

Abiotic modulators of *Podocnemis unifilis* (Testudines: Podocnemididae) abundances in the Peruvian Amazon

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ABSTRACT. Previous studies have demonstrated that river-based surveys can provide an inexpensive source of information for neotropical zoologists, yet little information is available to inform the application of this technique for the long term monitoring of neotropical turtle species. We aimed to fill this gap by presenting an assessment of data collected during 333 river surveys over 50 months along rivers in a newly protected area in the Peruvian Amazon. A total of 14,138 basking *Podocnemis unifilis* Troschel, 1848 were recorded during 13,510 km of river-based surveys. We used generalized additive models (GAMs) to explore the influence of a series of abiotic and seasonal variables on the recorded abundances at two temporal scales: monthly and per trip. Our analysis revealed that there was a significant increase in turtle abundances during the study period and we also found a significant seasonal periodicity in monthly abundances. Abiotic factors strongly influenced trip level abundances, with more individuals per kilometer recorded during sunny days in the dry season, with temperatures between 25 and 30°C. The results demonstrate that turtle populations are increasing following the establishment of the protected area and that river-based surveys are likely to be more effective when carried out within a limited set of key abiotic conditions.

KEY WORDS. Basking survey; conservation; population monitoring; river turtles; sighting rates.

Lack of basic biodiversity data continues to limit global conservation efforts (PENNISI 2010, STOKSTAD 2010). Demographic parameters of wildlife populations are the foundation upon which our understanding of ecological changes are based and effective management actions for the sustainable use of wildlife populations can be developed (NOSS 1990, CERTAIN *et al.* 2011). Marine turtles are a classic example where quantifying stage specific population trends led to the application of effective management techniques and population recoveries (CROUSE *et al.* 1987, CROWDER *et al.* 1994). Yet due to the time and effort required for long term population studies the quantification of demographic parameters in wildlife populations remains a challenge.

Amazonian river turtles are threatened by harvesting and the habitat loss and degradation caused by human expansion along Amazonian waterways (MITTERMEIER 1978, AGOSTINHO *et al.* 2005, KEMENES & PEZZUT 2007). Recently proposed changes to Brazilian legislation also pose serious threats to riparian species (MICHALSKI *et al.* 2010). Generally, turtle population num-

bers, demographics and population growth rates are known to be strongly dependent on the number of adults and juveniles whereas the numbers of eggs and hatchlings are relatively unimportant (CROWDER *et al.* 1994, GARBER & BURGER 1995, HEPPELL 1998, CHALOUPIKA 2002). This pattern has also been confirmed in the Podocnemididae, including the Giant Amazonian river turtles *Podocnemis expansa* (PEARSE *et al.* 2006, MOGOLLONES *et al.* 2010), where for example increased hunting of adult females led to population collapses (reviewed in THORBJARNARSON *et al.* 2000). The longevity and population demographics of these turtles mean that monitoring the number of adults is therefore particularly critical (MOGOLLONES *et al.* 2010).

Podocnemis unifilis Troschel, 1848 is classified as Vulnerable by the IUCN (TORTOISE & FRESHWATER TURTLE SPECIALIST GROUP 1996) and is listed on CITES appendix II (<http://www.cites.org/eng/app/appendices.shtml>). Despite their widespread distribution throughout the Amazon basin there remains little data on *P. unifilis* abundances to enable meaningful comparison or the development of testable hypothesis for explaining why differ-

ences in abundances exist. Behavior such as basking on logs, boulders and rocky outcrops makes *P. unifilis* one of the most common species seen during river-based boat surveys in Amazonia (PITMAN *et al.* 2011) and for the semi-aquatic *P. unifilis* river-based survey counts (sighting rates) may represent “true” counts over a known area as they are restricted to aquatic habitats (TOWNSEND *et al.* 2005). Maximum counts from river-based surveys can therefore represent the minimum number of turtle individuals per river (TOWNSEND *et al.* 2005). Yet maximum counts do not enable comparisons or hypothesis testing.

The importance of comparative data on *P. unifilis* population levels is highlighted by recent genetic studies that suggest geographically proximate populations are demographically independent units (ESCALONA *et al.* 2009a) and may therefore constitute distinct conservation management units (FRANKHAM *et al.* 2004: 101-121). Yet few studies evaluate the use of river-based surveys for monitoring river turtles or provide data to enable the standardization of the technique and or the generation of scientific data for basin wide comparative analysis. To contribute to the development of standardized monitoring techniques and comparative analysis of river turtles our study i) uses data collected on *P. unifilis* sighting rates (hereafter interchangeably referred to as abundances or individuals per km) from an extensive river-based survey effort to identify optimum river turtle survey conditions and ii) apply a simple, reproducible modeling process to generate data applicable for comparative analysis.

MATERIAL AND METHODS

Boat surveys were conducted continuously for 50 months between April 2004 and June 2008 in the Los Amigos River watershed at the base of the Andes in southern Peru (Fig. 1). Here we present a summary of the boat survey methodology which is fully described in PITMAN *et al.* (2011). All surveys were carried out inside the Los Amigos Conservation Concession (LACC), a 145,918-ha protected area managed by a Peruvian conservation organization since 2003 under the supervision of the Peruvian forest service. The stretches of river we surveyed included both the main stem of the Los Amigos and its largest tributary, the Amiguillos; both are low-gradient, actively meandering rivers that are born in the Amazonian lowlands and typically classified as whitewater. Survey data were grouped into three geographic sections (Fig. 1, Tab. I): I) “Lower Amigos,” consisting of data collected within the 46.9-km stretch of the Los Amigos River from its mouth to its confluence with the Amiguillos River, II) “Upper Amigos,” which includes data collected within a 82.0-km stretch of the Los Amigos River upstream from its confluence with the Amiguillos River, and III) “Amiguillos,” which includes data collected within a 29.7-km stretch of the Amiguillos River upriver from its mouth.

Monitoring of *P. unifilis* was carried out by park guards as part of a broader survey of 31 faunal species (PITMAN *et al.* 2011). Trips were not made on a fixed schedule, but took advantage of the park guards’ routine patrols and binoculars were not typi-

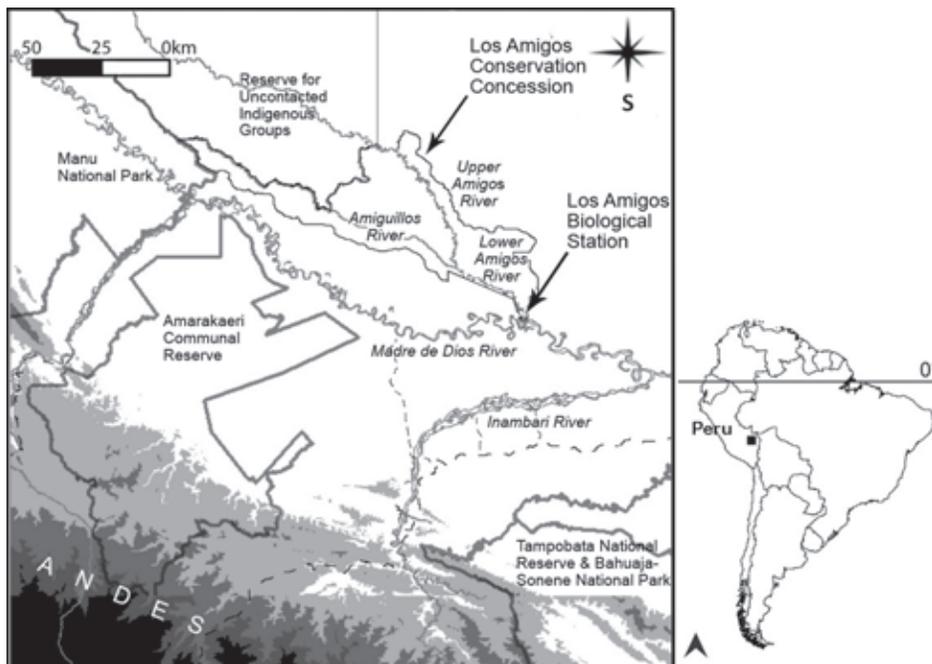


Figure 1. A map of the study area in southeastern Peru showing location of river sections surveyed. The white portion of the map is below 500 m elevation; darker gradations show 500-m intervals. Dotted lines represent roads. Several rivers have been omitted for clarity.

Table I. Summary of boat survey sampling effort with detection rates and number of *P. unifilis* individuals recorded per kilometer along three sections of river around the Los Amigos Biological Station, Amazonian Peru.

River stretch [trip length km: mean, (range)]	Trips with <i>Podocnemis</i> (%)	Total		Average speed (km/h)	Individuals per km (range)
		km	hours		
Amiguillos [21.3 (19.7-29.7)]	2/6 (33.3)	128.0	18.4	7.0	0.03 (0-0.10)
Los Amigos Lower [42.44 (7-46.9)]	254/290 (87.6)	12307.7	926.3	13.2	1.17 (0-10.18)
Los Amigos Upper [29.0 (3.1-82.0)]	33/37 (89.2)	1074.5	95.9	11.2	1.17 (0-4.33)
Overall [40.6 (3.1-82.0)]	289/333 (86.8)	13510.2	1040.7	13.0	1.14 (0-10.18)

cally used. Although the number of observers differed per trip (median = 2, range = 1-5) on each trip one guard was designated as principal observer and data recorder. Following a recent classification of monitoring approaches (DANIELSEN *et al.* 2008) the boat surveys can be classified as Category 3 (Collaborative Monitoring with External Data Interpretation). Park guards made an average of 7.7 trips per month (range 2-23). May and June had the highest mean number of trips, September and December the lowest. All boat travel was in 12-m wooden boats powered by 16-hp engines with a 3-m driveshaft. Upstream velocity was 11-17 km/h; downstream velocity was 18-22 km/h.

All analyses were performed in the R-software (R DEVELOPMENT CORE TEAM 2010) with associated packages. Non-parametric tests (Wilcoxon rank sum) were used to compare abundances (individuals per km) recorded during trips along the three river sections. To quantify the influences of series of abiotic and seasonal variables on monthly and trip level abundances we used generalized additive models (GAMs, package "mgcv" (WOOD 2010)) to model the number of individuals recorded per km. Previous studies have demonstrated that GAMs are particularly suited to modelling irregular time-series data such as ours (SIMPSON & ANDERSON 2009). With GAMs it is possible to model a combination of parametric variables (as commonly carried out in generalized linear models) and non-parametric "smoothed" variables, which allows the shape of the relationship between the response and the explanatory variables to be determined from the data, rather than following a prescribed functional form (e.g. linear). As a result, GAMs are able to model non-linear relationships between the response and the covariates, with the effect of the covariate varying across its range (WOOD 2008).

To quantify influences on the month to month variation in the response of *P. unifilis* abundances (for each month the total individuals from all trips/total survey km) a total of 4 weakly correlated (maximum Spearman correlation $r = 0.49$, across all pairwise comparisons) continuous variables were included as non-parametric smoothed predictors in a GAM, built using the package defaults for obtaining model knots and smoothing parameters. We used "month" (continuous values 1 to 50) to model the non-linear trends in abundances, mean river level was derived from daily records for the river level

relative to an arbitrary fixed point established on the bank of the Madre Dois river (data and recording details available from: http://atrium.andesamazon.org/meteo_station_display_info.php?id=14). Abiotic conditions were measured by mean air temperature and total precipitation per month, both of which were derived from daily records at the weather station at the Los Amigos Biological Station, near the mouth of the Los Amigos River (data and weather station details available from: http://atrium.andesamazon.org/meteo_station_display_info.php?id=12). For 5 months (April to August 2004) temperature and precipitation data were obtained from manual records at the Los Amigos Biological Station (data and recording details available from: http://atrium.andesamazon.org/meteo_station_display_info.php?id=13). These variables were selected as previous studies have shown their importance in relation to observed sighting rates and abundances (TOWNSEND *et al.* 2005, COWAY-GOMEZ 2007, ESCALONA *et al.* 2009b).

To evaluate modulators of trip level abundances and obtain estimates of optimum survey conditions we used 8 variables (data sources as per monthly abundances unless otherwise stated) to explain the variation in the response of the number of individual *P. unifilis* per km seen during a trip in a GAM. The mean air temperature during the trip (for 18 trips from April to August 2004 where weather station data was not available we used manually recorded maximum daily values), water level (daily mean) and two categorical factors of sunlight and rain (binary presence and absence) recorded during the trip were used to model abiotic conditions that are known to influence *P. unifilis* activity (TOWNSEND *et al.* 2005, COWAY-GOMEZ 2007, ESCALONA *et al.* 2009b). We also included a continuous linear measure of time to test for a temporal trend (i.e. a significant increase over time) in the observed abundances, plus two additional categorical factors that are also likely to explain variation in sighting records from our boat surveys: trip start period (i.e. 4 classes representing the time of day during which a trip was started) was included as detections of *P. unifilis* from boat surveys are strongly related to the time of day (COWAY-GOMEZ 2007) and finally observers. To test for an observer effect we retained as individual levels in our categorical factor only those observers ($n = 5$) who had a minimum experience of 23 trips and 2.5 years of surveys. Results from all other observers (a

total of 45 trips) were grouped together into one “less experienced” class. We did not include the total number of observers per trip (range 1-5) as it was the single designated observer who had primary responsibility for counting species and there was no significant influence of the total number of observers (categorical factor with 5 levels: 1-5) on *P. unifilis* abundances per trip (ANOVA, $F = 1.679_{4, 328}$, $p = 0.154$).

We used an information theoretic model averaging framework (BURNHAM & ANDERSON 2002) to examine the influences of the 8 variables on the *P. unifilis* abundances recorded per trip. This approach enables multimodel inference where our GAM models are ranked and scaled by some information criterion to allow an understanding of model uncertainty over the set of candidate models (BURNHAM & ANDERSON 2002: 281-284). We evaluated models based on their information content, as measured by AIC (Akaike Information Content implemented in R package “MuMIn” (BARTON 2011)). With a strong a priori justification for inclusion, we retained all predictors and all possible candidate models; therefore, all predictors were on equal footing to calculate their relative importance as measured by variable Akaike weights (BURNHAM & ANDERSON 2002: 75-77, 167-172), which is a scaled measure of the likelihood ratio that ranges between 0 (least important) and 1 (most important). A reduced subset of models for a 95% confidence set, based on the sum of Akaike weights across all models from largest to smallest that resulted in the sum of ≤ 0.95 , was used to calculate average values for slopes (BURNHAM & ANDERSON 2002: 169, 176-177). To reduce model selection bias model averaging was carried out using the full set of confidence models i.e. when a predictor was not present in the model its value was set to 0 (BURNHAM & ANDERSON 2002, pp. 152).

RESULTS

Park guards recorded a total of 14 138 individual *P. unifilis* over 50 months of surveys. Although the number of trips differed per month there was no significant correlation between the monthly abundances (total individuals/total km surveyed) recorded and the monthly total survey km (Spearman’s rank correlation, $r = 0.01$), which indicates that the effort per month was sufficient to ensure that differences in total kilometers surveyed did not influence the recorded abundances. Overall an average of 1.05 individual *P. unifilis* was recorded per km of river. Pairwise comparisons of individuals per km between trips on the three survey sections revealed that Amiguillos could be considered distinct from the Lower and Upper Amigos in terms of *P. unifilis* abundances. There was a significantly lower abundance on the Amiguillos when compared with Lower and Upper Amigos (Wilcoxon rank sum test, $p = 0.0007$, $p = 0.001$, Lower and Upper Amigos respectively). Although mean values between the “Upper” and “Lower” regions of the Los Amigos river were the same (Tab. I), median values were higher in the Upper Amigos (0.90 compared with 0.75 individuals per km,

Upper and Lower respectively) suggesting a slight but insignificant (Wilcoxon rank sum test, $p = 0.53$) increase in abundances along the Upper region.

There was a strong non-linear seasonal pattern in abundances, with more individuals per km recorded during trips in the dry season (Tab. II) and peak monthly abundances occurring when the river levels were declining or at their lowest (Fig. 2). Results from our GAM model showed that monthly abundances increased with time (Fig. 2, $p = 0.012$). The upper 95% confidence interval of the GAM model of monthly abundances provided the following minimum annual abundance (individuals per km) estimates along the 158.6 km of survey rivers: 1.74 (August 2004), 1.83 (July 2005), 2.44 (July 2006), and 2.56 (August 2008). These results from our GAM model provide values that correspond to an estimated 47% increase in the minimum number of turtles across the watershed from 276 individuals in 2004 to 406 in 2008. Although none of the other three variables (river level, mean temperature and total precipitation) were significant at the 95% level, comparisons of model AIC values (lower values indicate a relatively better model) showed that removing these “non-significant” variables did not substantially improve the model (AIC values: 94.67, 93.27, 94.04, 107.82 for the full model, and excluding river level, total precipitation and mean temperature respectively) as differences in AIC less than four are unlikely support any particular model (BURNHAM & ANDERSON 2002: 170) i.e. all variables are important to model the monthly *P. unifilis* abundances.

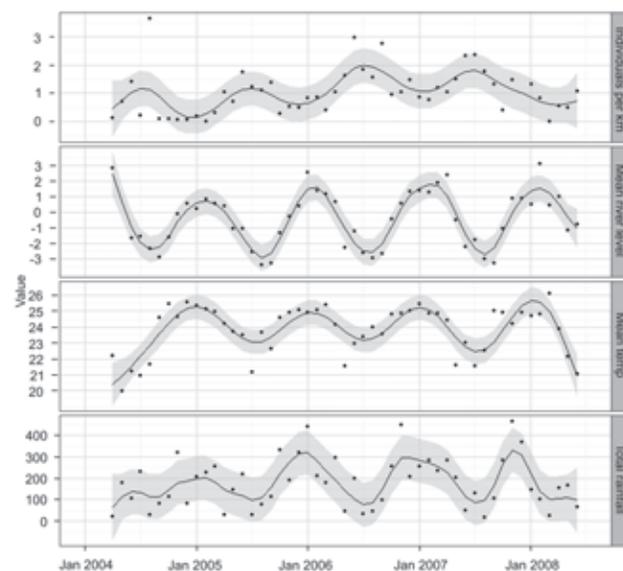


Figure 2. Monthly patterns in *P. unifilis* abundances and abiotic factors around the Los Amigos Biological Station, Amazonian Peru, from April 2004 to August 2008. Solid black lines and grey shaded areas show predicted values and confidence intervals obtained from generalized additive models, grey dots are the observed values.

Table II. Model weights and parameter (slope) estimates from information-theoretic analysis of predictors of the occurrence of *P. unifilis* monitored during four years of boat surveys. Generalized additive models were used to predict the abundance (individuals per km) recorded during 333 trips around the Los Amigos Biological Station, Amazonian Peru.

Model factor	Individuals per kilometer	
	Σw_i (rank) ^a	Slope (SE)
Temporal trend	0.83 (2)	*0.134 (0.074)
River level	1.00 (1)	-0.062 (0.050)
Sun (trips with compared to trips without)	1.00 (1)	***0.695 (0.161)
Season (wet compared with dry)	1.00 (1)	** -0.544 (0.181)
Rain (trips with compared to trips without)	1.00 (1)	*** -0.722 (0.213)
Mean trip temperature [§]	1.00 (1)	
Observer (compared with most experienced)	0.10 (3)	
	2	0.252 (0.212)
	3	0.146 (0.215)
	4	-0.121 (0.221)
	5	-0.386 (0.300)
	6	0.150 (0.243)
Start period (compared with start before 08:00)	1.00 (1)	
	8 – 10:59	***0.739 (0.191)
	11:00 – 13:59	**0.710 (0.249)
	After 13:59	*0.749 (0.307)

Parameter significance: *** < 0.001, ** < 0.01, * < 0.05, x < 0.1.

^a The sum of Akaike weights for all models within our set of candidate models with a given variable. Model averaging was carried out using the full set of confidence models, i.e., when a predictor was not present in the model its value was set to 0 (BURNHAM & ANDERSON 2002: 152).

[§] Non-parametric smoothed term.

At the trip level, seven of our eight explanatory variables provided important information content as demonstrated by the sum of Akaike weights and or were statistically significant in explaining the number of individual *P. unifilis* seen per km (Tab. II), with “Observer” being the only insignificant variable. Based on the results from our trip level analysis (Tab. II), the optimum conditions for conducting surveys of river turtles were: during the dry season, with sun and no rain, trip start times between 08:00 and 14:00 h, and temperatures ranging between 25 and 30°C. Visual inspection of mean abundances (number of individuals per kilometer) seen per hour showed that higher than average abundances were seen during trips that started after 8:00 and finished before 16:00 h and that the highest abundances were recorded during trips that started after 10:00 but finished before 13:00 h (Fig. 3).

DISCUSSION

Our analysis reveals important aspects relating to the use of river-based surveys for monitoring neotropical freshwater turtle populations. Previous studies have demonstrated that

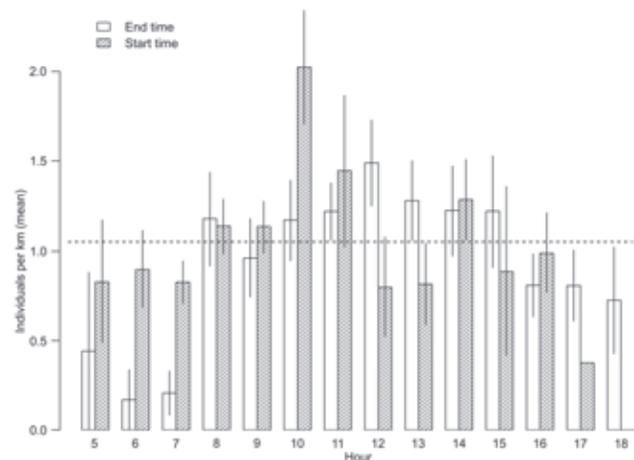


Figure 3. Abundance of *P. unifilis* by time of day. Mean (± 1 SE) abundances (individuals per kilometer) recorded by trip start (lined bars) and end times (open bars) during 333 river-based surveys around the Los Amigos Biological Station, Amazonian Peru, from April 2004 to August 2008. The dashed horizontal line is the average abundance recorded from all trips.

river-based surveys can provide an inexpensive source of information for neotropical zoologists (PITMAN *et al.* 2011), here we add information that we hope will encourage and facilitate both the use and standardization of this monitoring approach on a wider scale.

Our observed maximum abundances from the most completely surveyed Lower and Upper sections (10.18 and 4.33 individuals per km respectively) are within the range of those previously reported. During 5 years of surveys along 2 rivers (28 and 20 km) in Ecuador and reporting values that included “mostly” *P. unifilis*, TOWNSEND *et al.* (2005) found maximum abundances of 7.00 and 20.55 individuals per km. By combining observations of both *P. unifilis* and *P. expansa* from a total of 960 river-based survey km along three 40 km transects on two rivers in lowland eastern Bolivia COWAY-GOMEZ (2007) found maximum abundances of 1.93, 2.45 and 12.53 individuals per km. Previous studies from the northern Peruvian Amazon reported 14 individual *P. unifilis* per km (SOINI 1996). Based on these results it appears that along lowland, lower order rivers across the Amazon basin maximum abundances in the region of 2-20 individual *P. unifilis* per km of river can be expected. Although there is considerable variation in reported maximum abundances, what is clear is that these abundances represent decimated populations compared with accounts from early Amazon explorers (MEDINA 1934, MITTERMEIER 1978, JOHNS 1987).

Our monthly analysis confirms previous studies that reported strong seasonal influences on the distribution and sighting rates of *P. unifilis* (TOWNSEND *et al.* 2005, BALENSIEFER & VOGT 2006, ESCALONA *et al.* 2009b), which due to dramatic seasonal fluctuations in water levels are thought to be confined to permanent rivers and waterways during the dry season but during the wet season disperse into perennially flooded forest regions. Seasonality of water levels also influences the detectability of river turtles as during the dry season there is an increase in the availability of logs, rocks and beaches which may be used for basking. Additionally female *P. expansa* increase basking activity prior to nesting which coincides with low water levels during the dry season (VON HILDEBRAND *et al.* 1988), although this behavior has not been reported for *P. unifilis* it is possible that *P. unifilis* will also demonstrate behaviors that influence detectability. Previous studies have also demonstrated how abundances of *P. unifilis* and *P. expansa* differ spatially in relation to anthropogenic pressure (COWAY-GOMEZ 2007). Our results also suggest that there are spatial differences in abundances along the river sections studied. Yet, as we did not record differences in the density of suitable basking points we are unable to make any inference regarding why abundances on the Lower and Upper sections were the same and statistically higher than those recorded during trips on the Amiguillos. Further studies that develop standardized monitoring protocols for river turtles, specifically evaluating how the temporal and spatial distribution of potential basking points influences detectability and resulting abundance estimates are required before any firm

conclusions can be drawn relating to potential modulators of the spatio-temporal distribution of *P. unifilis*.

As expected based on the physiological constraints that limit the activity of the ectothermic *P. unifilis* we found that a series of abiotic factors had a significant influence on the observed trip level abundances. Although it is not possible to disentangle the effects of I) differences in detection probability and II) spatio-temporal patterns in the distribution of *P. unifilis*, we were able to establish some key thresholds that provide for optimum sampling conditions. Highest abundances were found on warm (25-30°C), sunny days during the dry season during trips that started after 8:00 h but finished before 16:00 h. For neotropical zoologists that often have limited time and financial resources these conditions are likely to provide the most cost effective for studies that aim to quantify river-based abundances of *P. unifilis*.

Although river-based surveys have long been recognized as a relatively accurate source of population information compared with hand or hoop net based techniques (KOPER & BROOKS 1988) little use has been made of the technique by neotropical zoologists. We found that using park guard observers provided data that can be used for basin wide comparisons of river turtle populations. We believe that modeling the observed sighting rates has several advantages over simply presenting maximum counts as proposed by TOWNSEND *et al.* (2005). Maximum values are inherently biased by survey intensity, observer, weather, and location specific detectability (i.e. river width, density of logs, boulders, and beaches). Therefore, although maximum counts may provide a minimum estimate for a particular section of river at a particular time they do not allow comparison of abundances or population trends between different rivers/watersheds across the Amazon basin. By applying a simple and freely available modeling approach we provide data relating to *P. unifilis* populations that are suitable for such future comparisons. There do however exist limitations: I) basking surveys are obviously not appropriate for nocturnal turtle species, II) the ability to reliably identify different turtle species, for example (COWAY-GOMEZ 2007) had to combine data from sympatric *P. unifilis* and *P. expansa* due to difficulties in separating the species, and III) the use of river-based monitoring to provide reliable stage specific (e.g. juveniles compared with adults) abundance estimates remain untested. Recently geometric morphometric analysis of carapaces was used to successfully identify the gender of *P. expansa* hatchlings (LUBIANA & DIAS FERREIRA JÚNIOR 2009). Investigations into the application of similar morphometric analysis for the separation of species, age classes and gender from photos obtained during boat surveys may provide cost effective solutions to these limitations.

The use of park guards/community based monitors is one of the strongest benefits (community involvement, active participation and increased motivation (TOWNSEND *et al.* 2005, DANIELSEN *et al.* 2008, PITMAN *et al.* 2011)) and potential weaknesses (relative lack of training compared with “specialized”

scientific researchers) of our monitoring approach (DANIELSEN *et al.* 2008). By integrating the considerable volume of data collected with “expert” analysis we confirm that it is possible to provide reliable, comparative and cost effective data on neotropical turtle populations.

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