50 geographic distribution of species observations (Hutchinson, 1959; James et al., 1984).
51 Unfortunately, both of these data types are challenging to obtain for cryptic or endangered
52 species, and available data for *D. mawii* are scarce. Field surveys are often expensive and time
53 intensive, whereas SDMs can be run using available locality data from prior studies. Machine
54 learning algorithms, like Maximum Entropy (MaxEnt), predict areas of habitat suitability using
55 presence-only occurrence points while remaining robust against small sample sizes (Anderson
56 and Gonzalez, 2011; Guillera-Aroita et al., 2014), which often occurs with rare or endangered
57 species. In this study we i) extrapolate the extent of the suitable habitat of the Central American
58 river turtle using machine learning software, ii) determine the environmental variables that are
59 associated with the distribution, and iii) identify optimal regions for conservation efforts in
60 relation to human impact. We predict that habitat suitability will be constrained by elevation and
61 rainfall. By using confirmed presence points and a combination of pertinent variables to train the
62 model, we can map areas of high habitat suitability and areas of human impact on *D. mawii*.
63 Using this map, we can predict the likelihood of occurrence of *Dermatemys mawii* in Central
64 America as well as determine areas well-suited for conservation planning.

65 **METHODS**

66 **Presence points and predictor variables**

67 Locality coordinates were collected from previously published literature (Vogt et al., 2011;
68 Rainwater et al., 2012), unpublished surveys, and museum database searches using VertNet
69 (vertnet.org; Guralnick and Constable, 2010) for records containing *Dermatemys mawii*.
70 Presence data were compiled and georeferenced to ensure accurate coordinate data in ArcMap
71 (ESRI, ver 10.6.1). Sampling design for field surveys are assumed to be as randomly sampled as
72 possible from accessible rivers and lagoons, however, to avoid spatial autocorrelation and correct
73 for sampling bias in areas where multiple surveys occurred, presence points were systematically
74 subsampled in ArcMap within 1 km grids to reflect the resolution of the environmental variables
75 (Fourcade et al., 2014).

76 We obtained BIOCLIM environmental variable raster files from the CHELSA database (Karger
77 et al., 2017) averaged from 1979–2013 at a spatial resolution of 30 arc-seconds (1 km) in a
78 WGS84 projection (Table 1). We clipped these layers to the extent (xmin = -100, xmax = -85,
79 ymin = 12, ymax = 24) of our study region to include Guatemala and Belize, as well as portions
80 of Mexico, Honduras, and El Salvador. We also included topographical elevation data from
81 USGS GMTED2010, which is suspected to be biologically relevant due to this species’
82 reliance on permanent water bodies. This layer was then resampled to the same cell size and
83 clipped to match the extent as the environmental variables in ArcMap (ESRI, ver 10.6.1).

84 To reduce collinearity and overfitting (Warren et al., 2014; Zeng et al., 2016) applied a principal
85 component analysis (PCA) to identify the factors that best explain the variance at the presence
86 points (Demšar et al., 2013). To further reduce collinearity, we used a Pearson’s correlation test
87 to confirm that all environmental features were below a 0.7 cutoff value (Gogol-Prokurat, 2011).

88 **Model parameters and assessment**

89 We used the ENMeval package (v. 0.3.0; Muscarella et al., 2014) to set data-specific parameters
90 and run the model implementing the MaxEnt algorithm (Phillips et al., 2006) in *R* (R Core Team,
91 ver.1.3.1073). A minimum convex polygon hull was created to encircle the outer presence
92 points, within which 10,000 background points (Muscarella et al., 2014) were randomly selected
93 for use in characterizing the environment. Model complexity was balanced by running models
94 across various regularization multipliers and feature classes: linear, linear quadratic, and linear
95 quadratic product (Muscarella et al., 2014; Peterson et al., 2011). Regularization multipliers from
96 one to three at intervals of 0.5 were applied to the model to correct for overfitting (Merow et al.,
97 2013). After models were completed, we determined the best fit model from the lowest Akaike
98 information criterion (AICc) value, which corrects for small sample sizes (Warren and Seifert,
99 2011). We evaluated the importance of environmental variables using permutation importance
100 rather than percent contribution because permutation importance relies on the final model rather
101 than the paths used in a particular run (Songer et al., 2012). Models were run and averaged using
102 a 5-fold cross validation (Muscarella et al., 2014). The output habitat suitability map is a cloglog
103 raster, which rescales the habitat suitability scores from zero to one, where zero represents lowest
104 predicted suitability and one represents highest predicted suitability (Phillips et al., 2017).

105 **Habitat calculation and human impact**

106 We used the mean habitat suitability value from the MaxEnt output to determine the cutoff for
107 high habitat suitability (Liu et al., 2005; Cramer, 2003). We calculated the total amount of high
108 habitat suitability by multiplying the total number of cells by the cell size. To represent regions
109 of higher human hunting pressures, we included a human settlement polygon to the habitat
110 suitability map. We transformed the point layer GHS POP (Schiavina et al., 2019; Freire et al.,
111 2016) from the Mollweide projection to WGS84 to match the environmental layers and clipped it

112 to the output of areas of high habitat suitability. A 5 km radius buffer was then added to each
113 human settlement to represent the likely concentration of hunting using boats and freediving near
114 settlements (Peck et al., 2011) before merging all points into one polygon. We calculated the area
115 of human impact layer with the same procedure as the area of high habitat suitability and
116 determined the amount of overlap in suitable habitat with potentially high hunting pressure.

117 **RESULTS**

118 **Species distribution model**

119 We used a total of 68 locality points across Mexico, Guatemala, and Belize to train the model,
120 after data quality checks and subsampling highly clustered localities.

121 With regard to the PCA used to evaluate which of the factors best explain the variance at the
122 presence points, the first two principle components explain 71.9% (PC1: 40.9% and PC2:
123 31.0%) of the variance. Precipitation of the wettest month, precipitation of the wettest quarter,
124 precipitation seasonality, and precipitation of the warmest quarter show the highest contributions
125 to PC1 and PC2 (Fig. 2).

126 The Pearson correlation test of the four variables selected from the PCA and the topographical
127 variable revealed high collinearity (0.995) between precipitation of the wettest month (Bio 13)
128 and precipitation of the wettest quarter (Bio 16), however all other variables were below the
129 cutoff value (0.7) (Table 2). We excluded Bio 16 due to the high collinearity and lower relative
130 contribution to PC1.

131 The habitat suitability model with the lowest deltaAICc score was determined to be the best fit
132 model for the data with an acceptable AUC value of 0.795 (Gogol-Prokurat, 2011; Hosmer et al.,
133 2013) using the linear quadratic product feature class at regularization multiplier 2.

134 **Habitat suitability and human impact area**

135 Elevation shows the highest permutation importance (57.2%) followed by precipitation
136 seasonality (27.3%), precipitation of wettest month (8.8%), and finally precipitation of the
137 warmest quarter (6.7%) (Table 3). At lower values, elevation, precipitation of wettest month, and
138 precipitation seasonality, habitat is predicted to be more suitable (Fig. 3). Conversely,
139 precipitation of the warmest quarter of the year predicts suitable habitat at higher values.

140 The overall habitat suitability values range from $3.67e-09$ to 0.9518 across the study extent. The
141 mean habitat suitability value (0.213) was used for the threshold of high suitability. High
142 suitability habitats are located in lowlands of Mexico, Guatemala, Belize, and a small area in
143 Honduras covering approximately 281,722 km² (Fig. 4) The human impact area overlaps 51.6%
144 of this highly suitable area, leaving 136,000 km² of the environmentally suitable area with lower
145 human impact (Fig. 5).

146 **DISCUSSION**

147 Using MaxEnt for species distribution modelling, we set out to identify the extent of the suitable
148 habitat of *D. mawii*, ascertain environmental factors associated with its distribution, and identify
149 optimal regions for conservation efforts in relation to human impact. We determined that
150 climatic habitat suitability of *D. mawii* is over 281,000 km² in Central America, however, this is
151 not excluded solely to aquatic habitat. This identified suitable habitat notes highly suitable
152 habitat for translocations; and if the species is present in the contained aquatic habitats, would
153 expand the distribution range known from existing literature (Vogt et al., 2011; Legler and Vogt,
154 2013). Specifically, the potential range provided from the SDM extends the current range to
155 include suitable habitat further north into the Yucatan Peninsula and into Honduras where *D.*
156 *mawii* has not been documented. The species distribution model also refines the potential

157 distribution by excluding areas of low suitability from the wider known distribution range in
158 Belize and Guatemala. The model indicated that low elevation, moderate amounts of rainfall in
159 the wettest month of the year, lower precipitation seasonality, and high precipitation in the
160 warmest three months of the year are important factors for habitat suitability, therefore providing
161 insight into the ecological niche of *D. mawii*.

162 High habitat suitability is most strongly associated with lowland habitats and sharply declines
163 with an increase in elevation. Rather than functioning as a physiological constraint, changes in
164 elevation likely limits the availability of slow-moving, permanent streams and lagoons. Greater
165 amounts of rainfall are associated with high elevation in this region, therefore, areas with higher
166 rainfall show lower habitat suitability while conversely, low to moderate rainfall in both the
167 wettest month of the year and warmest quarter of the year are correlated with higher habitat
168 suitability. Mild precipitation seasonality, or moderately consistent precipitation throughout the
169 year with a few months receiving more rainfall than the rest, is also important to their habitat
170 suitability given their fully aquatic nature (García-Anleu et al., 2011; Legler and Vogt, 2013;
171 Briggs-Gonzalez et al., 2019) and apparent reliance on the inundation of floodplains for seasonal
172 dispersal (Briggs-Gonzalez et al., 2019; Legler and Vogt, 2013).

173 The SDM accurately predicts areas of high habitat suitability based on environmental
174 variables, however, there are geographical constraints that are not considered in our model. The
175 SDM shows high habitat suitability extending north into the Yucatan peninsula based on the
176 chosen variables. However, the peninsular region is primarily karst, and is therefore unlikely to
177 contain *D. mawii* due to the lack of surface water. Rainwater that does not evaporate is either
178 absorbed into a layer of decomposed limestone or seeps into the aquifer below (Perry et al.,
179 2003). Absence of major rivers or streams greater than 100 m in the northern Yucatan Peninsula

180 (Perry et al., 2003; Perez et al., 2011) likely prevents turtles from accessing regions of the
181 peninsula. Additionally, a lowland region in northern Honduras and a narrow stretch of land
182 along the Pacific coast of Mexico and Guatemala are indicated by the SDM as suitable habitat
183 but are unlikely to contain *D. mawii*. The area of suitable habitat in Honduras is marginally
184 adjoined along the coast with Belize, where the larger area of suitable habitat is located,
185 however, it is highly unlikely that *D. mawii* is found in Honduras. The high elevation,
186 mountainous terrain of the Cordillera de Celaque range that begins at the border of Honduras and
187 Guatemala likely forms a strong barrier to movement. Similarly, the Sierra de Chiapas separates
188 the larger contiguous area of high habitat suitability on the Atlantic side of the countries and the
189 isolated area of predicted suitable habitat on the Pacific coasts of Mexico and Guatemala, so it is
190 unlikely that turtles inhabit this region due to the distant, disjointed locations separated by a
191 mountain range.

192 Although MaxEnt is robust against small sample size (Hernandez et al., 2006; Anderson and
193 Gonzalez, 2011; Guillera-Arroita et al., 2014) and appropriate subsampling techniques were
194 applied to reduce sampling bias, our presence data includes a potentially biased, small sample
195 size. Due to the fully aquatic lifestyle and small population size (Briggs-Gonzalez et al., 2019),
196 locating individuals is difficult and results in a low sample size. Surveys for this species appear
197 to be repeated in some locations and often occurred near villages and cities due to the ease of
198 river access. Because of this, the majority of the points were not evenly distributed throughout
199 the known range but were concentrated in Belize. It is possible that *D. mawii* is more abundant
200 throughout its range than our locality points suggest, furthermore, a more thorough population
201 survey in Guatemala, Mexico, and Honduras may reveal some undocumented sites for *D. mawii*.

202 Besides narrowing the potential range for *D. mawii*, the SDM may provide insight for
203 successful reintroduction and protective conservation practices. We found that 31% of highly
204 suitable habitat falls within areas of potentially high hunting pressures. There are no quantifiable
205 data for the long-distance movements of *D. mawii* in existing literature, yet there are indications
206 that adults move long distances (Briggs-Gonzalez et al., 2019) making it highly likely that
207 individuals are traveling through highly suitable areas that are within the human hunting regions
208 (Ellsworth et al. *in prep*). Because overharvesting is the primary driver in local extirpations of *D.*
209 *mawii*, targeting non-fragmented areas, distant from human settlements increases the success of
210 protected areas and reintroduction programs. We cannot be certain that individuals will remain in
211 protected habitats, therefore, the combination of enforcing policy and increased monitoring is
212 even more critical to ensure the survival of this species.

213 We have identified areas that are candidates for protection and release sites, and we have also
214 noted the importance of continued monitoring and enforcement of protective regulations of this
215 endangered turtle, but further work is needed. By conducting additional surveys in more remote
216 locations of the species potential distribution in Guatemala, Mexico, and Belize and further
217 research on its ecological niche, the use of protected areas and reintroduction programs can have
218 improved outcomes for this and associated species. We can conduct more informed population
219 surveys in areas that have yet to be surveyed to expand our knowledge of finer scale distributions
220 and provide insight to the vulnerability of populations and areas of extirpation. This study also
221 provided environmental associations that create opportunities to compare niches between co-
222 occurring species and against native predators. Lastly, it is important to investigate other
223 potential range-limiting factors beyond those used in this study to identify other variables
224 affecting this turtle's distribution.

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367

368 **Table 1.** Bioclim codes for variables downloaded from the CHELSA database (Kanger et al.,
369 2017). The four variables indicated as important from the PCA (Fig. 2) are bolded.

Code	Variable
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range
BIO3	Isothermality
BIO4	Temperature Seasonality
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation

Code	Variable
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

370

371

372 **Table 2.** Pearson correlation values for environmental variables. The four variables used for the
 373 model are bolded.

Variables	Precipitation of Wettest Month	Precipitation Seasonality	Precipitation of Wettest Quarter	Precipitation of Warmest Quarter	Elevation
Precipitation of Wettest Month	1.0000	-0.0655	0.9951	0.3787	-0.2051
Precipitation Seasonality		1.0000	-0.0725	0.5265	0.3155
Precipitation of Wettest Quarter			1.0000	0.3756	-0.2039
Precipitation of Warmest Quarter				1.0000	-0.1626
Elevation					1.0000

374

375 **Table 3.** Permutation importance of environmental and geographic variables used in SDM
376 model.

Variable	Percent permutation Importance
Elevation	57.2%
Precipitation Seasonality	27.3%
Precipitation of the Wettest Month	8.8%
Precipitation of the Warmest Quarter	6.7%

377

378

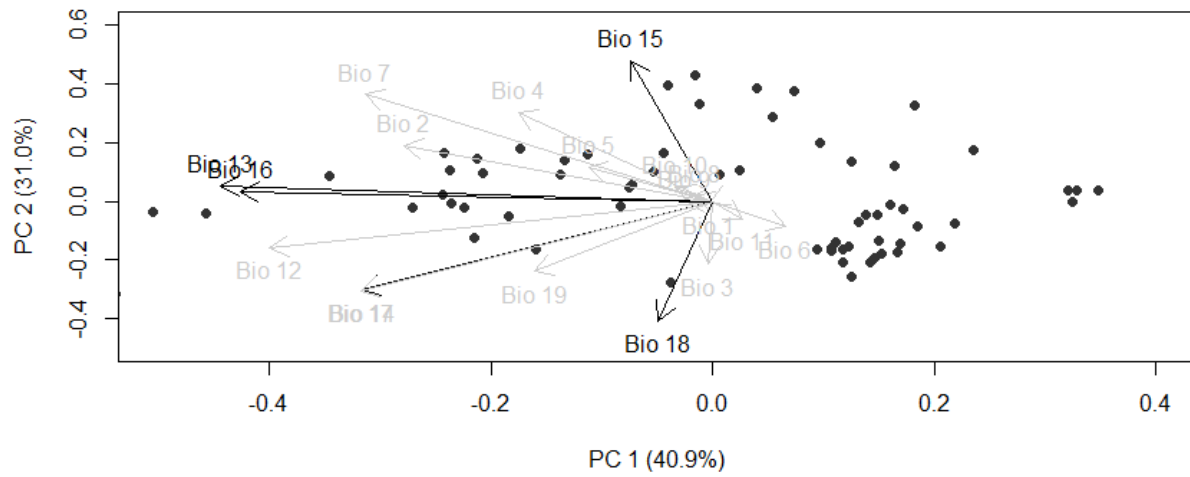


379

380 **Figure 1.** The approximate range of *Dermatemys mawii* in Central America, based on published
381 surveys (Vogt et al., 2011).

382

383



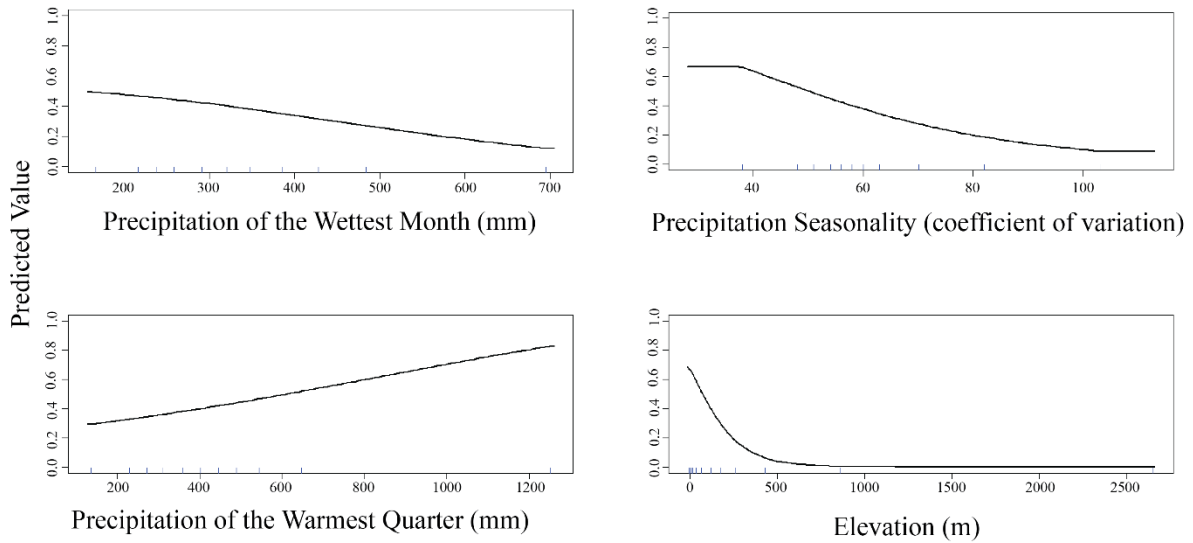
384

385 **Figure 2.** A Principal Components Analysis (PCA) of all Bioclim environmental variables at
 386 presence points with the top two highest contributing variables in each principal component
 387 bolded.

388

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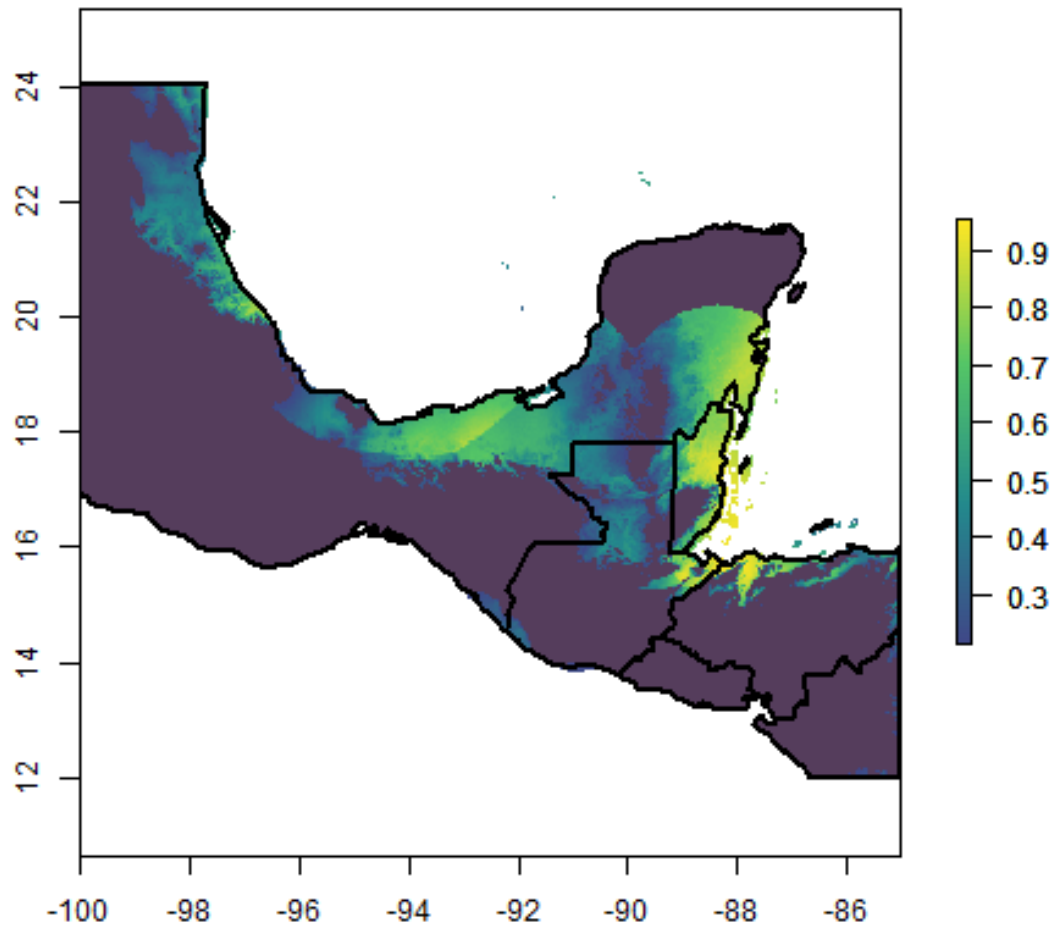
392 **Figure 3.** Response curves for each raw predictor variable used in the species distribution model.

393 Predicted value (y-axis) is the predicted habitat suitability from zero (low predicted suitability) to

394 one (high predicted suitability).

395

396



397

398 **Figure 4.** A habitat suitability map of *Dermatemys mawii* ranging from lowest habitat suitability

399 (0.21) to highest suitability (0.97).

400

401



402

403 **Figure 5.** High habitat suitability based on environmental conditions overlain with areas of high
404 human hunting pressure. High environmental suitability is indicated by the solid grey areas, with
405 buffered human settlements indicated by the shaded areas. Presence points are included. Large
406 areas of lower hunting pressures within the highly suitable areas are circled.

407

408

409 **Chapter 2: Home Range of Juvenile Central American River Turtles**

410 **(*Dermatemys mawii*) in Belize**

411 **ABSTRACT**

412 As anthropogenic factors are leading to species' population declines across the globe, many
413 conservation organizations are implementing initiatives to preserve imperiled species. The
414 Central American river turtle (*Dermatemys mawii*) is one such imperiled species that has been
415 extirpated from areas of its range in Mexico, Belize, and Guatemala. Although this culturally
416 important species has long been harvested for sustenance, more recent unsustainable hunting has
417 had a negative impact on populations. Home range information is crucial to conservation
418 initiatives that protect critical habitats and headstart programs. Here, we tracked movements of
419 juveniles at two sites: one with substantial human hunting activity and one protected site in a
420 river in Belize. We found that juveniles maintain relatively small home ranges with a mean of
421 3.4 ha, but occasionally move out of these ranges. Despite the difference in hunting pressure,
422 there were no difference in movement distances or home range size between the two sites.
423 Juvenile turtles had a higher capture rate relative to adults at the human activity site, suggesting
424 that human presence may reduce natural predators of juveniles, but such an advantage is likely
425 lost as turtles grow and become targets of hunting. Future studies assessing the effects of human
426 activity and overexploitation on the movement and survival of *D. mawii* are crucial in aiding
427 conservation initiatives.

428 **INTRODUCTION**

429 Habitat loss, habitat fragmentation (Fahrig, 1997; Marchand and Litvaitis, 2004; Böhm et al.,
430 2016), climate change (Thomas et al., 2004; Walther et al., 2002; Wiens, 2016), and

431 overexploitation (Klemens and Thorbjarnarson, 1995; Milner-Gulland and Bennett, 2003;
432 Allendorf et al., 2008; Ripple et al., 2019) are causing devastating population declines, putting
433 species at risk of extinction, and consequently impacting ecosystems. Turtle and tortoise
434 populations, in particular, have been impacted by landscape modification and overexploitation
435 causing nearly two-thirds of these species to be classified under a heightened risk of extinction
436 by the International Union for Conservation of Nature (IUCN Red List). Habitat alteration from
437 urbanization and agricultural development lead to a decrease in suitable nesting sites (Marchand
438 and Litvaitis, 2004), while increasing both the risk of vehicle collisions (Gibbs and Shriver,
439 2002; Bowne et al., 2006; Dorland et al., 2014) and predation from species associated with urban
440 and suburban development (Seigel, 1980; Congdon, 1993; Marchand and Litvaitis, 2004).
441 Similarly, over-harvesting of breeding populations for sustenance or commercial trade negatively
442 affects the viability and health of the remaining populations (Klemens, 2000; Zimmer-Shaffer et
443 al., 2014). Despite severe anthropogenic threats, freshwater turtles remain underrepresented in
444 conservation research (Burke and Gibbons, 1995; Roll et al., 2017; Lovich et al., 2018),
445 mirroring an overall gap in conservation of freshwater ecosystems (Abell, 2002) and further
446 complicating the ability to conserve freshwater turtles.

447 Combining knowledge of life history and environmental factors with field studies is critical to
448 improve conservation efforts (Wilson et al., 2006; Griffith et al., 1989; Fischer and Lindenmayer,
449 2000; Brooks et al., 2006; Berger-TAL and Saltz, 2014; Yang et al., 2018). For example, habitat
450 loss and overexploitation can be opposed with long-term conservation programs that offer
451 protection from human-induced mortality and assist in the breeding success of target species;
452 thus, these programs are fundamental to preserving biodiversity and the survival of threatened
453 turtle species (Ceballos and Ehrlich, 2010). Such conservation initiatives have a higher

454 likelihood of success when key components of a species' ecology, home range, and movement
455 patterns are incorporated into conservation strategies (Burt, 1943; Hart, 1983; Gibbons et al.,
456 1990; Powell, 2000, 2012; Lidgard et al., 2020). Spatial studies provide insight into population
457 distribution, dispersal patterns, and habitat selection (Bowler and Benton, 2005), which inform
458 potential release sites and allow for assessment of reintroduction success for programs aimed
459 toward augmentation and reintroduction (Fischer and Lindenmayer, 2000; Cadi and Miquet,
460 2004; Berger-TAL and Saltz, 2014). Home range studies provide minimal habitat requirements
461 that can also be used to designate protected areas and ensure adequate space for individuals to
462 carry out their activities with minimal human impact (Allen and Singh, 2016; Di Franco et al.,
463 2018); moreover, species' preservation in protected areas has a higher success rate when the size
464 of the protected habitat is considerably larger than the species home range size (Di Franco et al.,
465 2018; Green et al., 2015).

466 The Central American river turtle (*Dermatemys mawii*) is listed as Critically Endangered by
467 the IUCN (Vogt et al., 2006). This freshwater turtle is found primarily in lowland rivers, lakes,
468 lagoons, and brackish waters in the Yucatan peninsula region of Central America (Iverson and
469 Mittermeier, 1980; Legler and Vogt, 2013; Briggs-Gonzalez et al., 2019). The primary threat to
470 *D. mawii* is overexploitation, which has extirpated and fragmented populations across its range
471 (Iverson and Mittermeier, 1980; Alvarez del Toro et al., 1979; Vogt et al., 2011). In other turtles
472 and aquatic vertebrates, pressure from overhunting has caused population declines through
473 decreased clutch sizes (Daza and Páez, 2007; Eisemberg et al., 2017), reduced recruitment
474 (Marchand and Litvaitis, 2004; Walsh et al., 2006), and restricted genetic variability (Ratner and
475 Lande, 2000; Walsh et al., 2006; Allendorf et al., 2008). Similar to other turtles, *D. mawii* has
476 slow population growth because of low offspring survivorship and long maturation times,

477 making populations particularly vulnerable to over-harvesting (Dunham et al., 1989; Congdon,
478 1993; Gibbons et al., 2000). Although the exact time of reproductive maturity and longevity in
479 the wild is undocumented, the generation time for this species is thought to be approximately 10
480 years (Briggs-Gonzalez et al., 2019) and life expectancy exceeds 30 years in captivity (Briggs-
481 Gonzalez et al., 2019).

482 To counter the serious threats *D. mawii* is facing, spatial studies specifically investigating
483 home range size are needed to better understanding habitat use in order to inform conservation
484 initiatives that protect and bolster existing populations. The bulk of information on *D. mawii* has
485 investigated the species' population size (Rainwater et al., 2012), diet (Moll, 1989), population
486 genetics (González-Porter et al., 2011, 2013), habitat preference (Legler and Vogt, 2013), and
487 conservation threats (Rangel-Mendoza et al., 2009, 2014; Polisar and Horwich, 1994). However,
488 much of the current spatial information on *D. mawii* stems from published observations and
489 personal communications with people living near or within the species' range (Alvarez del Toro
490 et al., 1979; Iverson and Mittermeier, 1980; Moll, 1989; Polisar, 1992, 1996; Rainwater et al.,
491 2012; Vogt et al., 2011; Legler and Vogt, 2013). These studies, personal communications, and
492 anecdotes do not quantify movements, but suggest that adults undergo long-distance movements
493 and offer hypotheses about factors that may influence movement patterns and home range size,
494 including seasonal effects. The rainy season, especially, plays an important role in shaping home
495 ranges and movement patterns of adult *D. mawii* (Briggs-Gonzalez et al., 2019; García-Anleu et
496 al., 2010; Legler and Vogt, 2013). Specifically, turtle dispersal activity increases during the rainy
497 season when floodplains and flooded forests become inundated (García-Anleu et al., 2010;
498 Legler and Vogt, 2013). Conversely, during the dry season, the reduced rainfall and subsequent
499 low water levels limit the amount of available habitat. Low water levels force turtles to

500 aggregate, providing a prime opportunity to encounter other individuals, and eliminating the
501 need to travel long distances to search for a mate (Polisar, 1992, 1996; Briggs-Gonzalez et al.,
502 2019). Consequently, receding water levels and aggregated populations increase vulnerability to
503 human hunting. Although some factors that affect the movements of adult *D. mawii* are known, it
504 remains unclear whether juveniles follow the same home range attributes and seasonal
505 movement patterns as the adults.

506 Home range and movements of many animals are driven by a combination of intrinsic
507 biological and extrinsic environmental factors that may vary among seasons or over an
508 individual's lifetime. For example, reproductive maturity can influence home-range attributes
509 and result in disparities in home range size between juveniles and adults (Gibbons et al., 1990;
510 McNab, 1963; Beck-King et al., 1999; Sutherland et al., 2000). Reproductively mature
511 individuals of many species often expand their home range and increase movement to optimize
512 reproductive success (Morreale et al., 1984; Doody et al., 2002; Slavenko et al., 2016), whereas
513 reproductively immature individuals benefit from maintaining a smaller home range and short-
514 range movements, which can reduce predation (Morreale et al., 1984). Juvenile turtles heavily
515 invest into growth and development of the protective shell rather than overall size, leaving them
516 at a disadvantage to escape predation (Moll, 1986; Alvarez del Toro, 1982; Smith and Smith,
517 1980; Platt et al., 2016). Naturally high juvenile predation, in combination with increased
518 anthropogenic hunting, affect both ends of the age spectrum and have potential impacts on
519 population stability (Moll and Moll, 2004). Although not always the case (Crouse and Frazer,
520 1995; Sung et al., 2013), high juvenile representation often implies stable turtle populations.
521 Although survivorship rates have not been documented for *D. mawii*, populations would still
522 benefit from conservation efforts that protect juveniles.

523 Here, we aim to quantify home ranges and describe movement patterns of juvenile *D. mawii*
524 from two locations in central Belize using VHF (Very High Frequency) transmitters. Given that
525 juveniles are more susceptible to predation and lack the need to search for a mate, we expect
526 juveniles to move shorter distances and occupy a smaller area than adults. Investigating the
527 movement and home range size of juvenile *D. mawii* will provide critical data to improve
528 conservation efforts, inform policy makers, and increase our understanding of the species'
529 ecology.

530 **MATERIALS AND METHODS**

531 **Study site**

532 We conducted our study at two locations, during two different dry seasons in a large, slow
533 moving, perennial stream that flows through lowland tropical savannah into a series of lakes.
534 Over the period of study, air temperatures ranged from 23°C–29°C with a total of 4.6 cm of
535 rainfall (2019) and 23°C–31°C with 2.0 cm of rainfall (2020). Maximum water depth was 5 m.
536 The riparian vegetation at these sites is dominated by emergent plants such as *Mimosa pudica*
537 and *Paspalum paniculatum*. The prevailing trees, *Manilkara bidentata*, and *Haematoxylum* sp.,
538 provide canopy cover along the bank and contribute to the coarse woody debris found throughout
539 the stream. We chose the first site (A) based on accessibility and quality of habitat, then moved
540 to the second site (B), 10 km south of site A and within a wildlife sanctuary, due to the high
541 presence of human interference at site A. Site A, which was publicly accessible, had a high
542 occurrence of canoeing, net trapping, and poaching activity, whereas site B had minimal
543 anthropogenic activity. We tagged individuals at site A between January and March in 2019 and
544 between February and March 2020 at site B.

545 **Sampling**

546 In both 2019 and 2020, river accessibility limited our study to the dry season. Individuals of *D.*
547 *mawii* were captured and tagged at the beginning of the dry season between January and March,
548 just as daily precipitation declined, and water levels began to recede (Lambert et al.,1980).
549 Trammel nets (45 m long x 3 m deep, outer wall mesh size of 355 mm x 355 mm, inner wall
550 mesh size of 101 mm x 101 mm) were left open along banks or across the stream by tying the
551 ends to branches of overhanging trees, submerged logs, or available sturdy woody stems along
552 the bank during peak turtle activity time, largely between 1800 h and 0500 h (Rainwater et al.,
553 2012; Legler and Vogt, 2013) for 17 net nights at site A and 16 net nights at site B. Net checks
554 were conducted every 90 minutes to ensure the safety of the turtles; no turtles drowned during
555 the course of this study. All turtles, except one small hatchling that was captured by hand, were
556 captured using the trammel net. The large mesh opening precluded juveniles under 144 mm. For
557 each individual, we recorded the mass using a spring scale (Pesola) accurate to the nearest gram.
558 We recorded the straight-line carapace and plastron lengths using manual calipers to the nearest
559 1.0 mm.

560 Waterproof VHF transmitters (RI-2B, Holohil) were attached using an epoxy glue (Devcon) to
561 the fourth costal scute of the carapace to minimize any impacts on foraging, predator evasion,
562 and entanglement with vegetation. Transmitters had a pulse rate of 40 ppm, a pulse width of 24
563 ms, and a total weight of 15 g. In addition to the VHF transmitter, each individual was marked
564 with a prepackaged sterile passive integrated transponder (PIT) tag (GPT12, Biomark) with a
565 unique identification number. The PIT tag was inserted sub-dermally in the right hind limb of
566 each individual using sterile techniques. This tag allowed turtle identification in the event of
567 transmitter detachment. Individuals with a carapace length of greater than 365 mm were
568 classified as adults, and smaller individuals were classified as juveniles (Legler and Vogt, 2013).

569 The sex of each adult was determined based on the presence or absence of sexually dimorphic
570 characteristics. At sexual maturity, males display external, visual characteristics such as bright
571 yellow coloration of the head and a tail extending beyond the carapace, whereas females lack the
572 brightly colored head and long tails (Legler and Vogt, 2013). Juveniles could not be visually
573 sexed due to lack of sexual characteristics. No bias towards age or sex was intentional; all
574 individuals captured were tagged and used for this study. Duration of transmitter attachment was
575 limited by annual molting of the outer, keratinized layer of scutes, which often occurs in the late
576 dry season for *D. mawii* (Legler and Vogt, 2013). No individuals had visual signs of molting at
577 the time of capture. Animals were held for a maximum of 60 minutes to provide sufficient time
578 for the epoxy glue to set and cure prior to release at the site of capture. All appropriate research
579 permits were obtained (MSR permit 0015-20) and the study was approved by the University of
580 Oklahoma's Institutional Animal Care and Use Committee (R19-002, R19-002A).

581 **Radio telemetry, data collection, and distance measurements**

582 After we tagged and released turtles, they were tracked manually from a canoe using a handheld
583 radio receiver (R-1000 Telemetry Receiver, Titley Scientific, Columbia, MO) and a 3-element
584 Yagi antenna (Titley Scientific, Columbia, MO). For both sampling periods, tracking occurred
585 between 2 to 7 times per week following transmitter attachment. Individuals at site A were
586 tracked for five consecutive weeks (January–March 2019) and at site B, individuals were tracked
587 three weeks (February–March 2020).

588 Location data were predominately recorded during peak activity hours because of the species'
589 tendency to rest at the bottom of riverbed when not active (Briggs-Gonzalez et al., 2019) making
590 them difficult to locate. We occasionally tracked individuals at different times in a 24-hour
591 period to investigate movement activity at various times of the day. Our tracking area covered

592 over 500 meters both up- and downstream from the initial capture sites for a total of about 3 km
593 stretch of river. When an individual was located, we recorded the time of day and used a GPS
594 (GPSMAP 010-01199-10, Garmin, WGS84) to record coordinates of its location (or fix). All
595 distances were calculated using the Euclidean (straight-line) distance formula using the “dist”
596 function in the base R package. The sum of the distances between each locality fix was divided
597 by total number of fixes to calculate the mean distance per fix (mean displacement distance)
598 traveled by each individual. The mean displacement distance was then estimated for the mean
599 number of days between detections. Although measures were taken to prevent disturbing the
600 individuals from their location, if a turtle fled in response to being approached, GPS coordinates
601 were recorded after following individuals for five meters.

602 **Home range calculations and statistical analyses**

603 To estimate home range, we used 100% and 95% minimum convex polygons (mcp), which
604 provides a more accurate estimation of home range for small sample sizes (Boyle et al., 2009).
605 MCPs create a perimeter representing the minimum home range of each individual around the
606 five outermost GPS coordinates, so that it encompasses these points and all other points where an
607 individual was located using either 100% of the locality points, or the points that fall in the 95%
608 quantile. We then buffered the perimeter of each home range polygon by 15 m to account for any
609 variation in GPS signal, following the methods of Ryan et al. (2008). The area of each mcp was
610 calculated in the adehabitatHR package (Calenge, 2006) in R (R Core Team, 2019, Version
611 1.2.5019) and adjusted to fit along the river. We conducted a series of correlation tests using the
612 base cor.test function in R to detect relationships between carapace size, number of fixes, and
613 home range size. Spearman rank correlations were used to test the effect of size using carapace
614 length on the number of fixes we were able to obtain and on the association between turtle size

615 and home range size. A Spearman rank correlation was also used to determine whether the
616 number of GPS location points affected home range size. Due to inconsistencies in the tracking
617 effort, detection, and duration, we were unable to statistically compare home range or movement
618 between sites. We used a Fisher's exact test to determine if there was a difference in our ability
619 to locate juveniles or adults. We used $\alpha = 0.05$ as the statistically significant level for all tests.

620 **RESULTS**

621 **Sampling and detectability**

622 Seventeen juveniles and four adults were captured via trammel net or hand. Thirteen juveniles
623 and one adult were captured at site A over 17 net nights with an average of nine fixes per
624 individual over five weeks. Five juveniles and three adults were captured at site B over 16 net
625 nights with an average of five fixes over three weeks. On average, individuals were detectable
626 (i.e., had greater than one detection) at site A nearly every two days (47% of the attempted
627 tracking time), while individuals at site B were detectable approximately every four days (35%
628 of the attempted tracking time). Home range estimates and mean displacement distances were
629 calculated for a total of ten individuals that had a minimum of five locality fixes (Table 1) at site
630 A (Fig. 1) or site B (Figs. 2 & 3).

631 Tracking and trapping times indicate that individuals were more likely to be located between
632 2000h and 0600h, which coincides with their previously recorded peak activity times (Briggs-
633 Gonzalez et al., 2019). However, some individuals were active and relocatable during daylight
634 hours (0600 – 2000 h). The majority of the individuals captured were juveniles, with a smaller
635 proportion of adults to juveniles at site A (0.375) than site B (0.077). Three out of the four adults
636 captured for this study were re-detected after initial capture (Fig. 4).

637 **Home range size**

638 Juvenile home range size (95% mcp) varied from 0.27 ha to 2.14 ha at site A (Fig. 5a) and 0.48
639 ha to 21.14 ha at site B (Fig. 5b). Mean home range size (95% mcp) appears larger at site B (6.5
640 ha) than at site A (0.8 ha). One-half of the individuals tracked included one or two locality points
641 deviating from the core occupied area. We found that turtle size (carapace length) did not affect
642 the home range size ($S = 234$, $p = 0.2324$; Fig. 6a), nor the number of locality fixes ($S = 174.46$,
643 $p = 0.2198$; Fig. 6b). The number of fixes varied among individuals, but a greater number of
644 locality detections was not correlated with a larger home range area ($S = 112.68$, $p = 0.372$; Fig.
645 7).

646 **Movement**

647 Mean displacement movement between points of the nine tracked juveniles resulted in an
648 average movement of 127.4 meters per every two days at site A and an average movement of
649 277.1 meters every four days at site B. Turtle size had no effect on mean displacement distance
650 ($S = 372$, $p = 0.9432$; Fig. 6c), nor likelihood of detection ($p = 0.5865$).

651 The number of fixes were below the minimum required to calculate home range for all but one
652 adult (EDE 232). EDE 264 traveled 1780 m north from the initial capture site in less than 24
653 hours and was not located again within the 2 km of its original capture in the remainder of the
654 study. The other adult, EDE 262, was not located within the search area (2 km from the original
655 capture location) for a month before reappearing 277 m from its original net capture location.

656 **DISCUSSION**

657 Juveniles had relatively small home ranges and typically remained near the area where they
658 were initially captured, even when multiple individuals were captured in the same net. Our

659 results also indicate that juveniles occasionally travel outside a core area. These findings indicate
660 that allocating protected lands may be sufficient to benefit juveniles of this species during the dry
661 season. Both capture and detection rates for adults in our study were too low to allow direct
662 comparison of home range sizes between juveniles and adults; however, observations of adults
663 by local community members and previous studies indicate that adults make very long-distance
664 movements (Alvarez del Toro et al., 1979; Iverson and Mittermeier, 1980; Moll, 1989; Polisar,
665 1992, 1996; Rainwater et al., 2012; Legler and Vogt, 2013).

666 Our observations and inability to reliably track adults indicate that they are either occupying
667 extensive home ranges beyond our survey area or they make far-ranging movements that
668 provided us the opportunity to capture them while they traveled through our study site. However,
669 the latter can be detrimental if the adult is moving through an area with high human hunting
670 activity. These observations coupled with our data on juvenile movement also indicate a
671 potential ontogenetic change in the home range of this species.

672 Human disturbance by frequent boating activity, as occurs at site A, can impact nesting and
673 basking behavior (Moore and Seigel, 2006), stress levels, and overall health of individuals
674 (Selman et al., 2013). We suspect human activity plays a large role in the movements and home
675 ranges of these individuals based on studies of similar lotic species and from personal
676 observations. Although we could not directly compare home range size and mean fix distances
677 between sites, long-term data and a larger sample size may show that human activity and
678 disturbance result in smaller home range sizes and shorter movements. We observed longer
679 distances and greater home range size at site B which could likely be a consequence of the
680 difference in human activity between sites. At site B, hunting and fishing are regulated by local
681 personnel and very little boat activity was observed. Hunting activity could also be directly

682 responsible for the lack of adult captures. Interestingly, the human activity at site A could also be
683 suppressing the juveniles' natural predators, such as crocodiles, thereby decreasing juvenile
684 mortality rates and producing the observed higher capture rate of juveniles relative to adults at
685 site A. Any indirect protection of juveniles by hunting and other human activity would be lost as
686 turtles grow and become targets for human sustenance.

687 Only one-half of individuals that we captured for this study had the minimum number of fixes
688 to be used for the mcp calculations, possibly due to VHF limitations and the life history of *D.*
689 *mawii*. Although VHF technology is useful in pinpointing an individual, the signal attenuates
690 with depth or at great distances, which is likely the reason for few data points for adults. Other
691 technologies, such as GPS and satellite technologies, provide more spatial information with
692 higher accuracy, but both technologies are aerial systems that require an individual to breach the
693 surface to send a signal. As this species is wholly aquatic and does not leave the water to bask.
694 Based on current available technology, VHF provides better insight into fully aquatic freshwater
695 species that live in submerged holes along the bank (Skupien et al. 2016), however, testing a
696 combination of technologies that transmit a strong signal from greater distances, such as
697 ultrasonic transmission or acoustic tracking systems, is needed to determine the optimal tracking
698 method for this fully aquatic organism.

699 Our study provides quantitative data on the movements and home ranges of these individuals,
700 now identifiable with PIT tags, for future studies. With increased tracking duration and improved
701 technology, we can better understand the home ranges of *D. mawii* at various life stages and
702 across seasons. Our study was limited to the dry season when sites are most assessable, but
703 seasonality is a driver for movement in other freshwater turtles (Litzgus and Mousseau, 2004;
704 Fachín-Terán et al., 2006) and is therefore imperative to assess home ranges across seasons and

705 across years. Our study also suggests the difference in human presence potentially plays a role in
706 movement and home range of individuals, however extensive studies are needed to better
707 understand how anthropogenic activity affects this species.

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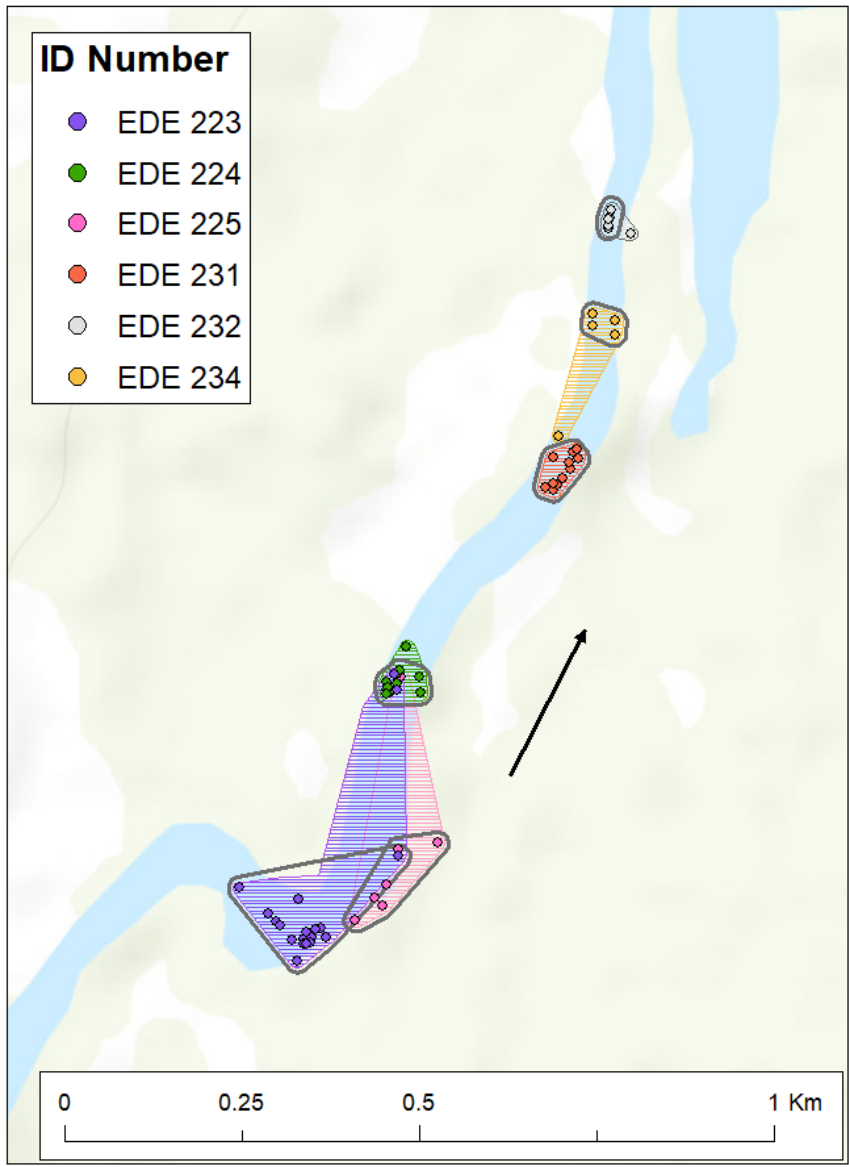
926

927 **Table 1.** Movement and home range data for each relocated individual.

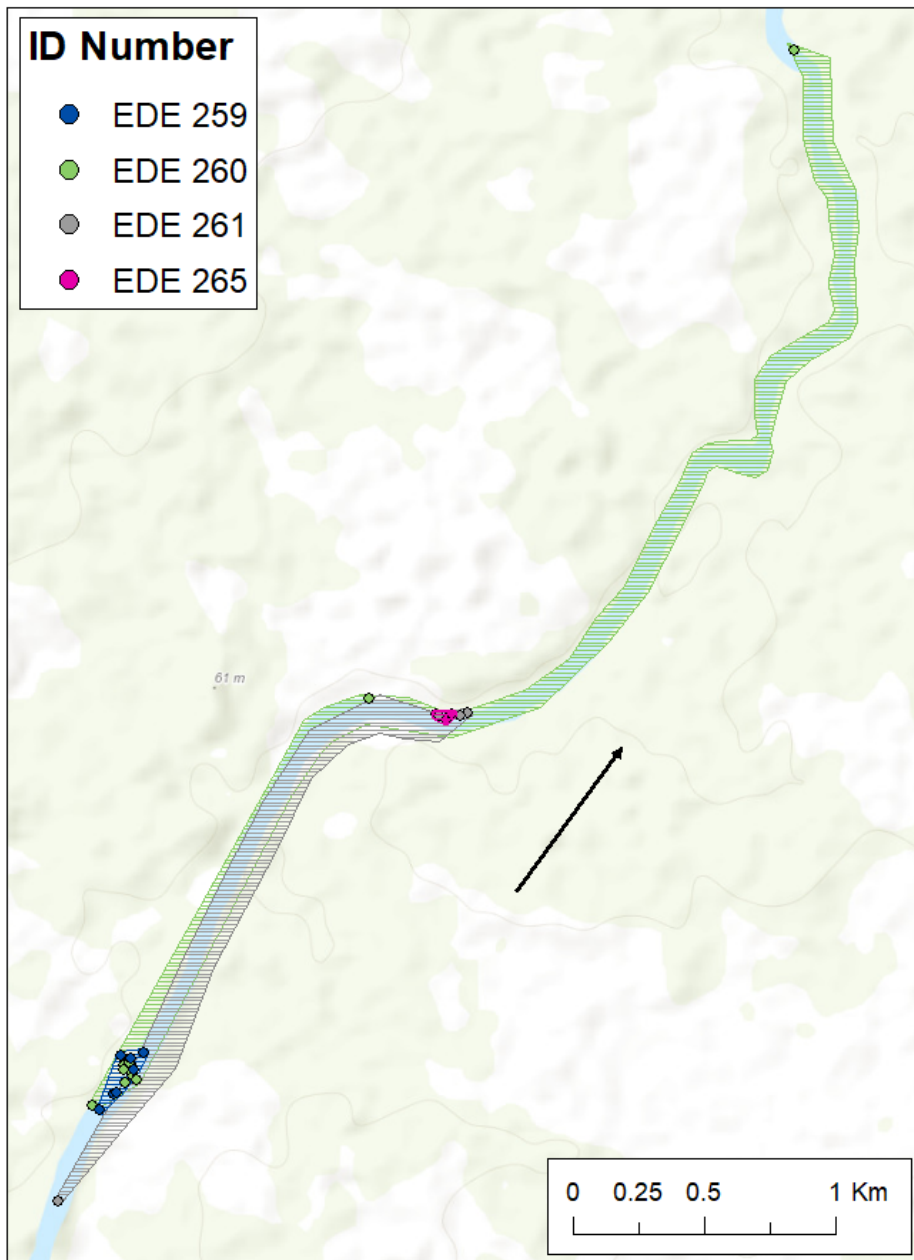
ID number	Age/ Sex	100% mcp (ha)	95% mcp (ha)	Number of Fixes	Maximum Distance Between Fixes (m)	Mean Displacement Distance (m)	Carapace length (cm)
Site A							
223*	Juvenile/ Unknown	3.830	2.14	21	608.90	175.44	28.0
224*	Juvenile/ Unknown	0.510	0.37	13	71.42	29.55	27.0
225*	Juvenile/ Unknown	2.520	0.87	8	522.59	197.29	28.2
226	Juvenile/ Unknown	NA	NA	1	NA	NA	30.1
227	Juvenile/ Unknown	NA	NA	1	NA	NA	27.1
228	Juvenile/ Unknown	NA	NA	1	NA	NA	35.4
229	Juvenile/ Unknown	NA	NA	1	NA	NA	34.2
230	Juvenile/ Unknown	NA	NA	1	NA	NA	33.1
231*	Juvenile/ Unknown	0.420	0.41	12	512.26	132.63	30.5
233	Juvenile/ Unknown	NA	NA	1	NA	NA	35.2
234*	Juvenile/ Unknown	0.950	0.27	5	270.61	101.84	27.5
235	Juvenile/ Unknown	NA	NA	1	NA	NA	17.4
232*	Adult/ Female	0.260	0.15	6	47.17	27.36	41.5

ID number	Age/ Sex	100% mcp (ha)	95% mcp (ha)	Number of Fixes	Maximum Distance Between Fixes (m)	Mean Displacement Distance (m)	Carapace length (cm)
Site B							
259*	Juvenile/ Unknown	1.930	1.39	8	341.04	225.00	26.1
260*	Juvenile/ Unknown	55.220	3.08	15	6,604.82	915.33	24.2
261*	Juvenile/ Unknown	28.469	21.14	6	3,522.11	811.46	28.7
263	Juvenile/ Unknown	NA	NA	2	30.08	30.08	29.3
265*	Juvenile/ Unknown	0.700	0.48	7	90.88	56.12	26.5
258	Adult/ Female	NA	NA	1	NA	NA	40.9
262	Adult/ Female	NA	NA	2	277.06	277.06	42.3
264	Adult/ Female	NA	NA	2	1,779.84	1,779.84	37.8

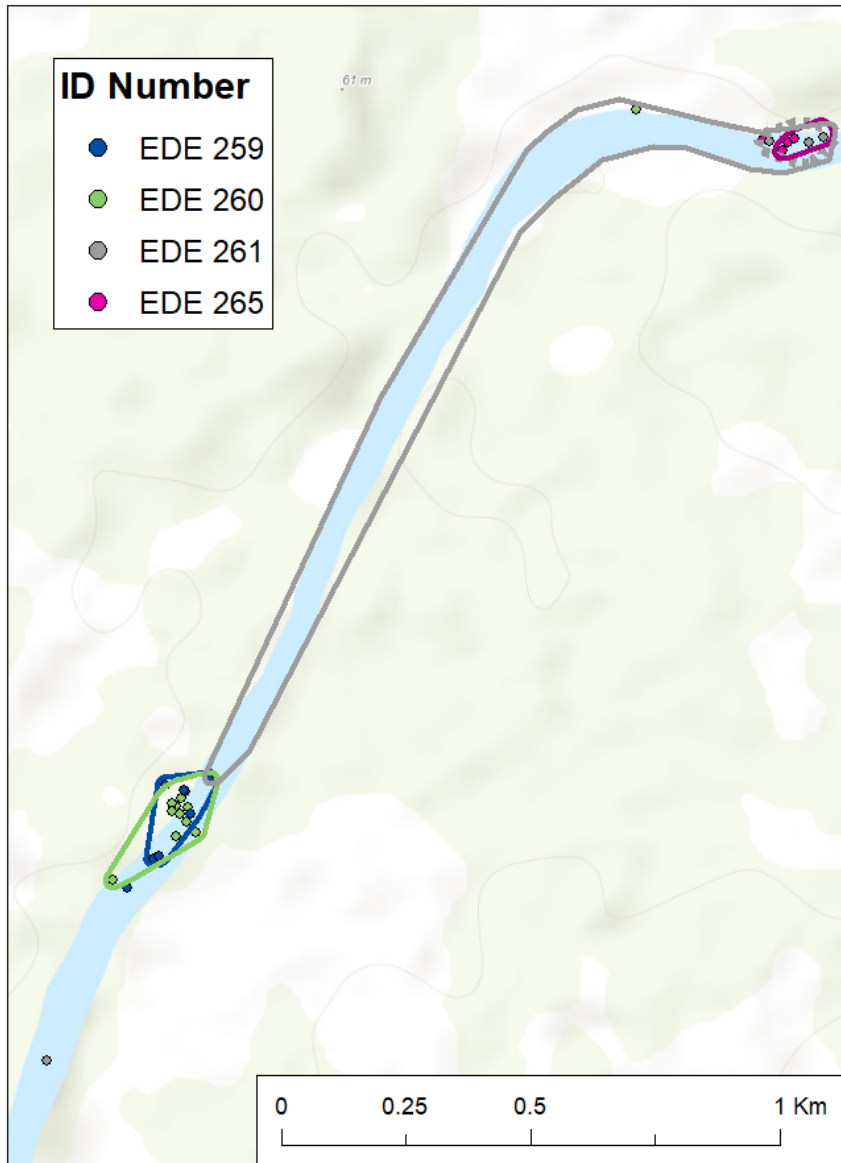
* Individuals used in mcp calculations



929 **Figure 1.** 100% and 95% minimum convex polygon (mcp) home range estimates for five
 930 juveniles and one adult (EDE 232) at site A, each represented by a unique color. Each point
 931 represents an individual fix and the surrounding color-shaded polygon shows the 100% mcp
 932 home range estimates. The grey band shows the 95% mcp home range of each individual. Flow
 933 direction is indicated by the arrow.

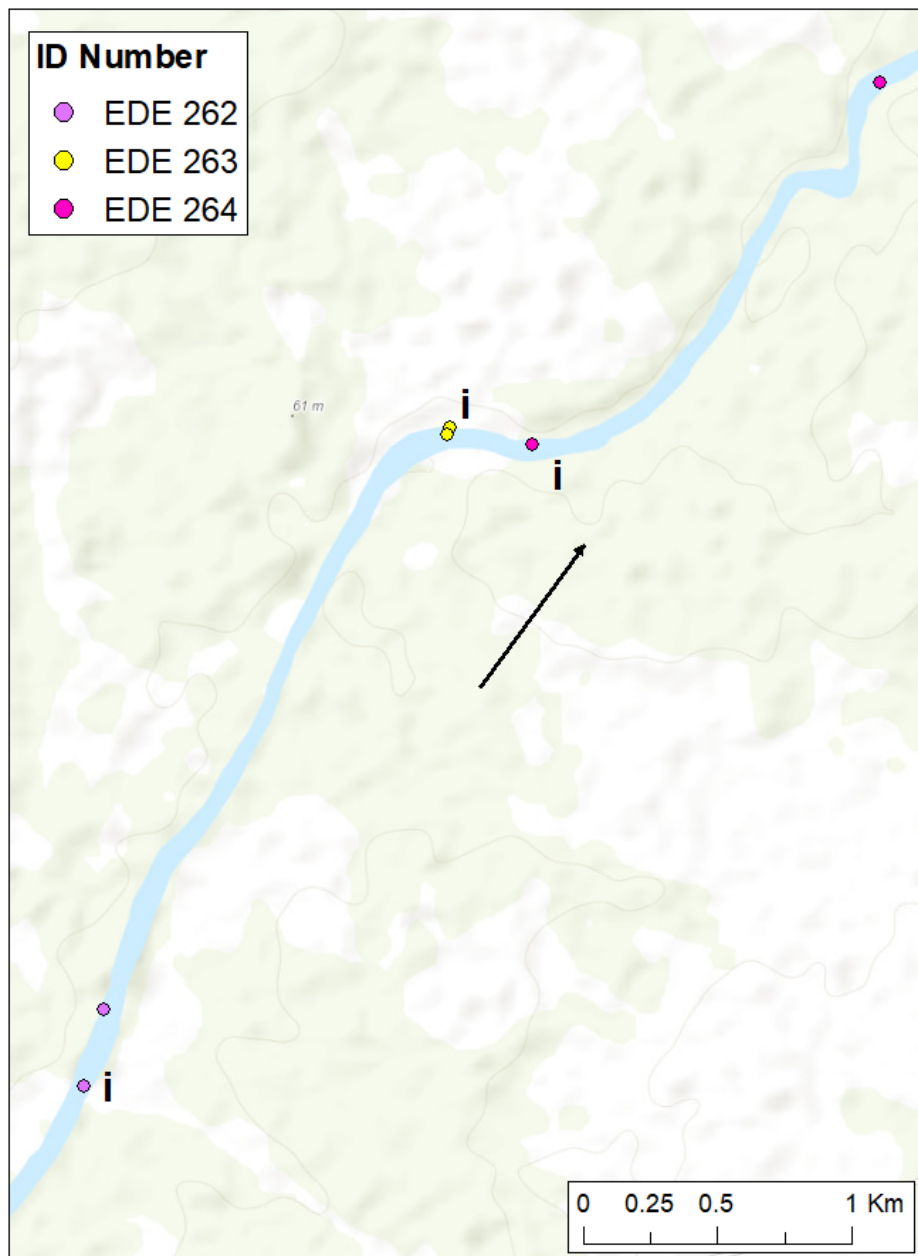


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 936 **Figure 2.** 100% minimum convex polygon (mcp) home range estimates for four juveniles at site
 937 B represented using unique colors. Each point represents an individual fix, and the surrounding
 938 color-shaded polygon shows the 100% mcp home range estimates.



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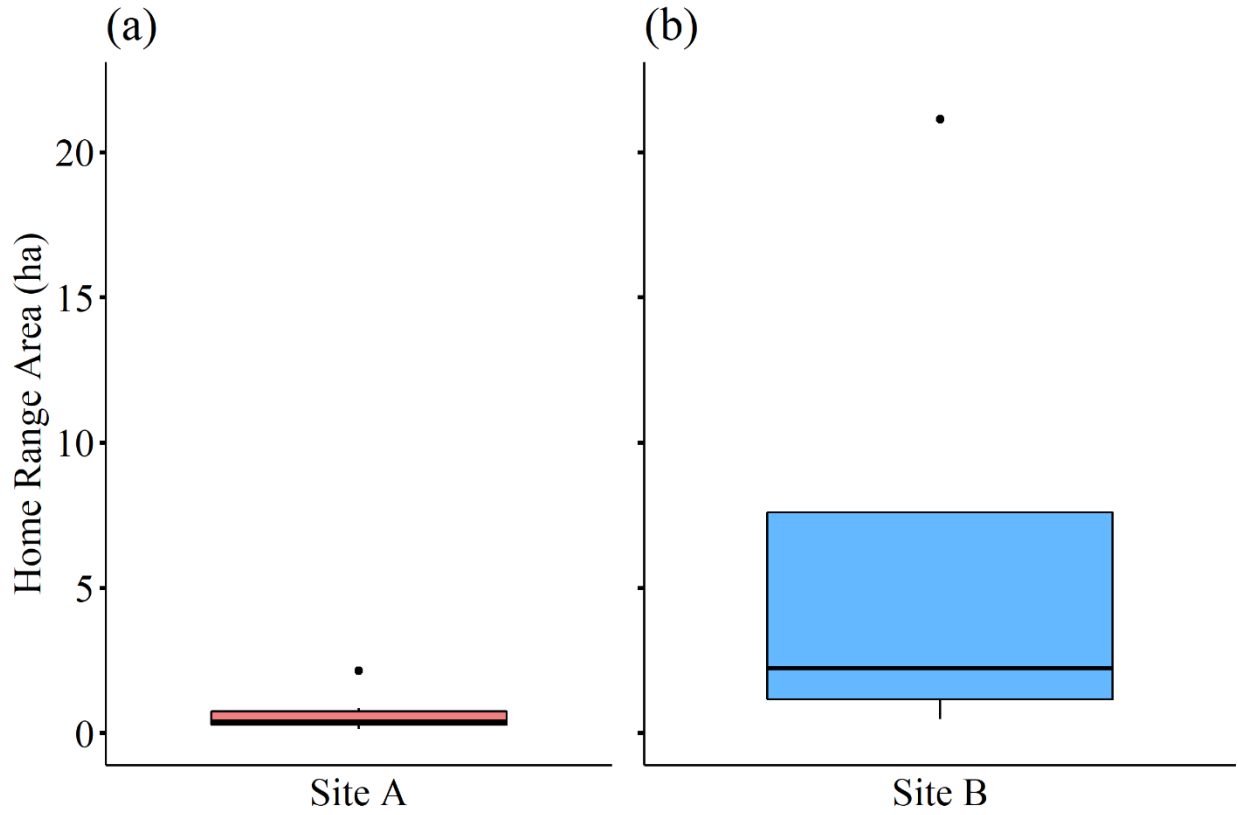
940 **Figure 3.** 95% minimum convex polygon (mcp) home range estimates for four juveniles at site B
 941 represented using unique colors. The grey band shows the 95% mcp home range of each
 942 individual. Flow direction is indicated by the arrow.



943

944 **Figure 4.** A map at site B indicating the three individuals that were only relocated a single time
 945 following initial capture. Initial capture is indicated by the ‘i’ adjacent to the locality fix. Stream
 946 flow is indicated with an arrow.

947

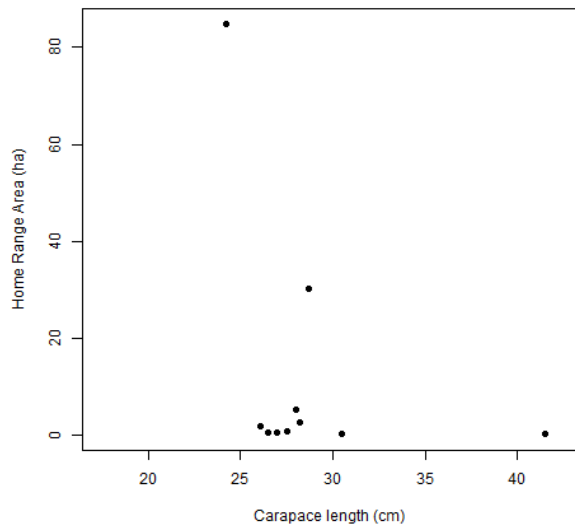


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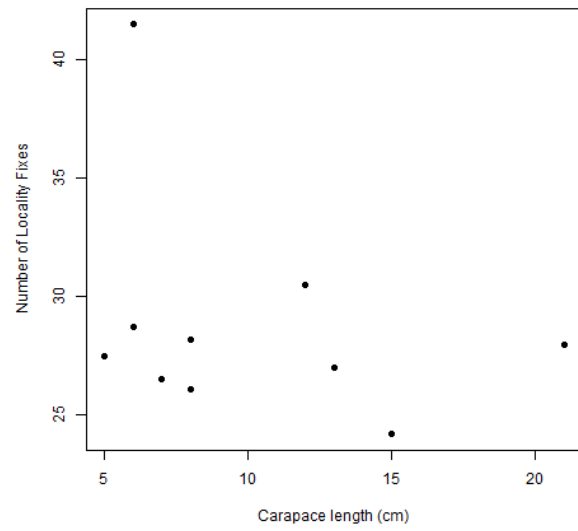
Figure 5. Variation in 95% mcp home range sizes at sites A (a) and B (b).

950

(a)



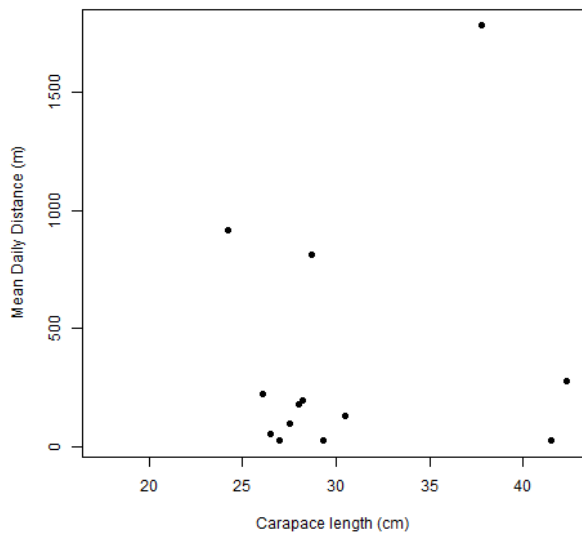
(b)



951

952

(c)



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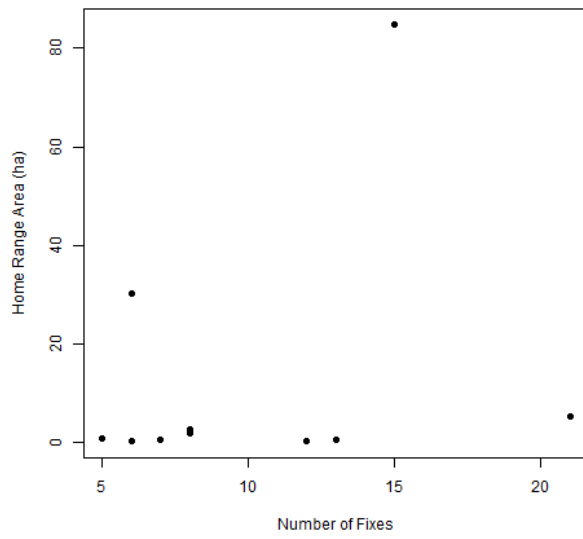
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Figure 6. Two plots showing no correlation between individual size (carapace length) and home range area (a), number of locality fixes (b), and mean displacement distance (c).

957



958

959 **Figure 7.** The number of fixes of each individual with greater than 5 fixes does not predict home

960 range size.