

Unanticipated effect of climate change on an aquatic top predator of the Atlantic rainforest

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ABSTRACT

1. From a biodiversity conservation viewpoint it is crucial to estimate the sensitivity of species and populations to climate change, especially of key species such as top predators.

2. Here, the El Niño-Southern Oscillation phenomenon (ENSO) was used as a natural experiment to estimate the sensitivity of a population of the rainforest-dwelling broad-snouted caiman, *Caiman latirostris*, to extreme floods.

3. Caiman abundance declined by 35% annually between 1996 and 1998, and then increased, without reaching 1996 levels, indicating a marked effect of the 1997 El Niño. Accordingly, the Southern Oscillation Index was positively correlated with caiman abundance, indicating lower caiman abundance with warm ENSO events.

4. The relationship between the relative annual mean abundance of caimans and the maximum daily annual discharge of the Iguazú River was analysed. This relationship was parabolic, with caiman abundance increasing at discharges from 500 to 1500 m³ s⁻¹ and then decreasing at discharges from 1500 to 2500 m³ s⁻¹, indicating an adverse effect of both extreme low and high river discharge. No effect of illegal hunting was measurable.

5. This study evaluated whether the negative effect of extremely high water levels on caiman abundance could be due to a decrease in the availability of the habitat more commonly used by small (<60 cm total length, TL) and medium (60–120 cm TL) caimans. Small and medium-sized caimans used herbaceous/shrub habitats more frequently than large caimans (>120 cm TL), i.e. the type of habitat flooded during extreme floods.

6. An increase in extreme floods, as forecast for the Atlantic rainforest owing to climate change, may seriously affect the population of rainforest caimans through the reduction of adequate habitat for juveniles. This counter-intuitive result, in which an excess of water reduces the abundance of an aquatic top predator, should be considered in conservation plans of rainforest-dwelling crocodylians.

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Received 24 April 2014; Revised 8 August 2014; Accepted 29 September 2014

KEY WORDS: *Caiman latirostris*; riparian habitat; Iguazú River; reptiles; tropical rainforest; El Niño-Southern Oscillation; climate change; Special Area of Conservation

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INTRODUCTION

From the viewpoint of biodiversity conservation, there is a need to move from measuring the extent of exposure of a species to climate change to estimating the sensitivity of species to climatic variables affected by climate change. Exposure to climate change is estimated by the extent to which the geographic range of a species or population is affected (Huntley *et al.*, 2010; Dawson *et al.*, 2011). Most current assessments and predictions of the effects of climate change on species and populations measure exposure (Dawson *et al.*, 2011). Sensitivity to climate change is the degree to which survival or fitness of individuals in a population is affected by climatic variables that are likely to change in the near future (Dawson *et al.*, 2011). To obtain a more precise assessment of the effects of climate change on species or populations, estimation of their sensitivity is needed (Huntley *et al.*, 2010; Dawson *et al.*, 2011), since different levels of sensitivity will produce different responses to the same levels of exposure. Sensitivity, then, is key for assessing the vulnerability of a population to climate change and for identifying the processes that operate throughout its geographic range (Parmesan, 2005). Such an assessment can be conducted by evaluating the change in population abundance along a gradient of a given climatic variable, while controlling for other factors.

The present warming trend of the world's climate is predicted to alter significantly the water balance of the South American rainforest. This includes the Atlantic rainforest biodiversity hotspot in southern Brazil, north-eastern Argentina and eastern Paraguay. Current trends indicate an increase in the amount of rainfall over this region (IPCC, 2007; Hirabayashi *et al.*, 2008; Knapp *et al.*, 2008), which will intensify as the 21st century unfolds (Hirabayashi *et al.*, 2008) and will significantly increase the frequency of large-scale floods (Milly *et al.*, 2002; Hirabayashi *et al.*, 2008). This forecast is of great concern because the Atlantic rainforest harbours a disproportionately large amount of the earth's biodiversity (Di Bitetti *et al.*, 2003; Mittermeier *et al.*, 2011; Ribeiro *et al.*, 2011), and it is essential to know how its

biota, particularly species of large habitat requirements (umbrella species), which ensure the protection of the rest of the community, will respond to these climatic changes.

Particularly important are the effects of climate change on top predators because these predators are increasingly being recognized as having substantial effects on the communities in which they live. Large predators of both terrestrial and aquatic (freshwater and marine) ecosystems usually control populations of predators at lower trophic levels (mesopredators), and play a key role in the maintenance of biodiversity and ecosystem processes (Estes *et al.*, 2011). In the food webs of streams and rivers of the Atlantic rainforest, broad-snouted caimans, *Caiman latirostris*, are the main top predators. The aquatic habitats of the Atlantic rainforest lack most of the big predatory fishes present in other tropical and subtropical South American ecoregions as a result of large waterfalls that act as barriers (Menni, 2004; Oyakawa *et al.*, 2006; Agostinho *et al.*, 2007; Buckup, 2011). Nowadays, many of those barriers have been obliterated by dams, allowing the invasion of upper waters by predatory fish (Agostinho *et al.*, 2007; Buckup, 2011; Vitule *et al.*, 2012). However, where these barriers still exist, as in the Iguazú River, a distinct aquatic community has evolved lacking large predatory fishes, such as piranhas (*Serrasalmus* spp.), giant freshwater stingrays (*Potamotrygon brachyura*), dorados (*Salminus* spp.), and large catfishes (*Pseudoplatystoma* spp., *Zungaro jahu*) (Menni, 2004; Gómez *et al.*, 2009); there, the largest predator is the broad-snouted caiman.

The El Niño–Southern Oscillation phenomenon (ENSO) is a semi-periodical climatic event with worldwide consequences. This phenomenon has two extreme phases: the El Niño phase is characterized by a warming of waters of the tropical eastern Pacific off Peru; the opposite phase, called La Niña, produces further cooling of the tropical eastern Pacific (Philander, 1990; Sarachik and Cane, 2010). ENSO has implications for many regional climatic systems around the world, producing inter-annual variability in these systems, with opposite consequences dependent on which ENSO phase is occurring (Philander, 1990;

Sarachik and Cane, 2010). Climatic variability produced by ENSO events, especially the strong ones, can be interpreted as natural experiments to elucidate the potential effects of climate change (Jaksic, 1998; Holmgren *et al.*, 2001). Since climatic inter-annual variability produced by ENSO may resemble, in some regions, the forecasted effects of climate change (Jaksic, 1998; Karl and Trenberth, 2005), the years affected by ENSO can be useful for evaluating the sensitivity of species and populations to climate change.

Different phases of ENSO change dramatically the climate of the Atlantic rainforest, which may have a considerable effect on populations of broad-snouted caimans. During an El Niño phase, southern Brazil, north-eastern Argentina and eastern Paraguay experience heavier than normal rainfall that produces high water levels in the region's rivers and streams (Cervený, 1998; Casco, 2004). On the other hand, strong La Niña years are characterized by drought conditions with lower than normal river levels (Cervený, 1998; Casco, 2004). In this way, El Niño may *a priori* increase the available nesting habitat of broad-snouted caimans by flooding areas adjacent to river banks. In fact, a positive effect of El Niño on the number of broad-snouted caiman nests has been observed in wetlands of the middle Paraná River (Simoncini

et al., 2011). A less intuitive alternative hypothesis is that the newly-formed habitat, by being predominantly flooded forest, is of lower quality for broad-snouted caimans, since they need a more open habitat for nesting and thermoregulation (Platt *et al.*, 2008; Charruau *et al.*, 2010). Indeed, hatching success of broad-snouted caimans is lowest in nests built in forest areas, compared with savanna and floating vegetation areas (Montini *et al.*, 2006).

This study tested two hypothetical effects of the El Niño phase of ENSO on a broad-snouted caiman population of the Iguazú River, with the aim of evaluating the sensitivity of the Atlantic rainforest's largest aquatic predator to increased flood risk, and interpreting the potential effects of climate change on a rainforest-dwelling crocodilian population.

METHODS

Study area

The study was conducted along a 64 km stretch of the Iguazú River between 25°32'S–54°09'W and 25°42'S–54°25'W (Figure 1). The Iguazú River forms the border between Argentina and Brazil and the whole part of the river included in this



Figure 1. Map of the study area showing the location of the Parque Nacional Iguazú (Argentina) and the broad-snouted caiman surveys (dashed line) along the Iguazú River. NP: National Park; PP: Provincial Park; and NR: Natural Reserve.

study lies within protected areas of both countries: the Argentinian Parque Nacional Iguazú on the southern shore, and the Brazilian Parque Nacional do Iguazu on the northern shore. In this area the river is approximately 1000 m wide, has numerous islands, and its shores are covered mainly with continuous dense subtropical semi-deciduous rainforest with scattered patches of tacuaruzú bamboo, *Guadua chacoensis*, and shrubs such as sarandí, *Cephalanthus glabratus*, and marshes (Sruar *et al.*, 2009). The area has a wet subtropical climate with mean maximum monthly temperatures between 20.7°C (June) and 31.8°C (January), mean minimum monthly temperatures between 10.7°C (June and July) and 20.4°C (January), a mean monthly relative humidity of 73–87%, and a mean monthly rainfall between 114.8 mm (March) and 209.5 mm (November) (Servicio Meteorológico Nacional Argentina, <http://www.smn.gov.ar/?mod=clima&id=30&provincia=Misiones&ciudad=Iguaz%FA>).

Parque Nacional Iguazú (II Category of IUCN), situated in the Upper Paraná Atlantic Forest, which constitutes one of the most threatened ecoregions of the world (Ribeiro *et al.*, 2011; De Angelo *et al.*, 2013), aims for the conservation of a representative sample of subtropical rainforest, ensuring continuity of natural processes occurring in it, and implementing management measures to ensure the conservation of areas of particular ecological value.

Surveys

Broad-snouted caimans (Figure 2) – the only crocodylian species inhabiting the study area – were counted during nocturnal standardized surveys, each conducted over two consecutive nights and covering the whole extent of the study area. All surveys started at 17:00–19:00 h and lasted until 03:00–05:00 h, depending on time of the year, on full-moon nights (\pm two nights from full moon). They all started and finished at the same locations and were conducted with the same boat. In each survey, the southern (i.e. Argentinian) shore of the Iguazú River was surveyed with a spotlight looking for broad-snouted caimans, from a 3 m length boat



Figure 2. Adult broad-snouted caiman, *Caiman latirostris*, in a wetland of the Iguazú River within the Parque Nacional Iguazú, Argentina.

powered by a 4.5 HP motor. For most surveys, air and water temperature (°C), and river height (m) were recorded. Survey participants were not always the same but all surveys were headed by the same experienced observer.

Each caiman observed was counted and, whenever possible, assigned to one of the following size classes: (I) small: up to 60 cm total length (TL), (II) medium: between 60 and 120 cm TL, and (III) large: >120 cm TL. In addition, the type of habitat where each caiman was recorded was registered. Habitat types were categorized as: (S) shrub or herbaceous shore, or (F) rainforest-covered shore. Another two habitat types, rocky shore and mud/sand beach, were recorded, but not used in the analyses owing to the low incidence of these habitats and the low number of caimans seen in them.

Population trends and sensitivity to floods

To estimate population trends, surveys were used as sample units. The number of broad-snouted caimans recorded in each survey (N) was the dependent variable in a generalized linear model that included year (Y), river height (H), the Southern Oscillation Index for the month of the survey (SOI), and Julian date (D), as independent variables. Quadratic terms were included for variables that had a non-linear relationship with the dependent variable. SOI was included in the models to quantify the effect of ENSO on N , the lower the SOI , the more driven towards an El Niño

phase the system is (Cervený, 1998). *SOI* values were taken from the Climate and Global Dynamics section of the US National Center for Atmospheric Research (<http://www.cgd.ucar.edu/cas/catalog/climind/soi.html>). A Poisson error structure and a log link were assigned to the model because the dependent variable was a count that could take only positive or zero values. The estimated slope for the variable *Y* can be interpreted as an estimate of the instantaneous annual rate of increase (*r*) of the population. If *r* is positive, the population is increasing, if negative, the population is decreasing.

Since preliminary analyses indicated that there were opposing trends in *N* before and after 1998, a piecewise regression analysis was conducted. Piecewise regression allows an estimate of population trends of different sign (i.e. decreasing or increasing) within a time series, and has been used before in the analysis of population trends of other aquatic predators (Shepherd and Myers, 2005).

The best model was selected using the Information Theory framework, by minimizing the Akaike Information Criterion (AIC) (Anderson *et al.*, 2000). In this framework, if an independent variable has a significant effect on the dependent variable it is left in the best model; on the other hand, independent variables not included in the best model do not have a significant effect on the dependent variable (Franklin *et al.*, 2001). The magnitude of the effect of each variable is measured by the estimate of its coefficient (either an intercept or a slope) in the best model (Franklin *et al.*, 2001).

The importance of interannual variation in water levels on broad-snouted caimans was explored further by noting whether there was a relationship between the relative abundance of broad-snouted caimans and the maximum daily annual discharge (m^3s^{-1}) of the Iguazú River, for each year. The rationale was that maximum daily annual discharge of the Iguazú River is positively correlated with rainfall, so that years with extreme rainfall would have higher values of river discharge. This allowed an evaluation of the effect of ENSO using a different independent variable, as a check of the previous analysis.

For this analysis, annual estimates of abundance were used, derived from the best model relating *N* and *Y*. In this analysis, annual abundance estimates are relative to the abundance in the first year of the time series, i.e. 1996, not to absolute abundances. Maximum daily annual discharge values for the Iguazú River were taken from Garciarena (2009). The model had a Gamma distribution error and a log link because variance was not homogeneous and the response variable could take only positive values.

Since preliminary analyses with generalized additive models detected a non-linear relationship between river discharge and broad-snouted caiman abundance, power terms (up to the third power) were added to the general linear model.

To test the hypothesis that caiman abundance could be affected by illegal hunting rather than by river discharge, a model was also run with the number of patrols along the Iguazú River conducted by park rangers per year as an independent variable. The rationale was that patrol number was inversely correlated with the level of illegal hunting. Data on patrol number were obtained from logbooks of ranger activities kept at the Parque Nacional Iguazú management authority (Intendencia del Parque Nacional Iguazú). Since the records of ranger patrols were missing for 1996 and 2005, the river discharge model was run again with these two years excluded to make model comparison valid. No attempts were made to include patrol number and river discharge as predictors in the same model, since the two variables were highly correlated. These models also had a Gamma error distribution and a log link. The best model was selected using the Information Theory framework, as before.

Habitat use

To evaluate the hypothesis of differential habitat use by the three size classes of broad-snouted caimans, a generalized linear mixed-effects model was built, with habitat (herbaceous or rainforest) as the dependent variable and size class plus covariates of interest, i.e. water temperature, Julian date transformed to sine and cosine, time of the day transformed to sine and cosine, and year,

as independent variables. In this analysis, the sample units were individual caimans. For this reason, a factor indicating the particular survey in which every caiman was observed was incorporated in the model as a random effect, in order to avoid pseudoreplication arising from considering each caiman from the same survey as independent from each other (Faraway, 2006). The model had a binomial error distribution and a logit link because the dependent variable took only two possible values. As in previous analyses, the Information Theory framework was used to find the best model.

All statistical analyses were conducted with the statistical software R version 2.10.1 (R Development Core Team, 2009).

RESULTS

Population trends

In total, 20 surveys conducted between 1996 and 2006 were employed for the analysis of population trends. The analysis detected a steep population decline from 1996 to 1998, then a slow increase between 1998 and 2006, without reaching the 1996 population level (Figure 3). The coefficients of the best model (Table 1) were: intercept = -0.011 , slope of year before 1998 = -0.428 , slope of year after 1998 = 0.058 , $\sin(d) = -0.125$, $\cos(d) = -0.179$, $\cos(2*d) = -0.133$, river height = -0.278 , $SOI = 0.051$, $SOI^2 = 0.017$. According to this model, the broad-snouted caiman population declined at an annual rate of 35% between 1996 and 1998; then increased by 6% annually between 1998 and 2006 without reaching the level of 1996 (Figure 3). Broad-snouted caiman abundance was negatively related to river height, and positively associated with SOI (Table 1). These results imply that broad-snouted caimans are less abundant at high water and when global climate is not in the El Niño phase, i.e. when the eastern tropical Pacific Ocean is warmer than usual.

Consistent with the previous analysis, broad-snouted caiman relative abundance had a parabolic relationship with the Iguazú River daily maximum annual discharge (model coefficients: intercept = -0.834 , discharge = 1.03×10^{-3} , discharge² = -4.07×10^{-7}). Abundance increased at discharge

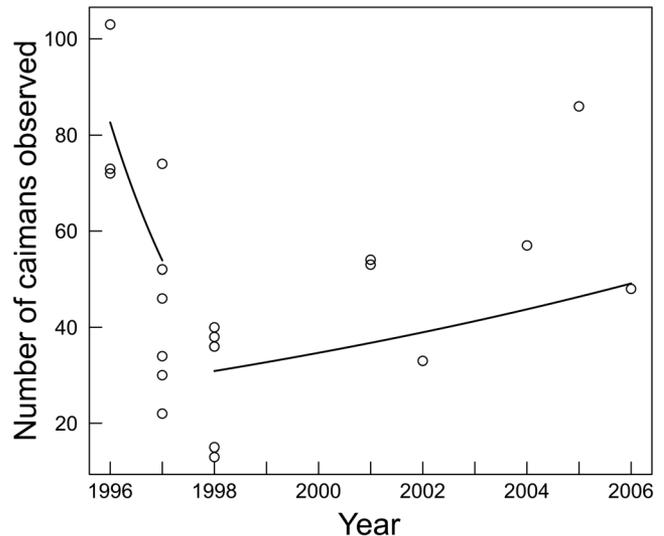


Figure 3. Temporal trend of the abundance of broad-snouted caimans, *Caiman latirostris*, in the Iguazú River. The lines are estimations of a piecewise regression generalized linear model with a Poisson error distribution and log link.

levels between 500 and $1500 \text{ m}^3 \text{ s}^{-1}$, then decreased to a minimum at a discharge of about $2500 \text{ m}^3 \text{ s}^{-1}$ (Figure 4). River discharge was a much better predictor (about 20 times) of broad-snouted caiman abundance than patrol number. The model containing only river discharge had an AIC of -11.507 , while the AIC of the patrol number model was -5.520 , which translates into Akaike weight (w) values of 0.952 and 0.048 , respectively. This indicates that illegal hunting was probably not a driver of the observed fluctuations in abundance.

Habitat use

In total, 379 sightings of broad-snouted caimans from 14 surveys were used in this analysis. Most of the sightings were of small and medium-sized caimans (size I = 138 sightings, size II = 129, size III = 112). For broad-snouted caimans there was a significant relationship between body size and habitat type used. The association with herbaceous/shrub habitat became weaker as size of caimans increased; individuals of size I used habitats with herbaceous/shrub cover more frequently than individuals of size II and III. The best minimal model included year, Julian date, time of the day, and size, but not temperature (Table 2).

Table 1. Statistical models corresponding to different hypotheses explaining broad-snouted caiman, *Caiman latirostris*, abundance in the Iguazú River. Models are ranked according to increasing Akaike Information Criterion (AIC); w is Akaike's weight, which measures the likelihood of the model given the data; d is Julian day; height is river height in metres; SOI is the Southern Oscillation Index, a measure of the state of the El Niño-Southern Oscillation phenomenon. All models are generalized linear models with a Poisson family distribution error and a log link. The best model is the one with the lowest AIC

Rank	Hypothesis	Model	AIC	w
1	density varies with year, season, river height, and SOI curvilinearly	$N \sim \text{year} + \sin(d) + \cos(d) + \cos(2*d) + \text{height} + \text{SOI} + \text{SOI}^2$	168.5610	0.6723
2	density varies with year, season, river height curvilinearly, and SOI curvilinearly	$N \sim \text{year} + \sin(d) + \cos(d) + \cos(2*d) + \text{height} + \text{height}^2 + \text{SOI} + \text{SOI}^2$	170.5609	0.2473
3	density varies with year, season, river height, and SOI	$N \sim \text{year} + \sin(d) + \cos(d) + \cos(2*d) + \text{height} + \text{SOI}$	174.2213	0.0397
4	density varies with year, season and river height	$N \sim \text{year} + \sin(d) + \cos(d) + \cos(2*d) + \text{height}$	175.8181	0.0179
5	density varies with year, season, river height curvilinearly, and SOI	$N \sim \text{year} + \sin(d) + \cos(d) + \cos(2*d) + \text{height} + \text{height}^2 + \text{SOI}$	176.0241	0.0161
6	density varies with season, year and river height in a curvilinear way	$N \sim \text{year} + \sin(d) + \cos(d) + \cos(2*d) + \text{height} + \text{height}^2$	177.8022	0.0066
7	density varies with year and river height	$N \sim \text{year} + \text{height}$	186.2988	0.0001
8	density varies with year and river height in a curvilinear way	$N \sim \text{year} + \text{height} + \text{height}^2$	188.2912	0.0000
9	density varies with season and river height	$N \sim \sin(d) + \cos(d) + \cos(2*d) + \text{height}$	245.4911	0.0000
10	density varies with season and river height in a curvilinear way	$N \sim \sin(d) + \cos(d) + \cos(2*d) + \text{height} + \text{height}^2$	247.3502	0.0000
11	density varies with season, height, and SOI curvilinearly	$N \sim \sin(d) + \cos(d) + \cos(2*d) + \text{height} + \text{SOI} + \text{SOI}^2$	249.3191	0.0000
12	density varies with season, height curvilinearly, and SOI	$N \sim \sin(d) + \cos(d) + \cos(2*d) + \text{height} + \text{height}^2 + \text{SOI}$	249.3235	0.0000
13	density varies with season, height curvilinearly, and SOI curvilinearly	$N \sim \sin(d) + \cos(d) + \cos(2*d) + \text{height} + \text{height}^2 + \text{SOI} + \text{SOI}^2$	251.2258	0.0000
14	density varies with river height only	$N \sim \text{height}$	252.0740	0.0000
15	density varies with height and SOI	$N \sim \text{height} + \text{SOI}$	252.9121	0.0000
16	density varies with river height only in a curvilinear way	$N \sim \text{height} + \text{height}^2$	254.0688	0.0000
17	density varies with river height and SOI not linearly	$N \sim \text{height} + \text{SOI} + \text{SOI}^2$	254.6527	0.0000
18	density varies with river height not linearly, and SOI	$N \sim \text{height} + \text{height}^2 + \text{SOI}$	254.8992	0.0000
19	density varies with river height and SOI, both in a curvilinear way	$N \sim \text{height} + \text{height}^2 + \text{SOI} + \text{SOI}^2$	256.6214	0.0000
20	density varies with year, season and SOI in a curvilinear way	$N \sim \text{year} + \sin(d) + \cos(d) + \cos(2*d) + \text{SOI} + \text{SOI}^2$	257.2682	0.0000
21	density varies with season and year	$N \sim \text{year} + \sin(d) + \cos(d) + \cos(2*d)$	270.2677	0.0000
22	density varies with year, season and SOI	$N \sim \text{year} + \sin(d) + \cos(d) + \cos(2*d) + \text{SOI}$	270.7421	0.0000
23	density varies with year and SOI in a curvilinear way	$N \sim \text{year} + \text{SOI} + \text{SOI}^2$	281.2874	0.0000
24	density varies with year only	$N \sim \text{year}$	284.1628	0.0000
25	density varies with year and SOI	$N \sim \text{year} + \text{SOI}$	285.7576	0.0000
26	density varies with season and SOI in a curvilinear way	$N \sim \sin(d) + \cos(d) + \cos(2*d) + \text{SOI} + \text{SOI}^2$	367.7803	0.0000
27	density varies with season and SOI	$N \sim \sin(d) + \cos(d) + \cos(2*d) + \text{SOI}$	382.5282	0.0000
28	density varies with SOI only in a curvilinear way	$N \sim \text{SOI} + \text{SOI}^2$	393.5713	0.0000
29	density varies with season only	$N \sim \sin(d) + \cos(d) + \cos(2*d)$	398.2692	0.0000
30	density varies with SOI only	$N \sim \text{SOI}$	403.3882	0.0000
31	constant density	$N \sim k$	409.9083	0.0000

DISCUSSION

These results show that increased rainfall produced by the El Niño phase of ENSO has a negative effect on the population of broad-snouted caimans of the Iguazú River. The results support the hypothesis that the El Niño phase of ENSO reduces the population of broad-snouted caimans through a decrease in the availability of open habitat by flooding, because (1) there was a large decline in abundance during unusually rainy years, and (2) there is a positive association between herbaceous,

non-forest habitat and broad-snouted caiman abundance, especially for the smaller size classes. Rainfall and water availability are among the best predictors of habitat suitability for crocodilians. For example, niche models for Sunda gharials, *Tomistoma schlegelli*, include rainfall as one of the two most important variables for detecting suitable habitat for this endangered crocodilian (Rödder *et al.*, 2010). However, open habitat necessary for nesting and thermoregulation is also a limiting factor for crocodilian populations inhabiting densely vegetated ecosystems, such as

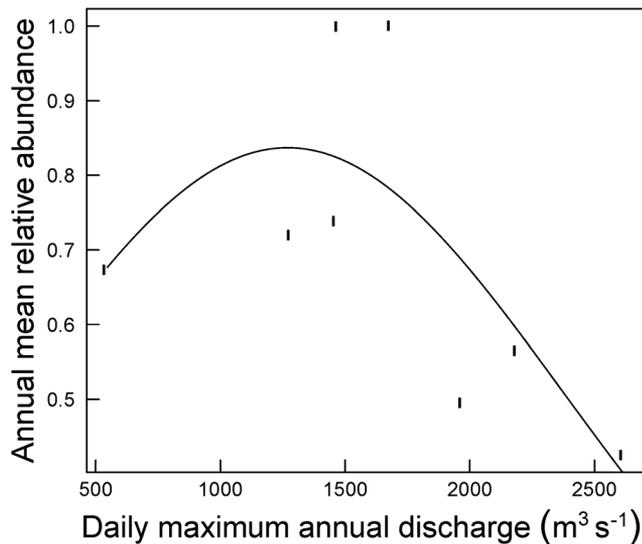


Figure 4. Relationship of annual mean relative abundance of broad-snouted caiman, *Caiman latirostris*, and maximum daily annual discharge of the Iguazú River (taken from Garciarena, 2009). The line is a regression line from a linear model with a Gamma error distribution and a log link.

Table 2. Coefficients of the best model explaining the relationship between habitat use and body size of broad-snouted caiman, *Caiman latirostris*. Size was classified as Size I (<60 cm total length, TL), Size II (60–120 cm TL), Size III (>120 cm TL). The coefficients for year are all relative to year 1996 and those for size are all relative to Size I. The response variable is a binomial factor (1 if caimans were in herbaceous habitat, 0 if they were in forest habitat). The model was a linear mixed-effects model with a binomial family distribution error, a logit link, and survey as a random factor

Explanatory variable	Estimate	Std. Error
Intercept	0.1727	0.7033
year1997	-0.1938	0.7933
year1998	1.4648	0.8271
year2006	-1.2798	1.1922
sin(day)	0.7941	0.3513
sin(2*day)	-0.4706	0.2283
cos(2*day)	-0.4507	0.2820
sin(hour)	0.5415	0.2025
sin(2*hour)	0.8347	0.2095
cos(2*hour)	-0.4194	0.1964
sizeII	-1.1006	0.3397
sizeIII	-2.6869	0.3967

rainforests. A population of American crocodiles, *Crocodylus acutus*, in a small atoll in the Caribbean was shown to be adversely affected in the short term by cyclones through egg mortality by drowning as a result of heavy rainfall (Charruau *et al.*, 2010). In the long term, however, the same population benefits from severe storms because storms clear land and make it available

for nesting – land that otherwise would be densely covered by mangrove forests (Charruau *et al.*, 2010). Based on the results, it is proposed that high water levels produced by heavy rainfall during El Niño years decreases habitat availability to small and medium-sized broad-snouted caimans, the most abundant size classes in the Iguazú River. Other hypotheses, such as disruption of the Iguazú River trophic web or increase in parasitic load or disease by ENSO events, may also explain the results, at least partially; however, no data are currently available to test these.

An alternative explanation for the observed abundance fluctuations could be that extreme floods dilute the population over larger inundated areas, reducing density by increasing the available area rather than by decreasing the number of individuals. If this were the case, the density at years immediately after the flood should be equal to the density before the flood, since water recession would reset the previous, smaller area. However, this was not observed in the time series, which shows a slow increase after the flood, and even 9 years after a strong El Niño event the population did not recover to pre-El Niño levels (Figure 3). In fact, this time lag to achieve full population recovery is consistent with observations on populations of saltwater crocodiles, *Crocodylus porosus*, in northern Australia, which took much longer than 9 years to achieve recovery (Fukuda *et al.*, 2011). While it is not possible to rule out completely a detectability contribution to the observed population trend, it may be concluded that the observed pattern (i.e. a gradual increase after a steep decline) is more consistent with a real population decline than with low detectability because of high water levels. Other crocodylian populations are known to be adversely affected by high water levels. Ballouard *et al.* (2010) remarked that gharials, *Gavialis gangeticus*, were washed out of protected areas with the release of monsoon overflow waters from a dam in Nepal.

Habitat differences may explain the observed opposite effects of El Niño on middle Paraná and Iguazú River populations of broad-snouted caimans. High water levels produced by El Niño actually increase the habitat for broad-snouted

caimans in the predominantly flat wetlands of the middle Paraná River, which explains the positive effect of El Niño on broad-snouted caiman nest numbers in this area (Simoncini *et al.*, 2011). On the other hand, an increase in water levels of the Iguazú River results in a decrease of adequate habitat for broad-snouted caimans, because the Iguazú River has steep, densely vegetated shores.

Illegal hunting is still a problem in Parque Nacional Iguazú despite occurring at lower levels than in neighbouring protected areas (Paviolo *et al.*, 2009) and is a known source of mortality of the broad-snouted caiman population of the Iguazú River (Herrera pers. obs.). While the effect of illegal hunting on broad-snouted caimans is unknown, there is no apparent reason to believe that illegal hunting increased substantially during 1997 and then decreased, so as to produce the steep population decline and the slow recovery observed. In addition, illegal hunting in Parque Nacional Iguazú and neighbouring protected areas is negatively correlated with control measures, such as the number of park rangers and park ranger patrolling (Paviolo *et al.*, 2009). This suggests that illegal hunting, while a permanent stressor for the population, cannot explain the large changes in broad-snouted caiman abundance recorded in the present study. Nevertheless, initiatives in Parque Nacional Iguazú should aim to protect heavily depleted populations through regular park ranger patrolling, and improve the law enforcement system. The continuous network of protected areas formed, from north to south, by Parque Nacional do Iguaçu, in Brazil, and Parque Nacional Iguazú and Parque Provincial Urugua-í, in Argentina, is one of the largest unfragmented remnants of the Atlantic rainforest (Di Bitetti *et al.*, 2003). This network still harbours the original set of large vertebrates inhabiting the Atlantic rainforest, thus offering a unique opportunity to conserve viable populations of these species, including the broad-snouted caiman, and the communities of which they are part.

These results are counter-intuitive in that global warming, by increasing water levels of rivers, will increase the abundance of a lowland tropical aquatic predator. It is possible that this also has ramifications for populations of broad-snouted

caiman outside the study area. Present evidence indicates that the main threat to inland aquatic ecosystems from climate change is water scarcity caused by droughts (Finlayson and D'Cruz, 2005). Consequently, the local extinction of one crocodilian, the Nile crocodile, *Crocodylus niloticus*, from Israel and Algeria is thought to be a consequence of increased aridity owing to climate change (Ross, 1998; Brito *et al.*, 2011). However, these results show that the niche of crocodilian predators in the Atlantic rainforest will also be seriously affected if climate change produces the opposite trend, i.e. an increase in precipitation and flooding of marsh habitat. It is unlikely that the vacated niche would be filled by other crocodilian species, since the effect is through reduction of more open habitat suitable for nesting and thermoregulation, a habitat requirement common to all crocodilians (Montini *et al.*, 2006; Platt *et al.*, 2008; Charruau *et al.*, 2010; Katdare *et al.*, 2011; Ugarte *et al.*, 2013).

The parabolic relationship between abundance of broad-snouted caimans and maximum annual daily river discharge suggests that this population is sensitive not only to flooding, but also to lower than normal water levels. This is not surprising, given the dependence on water and riparian habitats that crocodilians have for feeding and nesting. Heavy flooding is a known source of mortality for nests of many species of crocodilians (Montini *et al.*, 2006; Platt *et al.*, 2008; Charruau *et al.*, 2010; Ugarte *et al.*, 2013). For example, a population of the Morelet's crocodile, *Crocodylus moreletii*, in Belize has high nest losses both from high water levels that flood nests and low water levels that facilitate access to nests by terrestrial predators (Platt *et al.*, 2008).

Once populations are depleted, re-colonization of Atlantic rainforest streams and rivers by broad-snouted caimans seems unlikely. Genetic exchange among populations of broad-snouted caimans appears to vary significantly among habitat types. In open wetland habitats of the middle Paraná River, population exchange is high and most genetic variation occurs within populations (Amavet *et al.*, 2007, 2009). On the other hand, in streams and rivers of the Atlantic rainforest with less open habitat, there is significant genetic population

structuring, with different streams harbouring different populations (Verdade *et al.*, 2002). This suggests that there is less opportunity for dispersal and colonization in the Atlantic rainforest than in the more connected and continuous waterways of the middle Paraná River wetlands.

Despite the marked, fast decline in abundance of broad-snouted caimans because of increased water levels, it is expected that this population will persist if the floods are not regular. The results show that the effect of floods is mostly to limit habitat availability for juvenile broad-snouted caimans, not the adult population. In this way, if flood events are non-recurrent (as they were historically) they should not threaten the survival of the complete population, since recruitment failures would be only occasional. However, this situation could change if floods become a permanent stressor of this population.

The survival of broad-snouted caimans, and perhaps other crocodylians, as a species is not likely to be threatened by an increase in precipitation from global warming; what may be threatened is the persistence of rainforest-dwelling populations and the ecological roles they play in such ecosystems. Climate change, by increasing temperature and precipitation in some areas, may actually increase the available habitat for crocodylians, provided these habitats remain unchanged by human influence. However, the loss or a significant reduction of forest-dwelling crocodylian populations by climate change may alter the aquatic food webs through decreased predation pressure on fishes and smaller vertebrates. This effect would be exacerbated in areas where crocodylians are the sole top predators of aquatic food webs, such as the rivers and streams of the Atlantic rainforest.

ACKNOWLEDGEMENTS

We thank all the volunteers who participated in these 10 years of surveys for their important support, and appreciate the donations provided by the National Parks Administration of Argentina, and Iguazú Jungle. We thank one anonymous referee and the Chief Editor for comments that improved this paper.

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