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INSIGHT

Heads nods and boat bobs: Behavior of *Iguana iguana* is affected by environment and boat traffic in riparian tropical forest

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Abstract

Although frequently studied in captivity, less is known about wild *Iguana iguana*. Herein behavior of riparian *I. iguana* was collected alongside climate, vigilance, and boat traffic data. Observations showed boat tourism potentially affects *I. iguana* negatively. We recommend minor changes by the ecotourism industry to alleviate visitor pressure on *I. iguana*.

Abstract in Spanish is available with online material.

KEYWORDS

behavior, boat traffic, conservation, Costa Rica, gllvm, *Iguana iguana*, tropical, vigilance

1 | INTRODUCTION

Noise impacts on wildlife have mostly focussed on actions that have impeded communication or masked natural sounds (Francis & Barber, 2013; Laiolo, 2010). Studies have ranged across bony fish, small mammals, amphibians, and more extensively birds and marine mammals (Kunc et al., 2016; Shannon et al., 2016). Noise impacts specifically are known to affect wildlife and cause behavioral changes, enhanced vigilance, and escape/evasion across a variety of taxa (Barcelo-Serra et al., 2021; González Correa et al., 2019; Gospić & Picciulin, 2016; Grant & Lewis, 2010; Monti et al., 2018; Wang et al., 2020; Wright et al., 2020). However, the majority of evidence on impacts of noise associated with boat activity are seen in studies on echolocation and communication in cetaceans (Filiciotto et al., 2014; Heiler et al., 2016; Shannon et al., 2016). Knowledge about noise and boat activity impacts on reptiles is limited. French et al. (2017) study on behavior of marine iguanas (*Amblyrhynchus cristatus*) is one of the very few applied examples focussing on disturbances caused by the presence of eco-tourism boat activity.

Iguana iguana is a large (30–42 cm SVL), sexually dimorphic lizard, native to Central and South America, and the Caribbean and Pacific islands (Donoghue et al., 1998; López-Torres et al., 2011). It is "least concern" under IUCN and invasive across 20 countries (Bock et al., 2020). Despite this, factors such as poor environment quality, human disturbance, harvest, and predation impact the species ecology and survival (Bock et al., 2020). Despite much captive care information, significantly less is known about wild *I. iguana* (Burghardt, 2004). Information regarding natural behaviors and impacts of disturbance could therefore strongly aid its conservation in both native and invaded countries (Falcón et al., 2013).

Generally, *I. iguana* display similar gregarious behavior to other lizards (Gómez et al., 2020). Its hierarchies have dominant and subordinate males that communicate and court females for reproduction using social behaviors that include head bobbing movement and dewlap flashing (Falcón et al., 2013; Moss et al., 2018;

Rivera-Milán & Haakonsson, 2020). Dewlap flashing serves multiple purposes, contributing to thermoregulation, communication, mate attraction, dominance, territory, and predator warning (Figure 1) (Bro-Jørgensen, 2016; Dugan, 1982; Falcón et al., 2013; Harrison & Poe, 2012; Inbar & Lev-Yadun, 2005; Kabelik et al., 2018; Vicente, 2018; Waters et al., 2017). The species also uses visual social cues to avoid predation by capuchin monkeys (*Cebus* spp.), hawks (Accipitridae), caimans (Alligatoridae), and constrictors (Boidae), relying on group vigilance by conspecifics to sense threats (Ayala-Guerrero & Mexicano, 2008; Ferreira et al., 2017; Iglesias-Carrasco et al., 2016; Pereira et al., 2020). These known natural behaviors ideally position *I. iguana* for study about whether boat activity causes an impact to the species daily ecological routines.

Previous knowledge about escape and evasion by *I. iguana* has suggested that thermoregulating *I. iguana* are physiologically affected when interrupted from normal basking (Garrick, 2008; Gifford et al., 2012; Lattanzio, 2014; Muñoz & Bodensteiner, 2019; Porter & Witmer, 2019), leaving them vulnerable to predation (Bouazza et al., 2016; Libourel & Herrel, 2015; Muñoz & Bodensteiner, 2019; Radzio & O'Connor, 2017). Therefore, vigilance behavior has likely evolved to respond to and mitigate disturbances caused by noise (Ito & Mori, 2009). The potential for vigilance to trigger escape and evasion by *I. iguana* when disturbed by boat traffic in the wild is poorly documented and therefore of conservation interest (González Correa et al., 2019). Deciphering solutions to eco-tourism boat/wildlife conflict is therefore important considering the rise in wildlife tourism globally (Chion et al., 2017; Techera & Klein, 2013).

This study investigated the behavior of a small group of riparian *I. iguana* from a lowland tropical *Manicaria* swamp forest (Lewis, 2009) at Caño Palma Biological Station, Costa Rica (CPBS) (Figure 1). We modeled the effects of environment and boat traffic on behavioral responses and thermoregulation patterns for individual *I. iguana*, and hypothesize that the species is affected in its

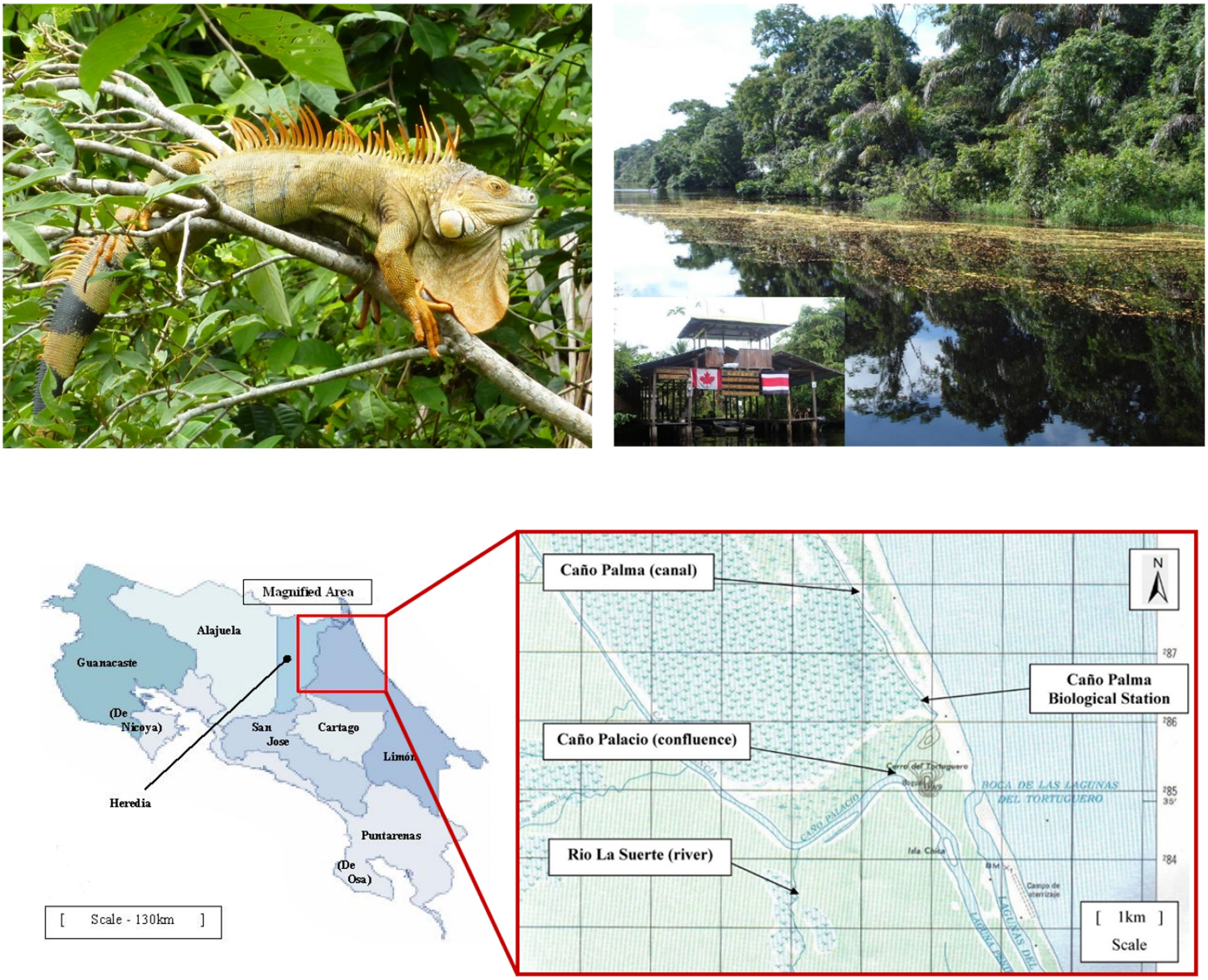


FIGURE 1 Adult male *Iguana iguana* from Caño Palma showing typical physical characteristics and prominent dewlap (photo by Michelle Haines), map of site location, Caño Palma Biological Station, and Caño Palma riparian *Manicaria* swamp forest opposite the boat dock/viewing gallery (modified from Lewis et al., 2011)

natural behavior by the regular movement of tourism boats within its native habitat.

2 | METHODOLOGY

Field observations of *I. iguana* took place from a viewing gallery dock tower that acted as a hide for observers above the Caño Palma (Figure 1). Data were collected during December 2004 (the breeding season for *I. iguana* regionally in northeast Costa Rica). Behavior observation was collected using scan sampling with frequency of behavior scored (Van Belle, 2017). Behaviors recorded included; thermoregulation (in sun/shade), vigilance, head bobbing, movement, foraging, displaying, retreating, feeding, dewlap displays (males), and time activity in sun/shade (Figure 2). Observations were recorded by two observers (one spotter and one recorder) that were kept consistent for the daily observations. Observation were recorded in 2 h intervals; 0600–0800 h, 0800–1000 h, 1000–1200 h, 1100–1300 h, 1200–1400 h, 1300–1500 h, 1400–1600 h, and 1500–1700 h. Abiotic data were collected to account for climatic influence and included; temperature, humidity, precipitation, cloud cover, canal height/state of water level measured from the center depth of canal in cm (flooding). The presence and number of boats were recorded during observation sessions and linked with predictors in the behavior model.

Generalized Linear Latent Variable Models (GLLVM) were performed in R package "gllvm" (Niku et al., 2019a; R Core Team, 2021) to contrast behavior responses by multiple *I. iguana* with environmental predictor factors and the presence of tourist boats (Figure 2). GLLVM use factor analytics to incorporate latent variables that combine values to model correlation between responses. Latent variables can be used in ordination, predict values, control variables, and assist model selection (Hui et al., 2015, 2017). *I. iguana* behavior multivariate data were constructed as a matrix with *n* rows (behaviors) and *m* columns of behavior response during observation sessions. GLLVM regressed mean behaviors μij against abiotic predictors as vectors of $d < md < m$ latent variables, $\boldsymbol{ui} = (u_{i1},\ldots,u_{id})'$;

$$g(\mu ij) = \eta ij = \alpha i + \beta 0j + \mathbf{x}' i\beta j + \mathbf{u}' i\theta j,$$

where $g(.)$ is a known link function, $\boldsymbol{u}'i$ are d-variate latent variables $(d < md < m)$, αi is an optional row effect at behavior i, $\beta 0j$ is intercept for predictor j, and $\boldsymbol{\beta} j$ and $\boldsymbol{\theta} j$ are column specific coefficients for covariates and latent variables, respectively.

Models used negative binomial, Poisson, and zero-inflated Poisson families via package TMB, with Laplace distributions (Kristensen et al., 2016). Dunn-Smyth residuals and Q-Q plots were used to inspect model fit. Model fit was assessed by AIC/BIC, and a for-loop iteration used to select appropriate numbers of latent variables. Models used a best of five run routines with the highest log-likelihood model selected (Niku et al., 2019b).

Latent variables induce correlation across response variables to estimate patterns. The getResidualCor function was used for this and visualized using package corrplot (Wei & Simko, 2017). To contrast response relationships alongside estimated correlation, latent variables were plotted using the ordiplot function in gllvm.

The final model was selected based on residual fit, AIC/BIC, moderation of correlation, suitable number of latent variables, and then estimated coefficients for predictors plotted with their confidence intervals and used for interpretation. Additional plots, figures, and tables related to analysis can be viewed in the supplementary material (Supplementary Figures).

3 | RESULTS

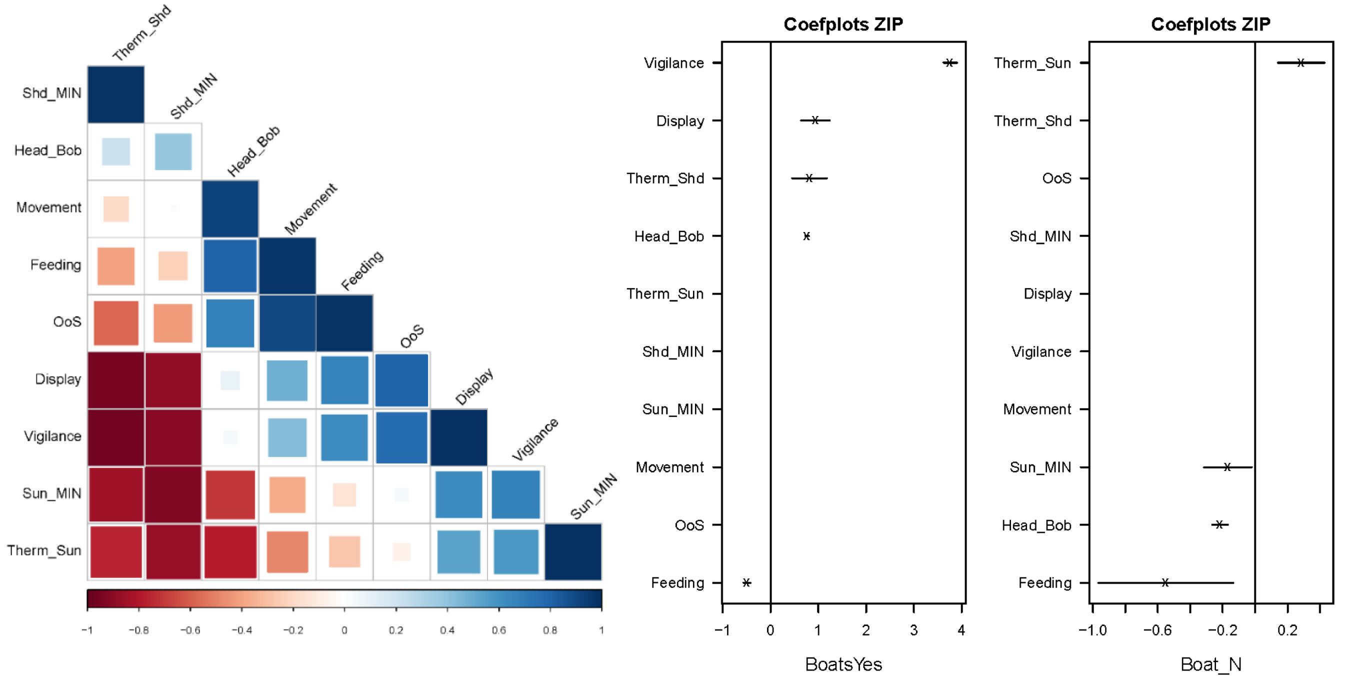
A total of 52 h of behavior observation over 30 days were recorded. All behaviors and predictors (see Figure 2) were analyzed. Summary plots of response behaviors and minutes spent in shade and sun by iguanas are presented in Figure S1. Figure 2 presents model correlations between behaviors. Figure S4 presents ordination of behaviors expressing similarity by proximity. Figures S5a–c are model coefficient plots showing positive and negative signals between all behaviors and all environmental predictor factors.

Three models (Model 1, 2 and 3) were fitted successfully. Model 1 was a GLLVM with negative binomial family, Model 2 the same model, only performed with Poisson distribution, and Model 3 used zero-inflated Poisson (ZIP). Dunn-Smyth residuals revealed a good fit, with minimal over-dispersion for all models (Figures S2a–c). AIC and BIC values confirmed Model 2 Poisson was the best fit due to its lower AIC/BIC and degrees of freedom (Table S1). However, coefficients for Poisson were poorly expressed, and the log-likelihood results suggested Model 3 was the best (highest) log-likelihood (Table S1). Considering the sensitivity of AIC/BIC values Model 3 (ZIP) was selected as the lead model for interpretation. The for-loop iteration utilized BIC values and recommended $N = 2$ latent variables as appropriate for all three Models (Figure S3).

Proceeding with Model 3, the getResidualCor function was used to plot a residual correlation matrix of all iguana response behaviors. Correlation was inspected using the adjust = command in gllvm. The adjust = 2 (from a choice of three) was found to reduce correlation the most across Model 3 (Figure 2). Appreciable levels of correlation in the model also confirmed that some iguana behaviors were naturally associated (either positively or negatively) in the model. Core clusters of response behaviors in the ordination confirmed the same associations of behaviors that were expressed in the correlations (Figure S4).

Coefficient plots were derived from Model 3. Plots expressed different *I. iguana* behaviors, both positively and negatively for each predictor variable (Figures S5a–c). Iguanas exhibited some behaviors that were common for the species and others that were more expressive of how specific individuals responded to specific predictors. Specific predictor relations are portrayed in the coefficient plots and evaluated in the discussion.

Models showed there was notable correlation among behaviors in *I. iguana*, including vigilance which was positively associated to



Abbreviation	Environmental Factor [Model Predictor]
Session	Session period [AM / PM]
ToD	Time [0600-0800; 08-10; 10-12; 11-13; 12-14; 13-15; 14-16; 15-17 h]
Minutes	Session length in minutes
Boats	Presence of tourist boats [YES]
Boat_N	Presence of tourist boats [NO]
ID	Individual iguana identification (where possible)
Temp	Temperature recorded (degrees C)
Prec	Precipitation during session period [AM / PM]
Humid	Humidity [%RH / session period
Cloud	Could cover [% cover / session period]
C_Depth	Rising canal depth (as indicator of floodwater rise)
Flood	Flooding to gallery forest [YES / NO]
Abbreviation	**Behaviour Factor [Model Response]**
Therm_Sun	Thermoregulation in sun
Therm_Shd	Retreating to shade
Vigilance	Behavioural vigilance
Head_Bob	Communication head-Bobbing
Movement	General locomotion (not associated with thermo-retreat)
Display	Dewlap displaying (males)
Feeding	Consumption of vegetation
OoS	Out of sight of surveyor
Sun_MIN	Number of minutes spent / individual in Sun
Shd_MIN	Number of minutes spent / individual in Shade

FIGURE 2 Behavior, response, and predictor variables and their code abbreviations, residual correlation: Blue = positively correlated behaviors, red = negative, coefficient caterpillar plots: Boat traffic frequency effects on iguana behaviors (black ticks to right of zero crossing = positive coefficients, left = negative, gray = non-significant)

thermoregulation in sun (basking) (Figure S2). Vigilance and dewlap display were strongly correlated, as were behaviors such as head bobbing, dewlap display and feeding. Basking (Therm_Sun) was positively correlated between 08:00 a.m.–10:00 a.m. and 10:00 a.m. – 12:00 p.m. As temperature increased, activity from movement, head bobbing, and feeding increased (Figure S5c). This trend was also reflected in time of day plots with activities occurring after individuals had been persistently basking. The opposite was true during cloudy and rainy periods, with activity decreased. Basking was observed more frequently with increasing cloud cover. As canal levels rose, and during presence of flooding, *I. iguana* movement decreased resulting in negligible activity, with the exception of heightened vigilance. Presence of boats (Figure 2: BoatsYes) was positively associated with higher vigilance and head bobbing signaling.

4 | DISCUSSION

The use of GLLVM for behavioral modeling is a new and novel approach to behavioral analysis. We interpret that the primary association between vigilance and thermoregulation in *I. iguana* is related to predator avoidance. Iguanids are vulnerable to predation when basking (Radzio & O'Connor, 2017), often from reduced mobility before they obtain optimal body temperature for locomotion (Ito & Mori, 2009). During this period of compromised activity, although lizards absorb sunlight efficiently, vulnerability is still increased (Sannolo et al., 2019).

We determine correlation in vigilance and dewlap display is explained by a combination of mating and predation risk (Cowles & Gibson, 2015). During mating season, *I. iguana* males compete intraspecifically with females choosing mates with the most impressive displays (Mitoyen et al., 2019). This attention and energy expenditure during mating makes lekking species such as *I. iguana* more vulnerable during mating (York & Baird, 2017). The data herein were collected during the regional mating season for *I. iguana* (Gómez et al., 2020), therefore, we suggest this as causal for correlation between vigilance and dewlap display. Increased activity from fighting, and dewlap displaying, can also attract predators (Thawley & Langkilde, 2017), which suggests a need for heightened vigilance during mating (Driessens et al., 2013).

Strong positive correlation between movement behaviors such as head bobbing, dewlap display and feeding, frequently occurred in unison after iguanas reached optimal body temperatures (Rowe et al., 2020). Ectotherms require optimal body temperatures to metabolize food (Tattersall, 2016). This connection, cross-behaviorally, with feeding, is reflected in the ordination plot (Figure S3).

Figure S5a presents behavior across different times of day with different behaviors expressed through periods (from 08:00 a.m.–05:00 p.m.). We consider the regular morning behaviors by *I. iguana* for this site are due to overnight body temperature loss (Rowe et al., 2020). Increased metabolism from morning basking elicits other behaviors; feeding, displays, movement, and head bobbing. Activity between 12:00 p.m.–02:00 p.m. reduced, except for shade thermoregulation (cooling). It is likely iguanas were cooling themselves during the hottest part of the day (Medina et al., 2016). As the afternoon progressed, activity reduced; 03:00 p.m.–05:00 p.m. behavior was minimal. Movement was negatively associated with this period, either because individual *I. iguana* were resting, cooling, and/or due to limited observer detection from iguanas retreating (Sylvester et al., 2013).

Display dewlaps are mostly a male behavior (Bro-Jørgensen, 2016; Harrison & Poe, 2012). We deduced sex of iguanas by their display behaviors and sexual dimorphism (Iguana 9 [IG9] was male). Some individuals were under-represented in the sample (e.g., IG5), and these were therefore less expressive for behaviors in the model (e.g., IG5 displayed more frequently [Figure S5b]). As temperature increased, activity from movement, head bobbing, and feeding increased (Figure S5c). This trend was also reflected in time of day plots with activities occurring after individuals had been persistently basking. The opposite was true during cloudy and rainy periods, with activity decreased. Basking was observed more frequently with increasing cloud cover suggesting general activity also decreased with suboptimal temperatures and lower sunlight (Kearney et al., 2009).

As canal levels rose and during presence of flooding, *I. iguana* movement decreased resulting in very low levels of activity, with the exception of heightened vigilance. As canal levels rose, water surface levels increased, making lower gallery basking iguanas more vulnerable to predation attempts by *Caiman crocodilus*, a species known to prey on *I. iguana* (Bontemps et al., 2016; Fernández et al., 2015). Such heightened risk of predation may explain the strong positive vigilance signal (Figure S5c), and reduced activity behaviors, as individuals were likely hiding (Iglesias-Carrasco et al., 2016) or had fled further into riparian tree canopy (Ito & Mori, 2009).

It is possible head bobbing is a threat response to boat presence (Vicente, 2018). One of the functions of head bobbing can be to communicate danger to conspecifics (Steinberg et al., 2014). Boat activity could provoke anti-predator behavior, due to their large presence and loud noise, which could be perceived as threatening for *I. iguana* (French et al., 2017). Our results of increased vigilance and head-bobbing during afternoons indicated a slight degree of disturbance to iguanas caused by presence of boats that could change through the day. This observation is in agreement with other lizard studies where frequency of vigilance and defensive strategies change daily and seasonally (Kerr et al., 2004; Lattanzio, 2019; Majláth & Majláthová, 2009).

Eco-tourism in the region has good conservation intentions with a focus on nature observation. It can help raise funds for wildlife protection and conservation (Mannon & Glass-Coffin, 2019). Promoting public education about local conservation issues, such as poaching and loss of habitat is progressive (Techera & Klein, 2013). However, in some cases, eco-tourism can increase infrastructure and contribute to degradation of local habitats (French et al., 2010; Knapp et al., 2013; Valverde Sanchez, 2018; Wang et al., 2020). Many eco-tourism companies have eco-certification, which requires sustainable, low impact work practices (Margaryan & Stensland, 2017). However, limited regulation within eco-certifications signal an opportunity exists to improve their effective contribution toward environmental protection (Blackman et al., 2014; Linsheng et al., 2007).

As well as behavioral, boat disturbances also have a proven physiological effect on some biota, such as altered stress hormones in response to visitor pressure (Ellenberg et al., 2007; French et al., 2010). Over time, this can affect the overall health of wildlife populations as has been demonstrated for other iguanids

(French et al., 2011). Our study shows a defensive/stress response to the presence of tourist boats for *I. iguana*. Therefore, mitigations should be considered to reduce impacts, including sensitive timing of eco-tours to limit disturbance levels. Notwithstanding, the pros and cons of eco-tourism, and its effect on the natural world, would benefit from reflective re-evaluation. The popularity of eco-tourism activities, such as whale watching, is still increasing (Hunt & Harbor, 2019) and the unseen effects of human disturbance could benefit from being monitored.

Preventing eco-tourism is unviable as it provides valuable local revenue and assists conservation costs (Blackman et al., 2014; Knapp, 2004; Sindiyo & Pertet, 1984). A more proactive solution could involve improving regulating eco-certification, ensuring inclusion of guidelines to minimize the impacts of public and boat-related disturbances (Dodds & Holmes, 2020). Possible solutions could include scheduling of boat numbers traveling between *I. iguana* viewing galleries along a canal per day. Repeated exposure to stressful stimuli has a more detrimental effect than less constant exposure (Scheun et al., 2020). Managing boat numbers passing repeatedly through selected areas could decrease any stress caused by boat traffic. We invite further study to our findings and recommend this may include investigating numbers of tourist and vigilance behavior, measuring noise output of motors and their impact on iguanas, designing a regional population census for *I. iguana*, and education work with local people, schools, and tourists.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.573n5tb9n (Rice et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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