Title: Population Dynamics and Biological Feasibility of Sustainable Harvesting as a Conservation Strategy for Tropical and Temperate Freshwater Turtles

Short title: Biological Feasibility of Sustainable Harvesting for Freshwater Turtles

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Abstract

Background: Conservation strategies are urgently needed for tropical turtles. Studies conducted exclusively in the temperate zone have revealed that the suite of life history traits that characterizes turtles and includes delayed sexual maturity and high adult survivorship makes sustainable harvest programs an unviable strategy for turtle conservation. However, most turtles are tropical in distribution and the tropics have higher, more constant and more extended ambient temperature regimes that, in general, are more favorable for population growth.

Methods: To estimate the capacity of freshwater turtle species from temperate and tropical regions to sustain harvest we synthesized life history traits from 163 freshwater turtle species in 12 families (Carettochelydae, Chelidae, Chelydridae, Dermatemydidae, Emydidae, Geoemydidae, Kinosternidae, Pelomedusidae, Platysternidae, Podocnemididae, Staurotypidae and Trionychidae). The influence of climate variables and latitude on freshwater turtle life history traits (clutch size, clutch frequency, age at sexual maturity, and annual adult survival) were examined using Generalized Additive Models. The biological feasibility of sustainable harvest in temperate and tropical species was evaluated using a sensitivity analysis of population growth rates obtained from stage structured matrix population models.

Results: Turtles at low latitudes (tropical zones) exhibit smaller clutch sizes, higher clutch frequency, and earlier age at sexual maturity than those at high latitudes (temperate zone). Adult survival increased weakly with latitude and declined significantly with increasing bioclimatic temperature (mean temperature of warmest quarter). A modeling synthesis of these data indicates that the interplay of life history traits does not create higher harvest opportunity in adults of tropical species. Yet we found potential for sustainable exploitation of eggs in tropical species.

Conclusions: Sustainable harvest as a conservation strategy for tropical turtles appears to be as biologically problematic as in temperature zones and likely only possible if the focus is on limited harvest of eggs. Further studies are urgently needed to understand how the predicted population surplus in early life stages can be most effectively incorporated into conservation programs for tropical turtles increasingly threatened by unsustainable exploitation, climate change and deforestation.

Introduction

Vertebrate animals are important for human welfare and wellbeing [1-3], particularly as food, medicine, and cultural uses by rural and aboriginal communities [3-6]. Freshwater turtles are a good example — they are frequently targeted for both subsistence and commercial harvest, primarily by local communities that live in the vicinity of river and wetlands [7-9]. High biomass [10, 11], ease of capture, and extended survival with minimal care in captivity make freshwater turtles a focus for harvest [7-9].

Unsustainable harvesting is recognized as one of the major factors driving global freshwater turtle decline [12-15] . Over 40% of turtle species are endangered as a result of overexploitation [13, 15, 16]. Although turtles are harvested for various purposes (e.g. pets, medicine, and curios), the most heavy use of turtles is for food [7, 16, 17]. Large adult turtles [18-21] and eggs [18] are usually the primary target of harvesting, because these life stages are the most valuable for food [7, 8, 16] and the easiest life stages to encounter. The greatest harvesting pressure occurs in tropical areas [7, 8] where the most freshwater turtles occur [22]. For many local people in these areas, turtle meat and eggs are not only important as sources of protein and lipid, but also support them economically [7, 16, 23]. Additionally, unsustainable exploitation in tropical areas can also lead to regional population collapse and as a consequence create pressures in other regions of the world [24].

Sustainable harvesting programs have been widely promoted as a strategy for wildlife conservation [25, 26]. Moreover, active involvement of local people in these sustainable harvest programs generally creates better outcomes for conserving wildlife [26, 27]. However, this conservation strategy is assumed not viable for turtle conservation [7, 28]. A corpus of research

on the topic has revealed that turtles are poor candidates for any sustainable use program [29-31]. In general, turtles exhibit delayed sexual maturity, high adult survivorship, low fecundity, and long life span [29-34]. This combination of life history traits limits their ability to compensate for additive adult mortality from harvesting [9, 28, 32, 34, 35].

It is notable, however, that virtually all research on sustainability of harvest as a conservation strategy for turtles has been conducted in temperate zones. Variation in life history traits occur within and between turtle species that inhabit different environments [32, 36-40]. Variation in clutch size [36, 41], clutch frequency [33], growth rate, and age at sexual maturity [36] in relation to latitude have been observed in turtles. The interplay of these different life history traits has been suggested to create more opportunity to harvest turtles sustainably, at least in one tropical freshwater species in Northern Australia [19, 42]. Earlier age at sexual maturity, higher fecundity, and faster growth rates in this tropical freshwater turtle compared to other turtles [42] may allow their populations to be harvested at 20% annual harvest rate [19], suggesting that the widely held assumption of the biological infeasibility of sustainable harvest programs for freshwater turtles based almost entirely on temperate zone species should be reassessed given the challenges of conserving turtles in rapidly developing tropical regions where most turtle diversity occurs [9, 13].

In this study, we investigated global patterns of life history traits (clutch size, clutch frequency, age at sexual maturity, and adult survival) in freshwater turtles using published data and contrasted them between freshwater turtle species from temperate and tropical regions. We then developed a population projection model to estimate the capacity of freshwater turtle species from temperate and tropical regions to sustain harvest. The primary goal of this study was to evaluate the hypothesis that freshwater turtle species from tropical and temperate regions

have the same, widely speculated incapacity to absorb additive mortality caused by population harvest [29, 30, 35].

Materials and Methods

Data Collection

Life history traits of freshwater turtle species were quantified along with locality of each report (latitude and longitude) from the published literature. We used keywords “life history”, “clutch size”, “clutch frequency”, “reproduction”, “age at sexual maturity”, “survival”, “growth”, “natural history”, and “turtle” to explore the published literature as indexed in the databases of EBSCO, Google Scholar, and Web of Science. The mean, median, or range values of reproductive parameters (clutch size, clutch frequency), demographic parameters (age at sexual maturity, annual adult survival rate), and morphological characters (carapace length) were extracted from each report acquired. Annual adult survival values were also checked and confirmed against those available for 15 freshwater turtle species in an online demographic database COMADRE [43] (version 3.0.0, accessed 2 September 2019 http://www.comadre-db.org/Data/Comadre).

When the exact coordinates of locality were not described, we estimated location from the nearest locality described in a given report. The coordinates of each turtle life history report were also combined with GBIF records (accessed via GBIF.org on 2019-01-13) and published data [38] to establish species distribution across four latitudinal classes: Temperate (species with latitudinal median and range within temperate zone), Temperate-tropical (“Temp-trop”, species with latitudinal median within temperate and range overlapping tropical zone/s), Tropical-

temperate ("Trop-temp", species with latitudinal median within tropical and range overlapping temperate zone/s), Tropical (species with latitudinal median and range within tropical zone). The tropics of Capricorn and Cancer (latitude -23.5^{o}, 23.5^{o}, respectively) were used to define geographic limits of temperate and tropical zones.

Two bioclimatic variables relevant to freshwater turtle biology, Mean Temperature of Warmest Quarter (bio10, ^{o}C) and Precipitation of Driest Quarter (bio17, mm) were obtained from WorldClim – Global Climate Data (5-arc ≈ 10 km resolution, www.worldclim.org, [44]) and matched to the coordinates of each turtle life history report. These bioclimatic variables were selected as proxies to represent the metabolic, physiological and behavioral differences that freshwater turtles have developed to survive in regions that are not ideal for these temperature and water dependent species [10, 22, 32, 33, 38-41, 45]. Both bioclimatic variables were only weakly correlated with latitude (Spearmans correlation 0.40 and 0.04 for bio10 and bio17 respectively) and were therefore included to represent temperature and rainfall patterns distinct to those most strongly associated with latitudinal gradients.

Statistical Analysis

We used Generalized Additive Models (GAMs, [46, 47]) to examine the influence of climate variables and latitude on freshwater turtle life history traits (clutch size, clutch frequency, age at sexual maturity, and annual adult survival). We treated each freshwater turtle species as a replicate in this analysis (obtaining median life history values within species for species with $n >$ 1 reports) to avoid the pitfalls of pseudoreplication associated with treating individual reports as replicates. Because comparative life history studies are not independent from phylogenetic relationships among turtles, which can lead to phylogenetic bias on inference and trait value

136 estimation [41-42], we treated taxonomic family as a random effect (penalized smoothed
137 regression term) [48, 49] based on the Turtles of the World Checklist (8th edition, [50]). In
138 addition, we used carapace length (ln-transformed) as a parametric term to control for its well-
139 established influence on life history traits [33, 36, 38, 41].

140 A total of four models were developed for each life history trait: latitude as a continuous
141 variable included as a parametric term, latitude as a categorical variable with four classes
142 (Temperate, Temp-Trop, Trop-Temp and Tropical), and two bioclimatic variables (Mean
143 Temperature of Warmest Quarter and Precipitation of Driest Quarter) included as parametric
144 terms. All life history trait estimates were ln-transformed, except for adult survival (arcsine
145 transformed). The mgcv package [46] was used to perform the GAM analysis in R (www.r-
146 project.org, [51]). Akaike Information Criterion corrected for small sample sizes (AICc) that
147 measures fit versus complexity of a model was used to select "best" models based on lowest
148 AICc [52, 53].

149

150 Modelling Synthesis

151 To evaluate whether freshwater turtle species from tropical and temperate zones have
152 comparable capacities to absorb additive mortality caused by population harvest, we
153 implemented a density-independent, stage structured "Lefkovitch" matrix population model [34,
154 54, 55]. This type of model is commonly used in turtle population dynamics modelling, as age in
155 most turtle species is often difficult to determine [19, 34]. The model consisted of egg, juvenile,
156 and adult stages (Fig 1) projected with a stable stage distribution (with an initial population of
157 1000, allocated in proportions of 0.544, 0.401, 0.055 to egg, juvenile and adult stages

respectively). The discrete stage based lifecycle (Fig 1) can be presented as a population projection matrix "A" as follows:

$$\boldsymbol{A} = \begin{bmatrix} 0 & 0 & F \\ G_1 & P_1 & 0 \\ 0 & G_2 & P_2 \end{bmatrix}$$

where P is the annual probability of surviving and remaining in the same stage, G is the annual probability of surviving and growing into next stage, and F is the annual fecundity. These parameters were estimated using the following equations [56]:

$$\boldsymbol{P} = \frac{\left(1 - p_i^{d_i - 1}\right)}{\left(1 - p_i^{d_i}\right)} \boldsymbol{p_i} \qquad \text{Equation 1}$$

$$\boldsymbol{G} = \frac{p_i^{d_i}\,(1 - p_i)}{1 - p_i^{d_i}} \qquad \text{Equation 2}$$

where p_i is the annual survival probability of i stage and d_i is the duration of i stage. Annual fecundity (F) was estimated by multiplying clutch size with clutch frequency. The model was based on female fraction only; thus half of all eggs produced was assumed to be female [29, 30] . The stable distributions of individuals amongst stage classes, and intrinsic rate of population growth (r) were determined with functions available in the R [51] packages "popdemo" [57] and "popbio" [58].

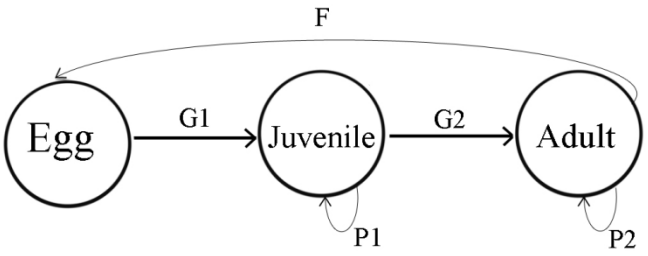

Fig 1. Conceptual diagram of population dynamics of freshwater turtles used for construction of a stage structure matrix model to estimate capacity for sustainable harvest in freshwater turtles.

Median values of clutch size, clutch frequency, age at sexual maturity and adult survival derived from the GAM predictions was used as input for this stage-structured model. Due to the sparsity of records for some traits (e.g. adult survival) predictions were aggregated across two latitudinal classes (temperate and tropical) to compare the intrinsic rate of population growth (*r*) between stages and latitude. Predictions for each trait were obtained from a final model that included all variables in a 95% confidence subset of models [52]. This confidence set was obtained by summing the Akaike weights of the set of all candidate models ordered by Akaike weight from largest to smallest until a sum of ≥0.95 was obtained ([52] pp. 169, 176-177). We estimated the annual survival probability of juvenile stage as 13% less than the annual survival probability of adult stage [59]. Due to lack of available nest / hatchling survival data the annual survival probability of egg stage for all turtle species was set at 0.2 [29, 30, 32]. To simulate the impact of harvest on populations of tropical and temperate freshwater turtle species, we

performed a sensitivity analysis by varying each demographic parameter systematically while holding all other parameters constant [29, 30]. In addition, we performed Jackknife randomizations [60] drawing deviates (n = 500 iterations) for each model parameter from the distributions observed in the literature (S1 Table) for these variables to estimate confidence intervals around the estimated intrinsic rates of growth of temperate and tropical species in sensitivity analysis.

Table 1. Demographic parameters in freshwater turtles. Demographic parameters used in population modelling to estimate capacity for sustainable harvest in freshwater turtles. Estimates are median values derived from the scientific literature (S1 Table) and summarized based on the species distributions across four latitudinal classes.

Distribution[a]	Families	Species	Lat[b]	Carapace Length	Clutch Size	Clutch Frequency	Age at sexual maturity	Fecundity
Temperate	6	41	34.0	181.0	8.4	2.0	8.7	7.8
Temp-Trop	6	43	29.1	221.7	11.2	1.7	8.3	6.6
Trop-Temp	10	37	18.3	197.3	6.1	2.5	6.5	6.0
Tropical	10	44	9.6	231.5	7.3	2.0	9.0	3.5
Overall	12	164	23.1	208.0	8.0	2.0	8.3	6.3

[a] Distribution of freshwater turtles in four latitudinal classes: Temperate (species latitudinal median and range within temperate zone), Temp-trop (species latitudinal median within temperate and range overlapping tropical zone/s), Trop-temp (species latitudinal median within tropical and range overlapping temperate zone/s), Tropical (species latitudinal median and range within tropical zone). This classification is unique for each species i.e. a species is only included in one class.

[b] Median latitude from species locations within each distribution class.

Results

A total of 461 reports of life history traits was obtained from 165 species (63% of living freshwater turtle species) among 12 taxonomic families (Fig 2, S1 Table). The data once aggregated represent: 84 species from 7 families in the temperate zone (Temperate and Temperate-Tropical classes) and 81 species from 12 families in the tropical zone (Tropical-Temperate and Tropical classes). Sixty percent of these studies were from temperate areas, with most of these (73%) from North America (Fig 2). Forty percent of these data were from tropical areas, with most of these (36%) from Asia. Only 12 of these life history trait reports were from captive breeding situations while the remainder were from wild populations.

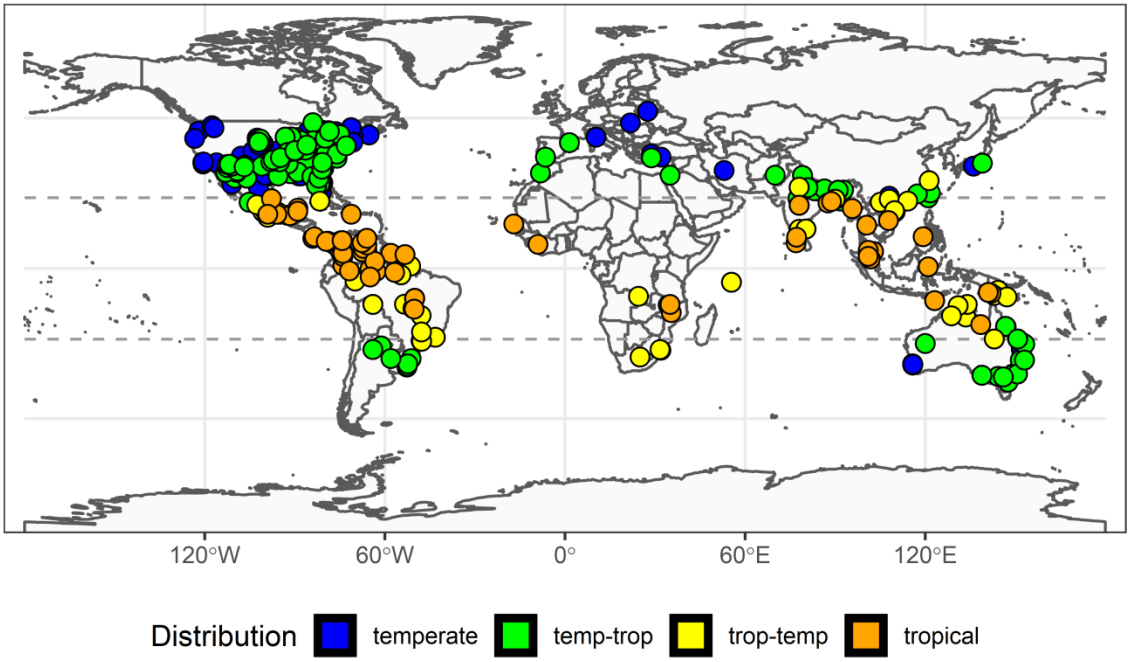

Fig 2. Distribution of freshwater turtle studies. Geographic distribution of data on freshwater turtle life history traits obtained from the literature (S1 Table) to estimate capacity for sustainable harvest in freshwater turtles. Color of study locations represent the distribution of the study species across four latitudinal classes: Temperate (species with latitudinal median and range within temperate zone), "Temp-Trop" (species with latitudinal median within temperate and range overlapping tropical zone/s), "Trop-Temp" (species with latitudinal median within tropical

and range overlapping temperate zone/s), Tropical (species with latitudinal median and range within tropical zone). Dashed horizontal lines show Tropic of Cancer and Tropic of Capricorn (latitude -23.5°, 23.5°, respectively). The background map was obtained from the 1:110m Natural Earth country and geographic lines maps (http://www.naturalearthdata.com).

Latitude as continuous variable significantly influenced all life history traits, except adult survival (Table 2, Table 3). Indeed, latitude was the most informative variable for clutch size, clutch frequency and age at sexual maturity (Table 3). Natural logarithm of clutch size ($\beta = 0.13$; $P < 0.001$) and age at sexual maturity ($\beta = 0.06$; $P < 0.01$) were positively related to latitude, whereas natural logarithm of clutch frequency ($\beta = -0.09$; $P < 0.05$) exhibited a negative relationship with latitude (Fig 1, Table 2). When latitude was treated as categorical variable, only the natural logarithm of clutch size was significantly related to latitudinal zones , such that Tropical ($\beta = -0.21$; $P < 0.001$) and Tropical-Temperate ($\beta = -0.13$; $P < 0.05$) species had reduced clutch size relative to temperate species (Table 2).

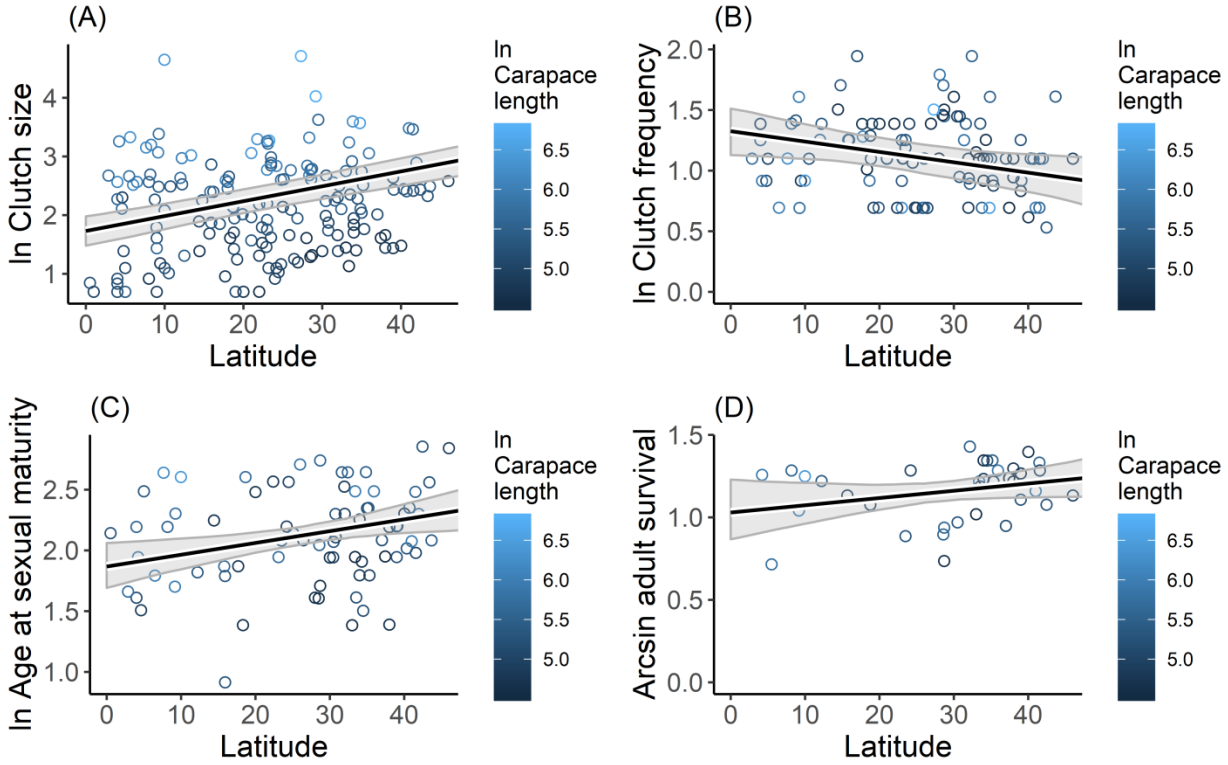

Fig 3. Relationships between latitude and (A) clutch size, (B) clutch frequency, (C) age at sexual maturity, and (D) adult survival rate of freshwater turtles. Points are the median species values obtained from the literature (S1Table), colored representing ln carapace length values. Solid black line is the GAM prediction. Grey shaded polygons show 95% confidence bands around the prediction.

Of the two bioclimatic variables assessed, only bioclimatic temperature (Mean Temperature of Warmest Quarter) was a contributor to life history variation (Table 2) and was also the most informative variable for adult survival (Table 3). The bioclimatic temperature models were included in the 95% confidence set for all life history traits, except clutch size (Table). Natural logarithm of age at sexual maturity (β = -0.06; $P < 0.01$) and arcsine adult survival (β = -0.08; $P < 0.05$) were both negatively related to Mean Temperature of Warmest Quarter (Fig 4).

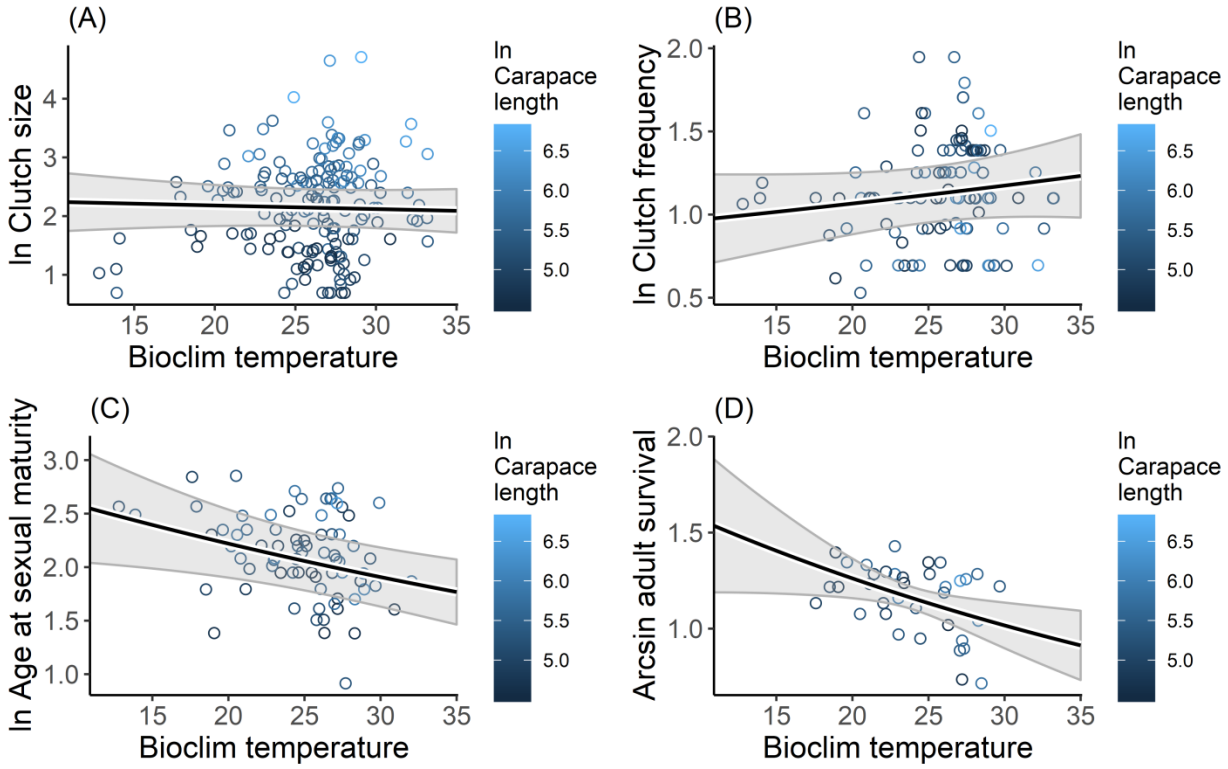

Fig 4. Relationships between bioclimatic temperature (Mean Temperature of Warmest Quarter) and (A) clutch size, (B) clutch frequency, (C) age at sexual maturity, and (D)

adult survival rate of freshwater turtles. Points are the median species values obtained from the literature (S1 Table), colored representing ln carapace length values. Solid black line is the GAM prediction. Grey shaded polygons show 95% confidence bands around the prediction.

The sensitivity analysis performed to examine the impact of harvest on freshwater turtle populations revealed that adult and juvenile survival rates had dramatically more impact on intrinsic rate of population growth than egg survival rate and fecundity (Fig 5). Tropical freshwater turtle species exhibited a moderately higher intrinsic rate of growth than temperate freshwater turtle species (Fig 5). Although, fecundity tended to be less in tropical species (Table 2, Table 4), comparing the minimum values necessary to result in positive population growth with GAM predictions showed that fecundity could be reduced by 28% in tropical compared with only 12% in temperate species (Table 4). Survival rates were estimated to be reducible by 35% in eggs, 24% in juveniles, and 5% in adults for tropical species, and 15%, 16%, and 7%, respectively for temperate species, without causing negative population growth (Table 4). However, overlap in estimations of population growth in relation to survival rates was very broad between tropical and temperate turtle species suggesting that, in aggregate the capacity for sustainable harvest of adults as an additive source of turtle mortality is constrained in tropical turtle species largely as it is in temperate zone species (Fig 5, Table 4).

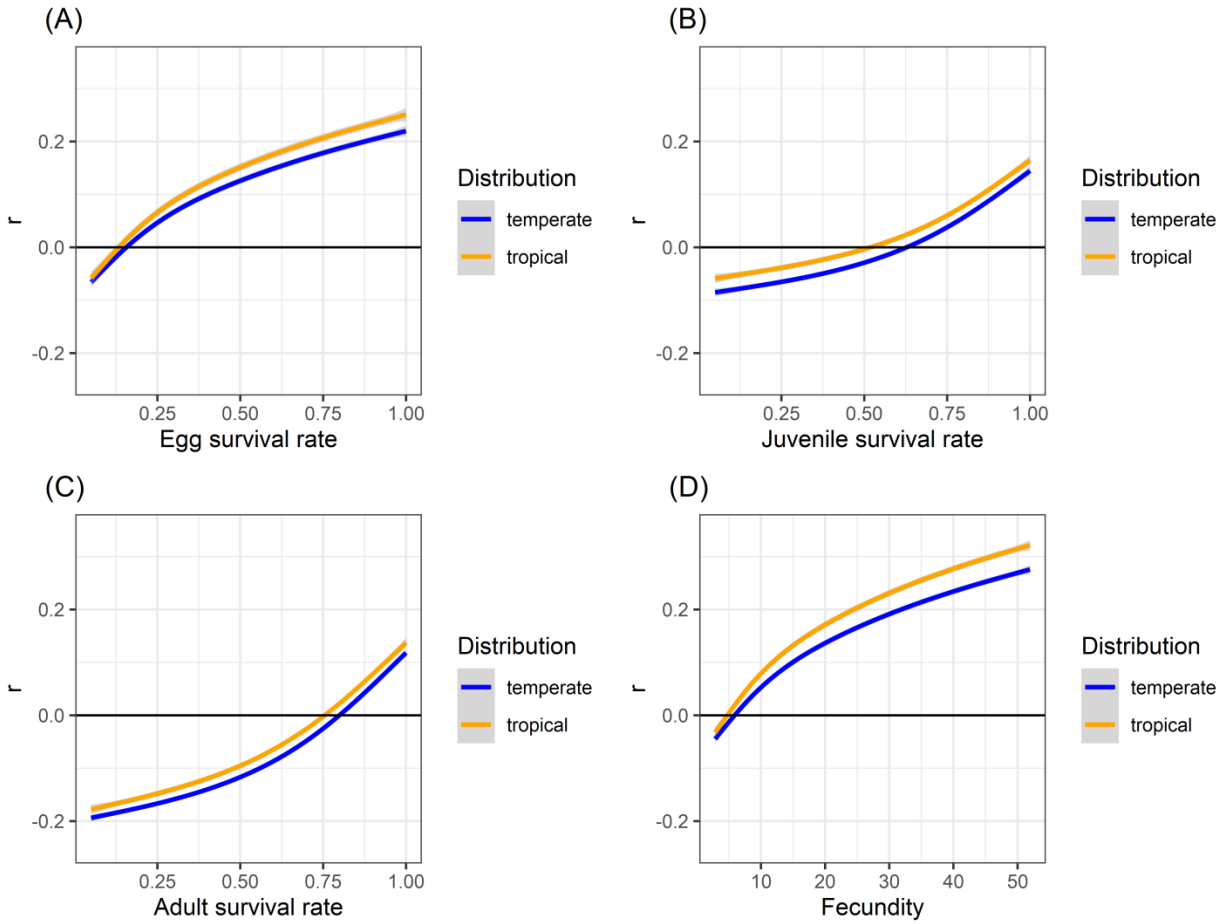

Fig 5. Relationships between intrinsic rate of growth (*r*) and survival rates of (A) egg, (B) juvenile, and (C) adult, and (D) fecundity in freshwater turtles of tropical and temperate zones. Solid lines are the intrinsic rate of growth for temperate and tropical species, respectively.

Table 2. Influence of climate variables and latitude on freshwater turtle life history traits. Generalized Additive Models were used to predict responses of four freshwater turtle life history traits: clutch size, clutch frequency, age at sexual maturity and adult survival.

Model		ln clutch size (n = 165)			ln clutch frequency (n = 102)			ln age at sexual maturity (n = 75)			arcsine adult survival (n = 37)		
Continuous latitude		**Est.** [a]	**SE**	***p***	**Est.** [a]	**SE**	***p***	**Est.** [a]	**SE**	***p***	**Est.** [a]	**SE**	***p***
Intercept		0.78	0.05	***	0.12	0.05	*	0.75	0.02	***	0.12	0.03	***
Log carapace length		0.29	0.02	***	0.01	0.03		0.09	0.02	***	0.01	0.03	
Latitude		0.13	0.00	***	-0.09	0.04	*	0.06	0.02	**	0.04	0.03	
Smooth		**Edf/ref**	**F**	***p***	**Edf/ref**	**F**	***p***	**Edf/ref**	**F**	***p***	**Edf/ref**	**F**	***p***
Family		8.1/11	6.48	***	5.0 / 11	1.2	*	0.0 / 10	0.0		0.0 / 7	0.0	
R^2 ajust / Dev. Exp [b]		0.78 / 77.6%			0.12 / 17.9%			0.19 / 20.2			0.01 / 6.7		
Categorical latitude		**Est.** [a]	**SE**	***p***	**Est.** [a]	**SE**	***p***	**Est.** [a]	**SE**	***p***	**Est.** [a]	**SE**	***p***
Intercept		0.85	0.06	***	0.12	0.06	.	0.76	0.05	***	0.10	0.06	
Log carapace length		0.29	0.02	***	0.01	0.03		0.06	0.03	*	-0.01	0.04	
Latitude	temp-trop	0.04	0.05		-0.06	0.08		0.02	0.05		0.08	0.06	
	trop-temp	-0.13	0.05	*	0.06	0.09		-0.11	0.07		0.07	0.09	
	tropical	-0.21	0.05	***	0.04	0.09		-0.02	0.08		-0.05	0.12	
Smooth		**Edf/ref**	**F**	***p***	**Edf/ref**	**F**	***p***	**Edf/ref**	**F**	***p***	**Edf/ref**	**F**	***p***
Family		7.9/11	6.27	***	2.7 / 11	0.4		4.7 / 10	0.9	.	2.5 / 7	0.6	
R^2 ajust / Dev. Exp [b]		0.76 / 75.8%			0.03 / 9.3%			0.24 / 32.2%			0.07 / 23.8%		
Bioclimate - temp		**Est.** [a]	**SE**	***p***	**Est.** [a]	**SE**	***p***	**Est.** [a]	**SE**	***p***	**Est.** [a]	**SE**	***p***
Intercept		0.76	0.05	***	0.12	0.04	**	0.72	0.04	***	0.11	0.03	**
Log carapace length		0.27	0.02	***	0.01	0.03		0.07	0.03	**	0.02	0.03	
Temp. warm quarter (bio10)		-0.01	0.02		0.03	0.03		-0.06	0.02	**	-0.08	0.03	*
Smooth		**Edf/ref**	**F**	***p***	**Edf/ref**	**F**	***p***	**Edf/ref**	**F**	***p***	**Edf/ref**	**F**	***p***

Family	7.0 / 11	4.39	***	3.4 / 11	0.6	.	5.4 / 10	1.2	*	0.0 / 7	0.0	
R^2 ajust / Dev. Exp [b]	0.72 / 69.8%			0.05 / 9.9%			0.31 / 37.7%			0.12 / 16.7%		
Bioclimate - rain	**Est.** [a]	**SE**	***p***	**Est.** [a]	**SE**	***p***	**Est.** [a]	**SE**	***p***	**Est.** [a]	**SE**	***p***
Intercept	0.76	0.05	***	0.12	0.04	**	0.73	0.05	***	0.15	0.03	***
Log carapace length	0.27	0.02	***	0.01	0.03		0.06	0.03	*	-0.01	0.03	
Rain dry quarter (bio17)	-0.03	0.02	.	0.02	0.03		0.00	0.02		0.02	0.04	
Smooth	**Edf/ref**	**F**	***p***	**Edf/ref**	**F**	***p***	**Edf/ref**	**F**	***p***	**Edf/ref**	**F**	***p***
Family	7.4/11	5.71	***	2.5 / 11	0.3		5.7 / 10	1.5	*	0.0 / 7	0.0	
R^2 ajust / Dev. Exp [b]	0.72 / 70.5%			0.02 / 7.0%			0.24 / 31.6%			-0.04 / 1.4%		

Each model contained Family as a random effect (smooth GAM term specified with "re" basis) and body size (ln transformed carapace length) as a parametric term; Asterisks indicate significant level of estimated parameters (*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; '.' $P < 0.1$).

[a] Standardized regression coefficient (obtained by dividing the centered response values by their standard deviations) and associated standard error (SE).

[b] Model adjusted r-squared and deviance explained (%)

Table 3. Freshwater turtle life history model comparisons. Comparisons of the Generalized Additive Models created for each life history trait to estimate capacity for sustainable harvest in freshwater turtles. Models for each trait ordered by decreasing AICc (Akaike information criterion corrected for small sample sizes) values.

Life history trait	Model[a]	Dev. Exp	Loglik	BIC	AICc	Δ AICc	W_i AICc[b]
Clutch size							
	Continuous latitude	77.6	-69.35	207.05	168.09	0.00	1.00
	Categorical latitude	75.8	-80.04	237.57	193.80	25.71	0.00
	Bioclimate - rain	69.8	-95.48	256.12	218.85	50.77	0.00
	Bioclimate - temp	70.5	-98.96	261.27	224.98	56.90	0.00
Clutch frequency							
	Continuous latitude	17.9	-14.42	81.83	54.94	0.00	0.93
	Bioclimate - temp	9.9	-19.25	85.31	61.22	6.28	0.04
	Bioclimate - rain	7.0	-21.01	83.69	62.00	9.79	0.03
	Categorical latitude	9.3	-19.61	91.34	64.84	12.62	0.01
Age at sexual maturity							
	Continuous latitude	20.2	-28.82	79.24	68.52	0.00	0.57
	Bioclimate - temp	37.7	-19.46	92.49	69.13	0.62	0.42
	Bioclimate - rain	31.6	-22.86	99.50	76.08	7.56	0.01
	Categorical latitude	32.2	-22.62	104.54	79.42	10.91	0.00
Adult survival							
	Bioclimate - temp	16.7	14.16	-10.39	-16.31	0.00	0.85
	Continuous latitude	6.7	12.09	-6.27	-12.19	4.12	0.11
	Bioclimate - rain	1.4	11.09	-4.26	-10.18	6.13	0.04
	Categorical latitude	23.8	15.77	7.28	0.73	17.04	0.00

[a] Models used to predict natural history traits. Each model contained Family as a random effect (smooth term with "re" basis) and body size (log transformed carapace length) as a parametric (not smooth) effect. Continuous latitude included median latitude from all records (Table S1). Categorical latitude included four latitudinal classes: Temperate (species with latitudinal median and range within temperate zone), "Temp-Trop" (species with latitudinal median within temperate and range overlapping tropical zone/s), "Trop-Temp" (species with latitudinal median within tropical and range overlapping temperate zone/s), Tropical (species with latitudinal median and range within tropical zone). Bioclimate - temp included Mean Temperature of Warmest Quarter (WorldClim: bio10). Bioclimate - rain included Precipitation of Driest Quarter (WorldClim: bio17). Coefficients for individual variables in all models are presented in Table 2.

[b] Akaike weights (W_i) from largest to smallest. Predictions for each trait were obtained using variables from the 95% confidence subset of models, obtained by first ordering all models in the set by decreasing Akaike weight (W_i), and then sequentially summing the model W_i's in rank order.

305 **Table 4. Demographic parameters used in population modelling to estimate capacity for**
306 **sustainable harvest in freshwater turtles.** Observed are median values derived from the
307 scientific literature (S1 Table) and predicted values are from the 95% confidence set of GAM
308 models (Table 3). "*r* min" are the minimum values necessary to obtain positive intrinsic rate of
309 growth (*r*) as determined via sensitivity analysis (Fig 5).

	Observed		Predicted		*r* min	
Parameter	**Temp.**	**Trop.**	**Temp.**	**Trop.**	**Temp.**	**Trop.**
Annual egg survival rate	0.200 [a]	0.200 [a]	0.200 [a]	0.200 [a]	0.170	0.130
Annual juvenile survival rate	0.766[b]	0.767[b]	0.746[b]	0.694[b]	0.630	0.530
Annual adult survival rate	0.880	0.882	0.857	0.798	0.800	0.760
Clutch size	8.8	7.0	7.3	5.2		
Clutch frequency	2.0	2.3	2.0	2.3		
Age at sexual maturity	8.3	7.8	8.6	7.3		
Fecundity	7.3	6.0	7.3	6.0	6.4	4.3

310 [a] Values derived from previous syntheses [32].
311 [b] Estimated as 13% less than the annual adult survival rates [59].
312

313 Discussion

314 The capacity of any species to cope with additive mortality is determined by the interplay of its
315 life history traits [61-63]. Turtles are often declared to share integrated life history features [64]
316 that make compensation for additive mortality associated with harvest infeasible [28]. Life
317 history traits of many organisms are related to variation in environment [65, 66], climate [67]
318 and their ecological interactions [61-63, 68, 69] and this study revealed that turtle life history is
319 strongly related to latitude and ambient temperature. Yet although these trends might suggest an
320 increase in capacity of tropical freshwater turtles to absorb additional mortality due to
321 anthropogenic sources than in temperate zone species, once integrated in a synthetic population
322 model tropical species appear to be as unable to absorb additive mortality as are temperate zone
323 species.

The positive relationship we observed between clutch size and latitude is consistent with earlier studies [36, 41]. Turtles that inhabit higher (temperate) latitudes, have larger clutch size than turtles that inhabit low (tropical) latitudes. Similar patterns have been observed in mammals [67] and birds [68, 70]. Tokolyi, Schmidt (67) and McNamara, Barta (68) suggest this pattern is related to climate variability. Iverson, Balgooyen (41) concluded that higher juvenile competition due to shorter time period for development along with higher egg mortality associated with winter and climate uncertainty that creates temporary periods of low competition may make it more advantageous for temperate turtle species to produce more offspring ("more eggs in one basket" [33]) as a "bet hedging" strategy to exploit temporary resources. In addition, temperate turtle species typically have small egg size to speed development as an adaptation to short incubation times in temperate zone [17, 41]. As such, our findings support the suggestion that temperature zone turtles may have evolved to produce smaller egg size with larger clutch size than tropical species [33].

Larger clutch size in temperate turtle species may also act as a mechanism to compensate for low nesting frequency [33, 41]. We found that clutch frequency was negatively related to latitude. The general model of the interaction of environmental factors and reproductive output in turtles [33] suggests that high latitudes yield short reproductive seasons for turtles, resulting in lower clutch frequency. In addition, timing of nesting in turtles is correlated with temperature [36, 71]. Because tropical zones have a more stable warmer temperature all year long, more opportunities are available for turtles to lay eggs than in the temperate zone. Additionally, clutch mass (number of eggs x egg size) can also vary with latitude [33, 41], further studies are necessary to examine how egg size correlates to differences in population growth rates,

346 especially as egg size has been shown to be an important predictor of age at sexual maturity [32,
347 33].

348 The relationship between age at sexual maturity and latitude observed in this study is also
349 in agreement with the earlier studies [72-74]. Turtles that inhabit high latitudes reach maturity at
350 a later age than those inhabit low latitudes. This result is likely due to more stable and more
351 productive climate conditions at low latitudes. As growth rate in turtles depends on temperature
352 and food availability [75, 76], thus stable warm temperature and continuous food availability in
353 low latitudes will generate faster growth rate to reach size at sexual maturity [33]. This
354 conclusion is also supported by the inverse relationship between Mean Temperature of Warmest
355 Quarter and age at sexual maturity. Although it has been suggested that turtles tend to have
356 larger body size at higher latitudes [77] a recent review (compilation of 245 species) failed to
357 uncover clear latitudinal trends in turtle body size [38]. These differences between studies (for
358 example [77] evaluated variation within species from a sample of 23 species of mainly northern
359 hemisphere and temperate turtles) seem to support the hypothesis that body size latitude
360 relationships (e.g. Bergmann's rule) maybe stronger for temperate turtle species. Large body size
361 is thought to provide evolutionary advantages for temperate turtle species to cope with
362 unfavorable environments e.g. via a relative increase in fasting endurance [36, 76]. As a result,
363 temperate turtle species require longer time to reach size at sexual maturity, but increased size
364 may provide for increased adult survivorship [32].

365 Adult survival and latitude were not strongly related perhaps because all turtles share in
366 common the unique morphological feature: a rigid shell [28, 78, 79]. Turtle shells not only
367 provide physical protection from predators [28], but also important physiological functions [78-
368 80]. The optimum benefits from the shell are achieved when a turtle has reached adult size [28]

369 such that different environmental conditions at low and high latitudes may have little effect on
370 adult survival rate because the shell ensures high survival regardless of ecological context.

371 It is important to note, however, that our failure to identify differences in survival rates
372 may result from a lack of statistical power [53, 81]. Relatively few reports were available for
373 survival rates of turtles at low (tropical) latitudes thereby possibly limiting the ability to detect
374 differences might they exist. Clearly more long-term studies of turtle population biology in
375 tropical regions are needed and would inform this analysis. This said, differences that may exist
376 but are currently obscured by sampling variation would likely be modest and not likely to change
377 the overall conclusions of this study.

378 The distinct life history characteristics of turtles at low latitudes (tropical zone) would
379 seem to translate into greater opportunity for sustainable harvest of early stages than those at
380 high latitudes (temperate zone, Fig 5, Table 4). However, our estimated annual sustainable
381 harvest rate (5%) of adult turtles is considerably lower than typical thresholds for sustainable
382 harvest rates (20%) estimated for long-lived animals [19, 82, 83]. In addition, similar to previous
383 studies [29, 30, 34, 73, 84-87], high adult survival rates are estimated to be critical to maintain
384 population stability due to their relatively greater contribution to population recruitment than
385 other life stages [34]. Considering these results, harvesting wild adults would appear to present a
386 high risk of causing population declines whether in the temperate or tropical regions, reinforcing
387 the need to develop appropriately enforced alternate management options such as farming of
388 captive reared turtles for meat [88].

389 Although adult harvest is clearly risky [9, 28, 87] there does appear to be some potential
390 for sustainable exploitation of early stages of tropical freshwater turtle species. Indeed, egg

391 harvest may be more feasible, because it has low risk of causing population declines (Fig 5).
392 Gibbs and Amato (28) suggest that significant additive mortality in the egg stage may not
393 threaten population persistence and, Thorbjarnarson, Lagueux (8) identified that harvesting of
394 eggs is the most promising strategy in the development of sustainable use programs for turtles.
395 Integrating the conservation and harvest of eggs (for consumption, sale and/or rearing of
396 hatchlings for the pet trade) has generated promising results for the conservation of some
397 threatened tropical turtles e.g. *Podocnemis unifilis* in Peru [89, 90] and our analysis supports the
398 idea that such actions could be feasible in other tropical turtle species.

399 We found that tropical populations could continue to grow if egg survival was reduced by
400 up to 35%. We suggest that this surplus of eggs can be applied for both sustainable exploitation
401 and conservation. A focus on management and sustainable exploitation of early life stages (e.g.
402 consumption, pet trade) would also complement conservation actions that generally protect the
403 most sensitive adult stages [9, 28]. We found that the margins for additive mortality are so tight
404 (<10% in both tropical and temperate species) that the sustainable harvest of adult turtles will
405 likely fail unless additional management actions are incorporated into conservation programs [9].

406 Integrated management that explicitly considers survival of all life stages is likely to
407 generate more robust and timely increases in exploited turtle populations. Although egg survival
408 produces a relatively small overall effect on population growth rates when compared to adult
409 survival [28, 34], demographic simulations show that increasing survival of eggs and hatchlings
410 can compensate for decreases in adult survival in at least one species of tropical turtle [91].
411 Additionally, increasing survival of early stages via community-based protection of turtle nesting
412 beaches has been shown to provide conservation success for local communities [90], target
413 species [90-93] and also non-target vertebrate and invertebrate taxa [92]. Further examples are

414 needed to understand how the predicted surplus in early life stages can be most effectively
415 exploited so that populations can still increase to replace adults that remain widely targeted and
416 threatened by additional anthropogenic impacts across tropical regions including climate change,
417 forest loss and pollution [1, 9, 12, 18, 19].

418 An important caveat is that the population dynamics of temperate and tropical species in
419 this study were evaluated using the same survival rate values for eggs due to lack of available
420 published data on these parameters both in temperate and tropical species. Mechanisms of
421 protection of egg and juvenile stages do not produce as large an effect on population growth as
422 protecting adult survival [28], so our conclusions are likely to remain valid despite this untested
423 assumption. That said, until data are available on typical nest and juvenile survival in temperate
424 and tropical zones, the relative impact of harvest on populations of temperate and tropical
425 species we estimated must remain tentative.

426 Together the results of this study imply that sustainable harvesting is difficult to apply as
427 a conservation strategy, both in temperate and tropical turtle species, due to the biological
428 limitations on turtle population growth imposed by their life history strategy everywhere. This
429 said, Eisemberg, Rose (18) suggests that complete prohibition of harvesting as a conservation
430 strategy in turtles will not be possible to implement in tropical areas and developing countries,
431 where local communities have long history in using turtle meat and eggs. Conservation strategies
432 that exclude local communities in their practices are often unsuccessful at protecting wildlife
433 [94]. We reject the assumption often employed in temperate-zone turtle research that "all turtles
434 are the same" yet also note that demographic differences we observed between temperate and
435 tropical turtles do not translate into obviously greater opportunity for sustainable harvest of
436 adults and juveniles in the tropics. Therefore, carefully constructed sustainable harvest programs

may present greater opportunities to succeed in the tropics if based on egg and hatchling stages, and should be considered further but cautiously for the regions that have a long history of harvesting turtles for subsistence use, particularly when the species possess density dependent mechanisms to compensate harvest, such as shown in *C. oblonga* [19, 42].

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Author Contributions

Conceived and designed the experiments: AR, JPG. Performed the experiments: AR, DN, JPG. Analyzed the data: AR, DN, JPG. Contributed reagents/materials/analysis tools: AR, DN, JPG. Wrote the paper: AR, DN, JPG.

Supporting Information

S1 Table. The life history traits data obtained from literature review. Available from the corresponding author on request.

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