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# Disturbance-specific behavioral responses of giant otters exposed to ecotourism and extractive activities

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## Abstract

Human activities increasingly result in disturbance of wild animal populations. Behavioral responses vary according to the type, duration, frequency and intensity of disturbance. Exposure to disturbance, for example, arising from ecotourism, may promote tolerance of humans and drive a decrease in vigilance and avoidance behaviors, whereas disturbance resulting from extractive activities is typically more intense and is likely to be perceived as a threat. To understand how animals cope with land transformation and human presence, it is imperative to study their responses under different disturbance regimes. We performed behavioral sampling of groups of the giant otter, a charismatic top carnivore, exposed to ecotourism, extractive activities (mining and fishing) and control sites without disturbance to compare their responses. Foraging efficiency was impacted by fish abundance and thus was reduced in mined and fished areas. Giant otters in lakes with managed ecotourism did not show avoidance of research vessels and demonstrated reduced rates of defensive behavior compared to control lakes. Groups from lakes with fishing and gold mining showed increased avoidance, suggesting that these types of disturbance may involve more direct conflict. Our findings suggest that noninvasive disturbance such as ecotourism may promote giant otter tolerance to the presence of humans, whereas extractive activities may be perceived as riskier. Current protected area conservation strategies of strict ecotourism regulation and the maintenance of no-access oxbow lakes may ensure the maintenance of behavioral flexibility in giant otter populations. However, resource depletion and more intense human-giant otter interactions in disturbed areas may not be sustainable. Further studies are necessary to determine whether distinct disturbance regimes drive longer-term demographic effects.

## Introduction

Human activity drives various types of disturbance to wildlife, with evident, increasing impacts on animal behavior across aquatic and terrestrial ecosystems (Tucker *et al.*, 2018; Samia *et al.*, 2019; Suraci *et al.*, 2019). Human activity can vary in type and intensity. This variation has implications for disturbance perceived by animals, which may include noise (Kunc, McLaughlin & Schmidt, 2016), habitat modification (Wilmers *et al.*, 2013) or the presence and movement of humans (Oriol-Cotterill *et al.*, 2015; Kays *et al.*, 2017). Animal behavioral responses to anthropogenic disturbances can vary by individual and include increased avoidance and changes in foraging patterns, reducing investment in fitness-related activities such as foraging, parental care and breeding (Sih, 2013). Thus, such responses can have consequences for the survival and reproductive output of individuals and affect population-level processes (Bejder *et al.*, 2006).

Ecotourism, involving recreational activities in which wildlife are often part of the experience or the focus of attention, is an important component of the conservation toolbox, having the potential to generate revenues that support nature protection and benefit local communities (Krüger, 2005). However, as ecotourism outcomes have been mixed, conservation objectives and economic benefits to local communities are not always fully realized (Kiss, 2004). Ecotourism can create disturbances arising from the presence of humans or vessels in the proximity of animal populations (Geffroy *et al*., 2015). Studies suggest that some types of recreation can have negative effects, because animals may perceive the presence of recreationists as a predation risk (Frid & Dill, 2002; Larson *et al*., 2016). However, recent evidence suggests that animals can behaviorally compensate for the presence of humans, especially when it is temporary, and are thus able to cope with relatively mild disturbances presented by ecotourism (Lusseau, 2004; Griffin *et al*., 2007). Whereas short-term behavioral responses are well studied, findings of long-term effects of recreational activities, such as behavioral tolerance or demographic declines, are not as common (Larson *et al*., 2016; Saltz *et al*., 2019). Meta-analyses have concluded that negative long-term consequences of ecotourism are poorly documented (Bateman & Fleming, 2017), that ecotourism is most often sustainable in the sense that it does not represent an immediate threat to the species or area (Krüger, 2005) and that incorporation of ecotourism can have a net effect of decreasing probability of extinction for at-risk species (Buckley, Morrison & Castley, 2016). In addition, because of publication bias, studies where effects of ecotourism on animal populations are statistically insignificant or positive may be underreported (Bateman & Fleming, 2017).

Disturbance intensity may interact with spatial and temporal human activity patterns to produce different behavioral responses with positive or negative consequences (Wilson *et al*., 2020). Animals may become sensitized to human presence when exposed to more intense or aversive human encounters, but may habituate to repeated exposure to non-threatening human activity (Blumstein, 2016). Compared to recreational activities, extractive activities of variable lengths such as fishing, hunting and mining can present more intense disturbance to wildlife. Because these activities are commonly conducted with motorized vehicles, vessels or engines, their effects are predicted to be more severe (Pirotta *et al*., 2015; Nordell, Wellicome & Bayne, 2017). Conflict may also arise when humans compete with wildlife for the same resource (Macdonald, 2016), as is the case in interactions between carnivores, including otters and fishermen (Lavigne, 2003; Loch, Marmontel & Simoes-Lopes, 2009; Akpona *et al*., 2015). To better understand how animal populations respond to distinct types of disturbance, studies are needed that quantify the various dimensions of their behavior under different conditions (Bro-Jørgensen, Franks & Meise, 2019; Swaisgood & Greggor, 2019).

The responses of animals subject to disturbance from human activity can be quantified in several ways. One commonly used method is to assess whether there is an avoidance response. This can be done by approaching animals to simulate a disturbance under the conditions of interest (e.g. in locations with or without tourist activities) and measuring their flight response (Stankowich & Blumstein, 2005; Nordell *et al*., 2017). Another aspect of animal behavior that can be measured is foraging. Animal time budgets can be modified by an increase in the periods necessary to meet nutritional needs (Verhulst, Oosterbeek & Ens, 2001). Such responses can be inferred by comparing animal foraging behavior with and without the presence of disturbance (Lusseau, 2003). Alternatively, vigilance and tolerance to the presence of human observers can be quantified under different disturbance scenarios (Saltz *et al*., 2019; Eastcott *et al*., 2020). Because different species can vary in their way of coping with disturbance, examining multiple dimensions of their behavioral responses can provide a more complete assessment of the influences of human activity on individuals and populations (Bateman & Fleming, 2017).

Ecotourism is often focused on large, charismatic predators, which can be particularly sensitive to human-driven disturbance (Macdonald *et al*., 2017). The giant otter *Pteronura brasiliensis* is an endangered top carnivore in neotropical freshwater ecosystems (Duplaix, Evangelista & Rosas, 2015; Groenendijk *et al*., 2015*a*,*b*). Because they are large and highly social, giant otters are significant tourist attractions in several South American countries, especially Brazil and Peru (Staib & Schenck, 1994; Georgiadis, Campello & Leles, 2015; Recharte, Bride & Bowler, 2015). In south-eastern Peru, giant otter ecotourism typically consists of unmotorized vessels from which small groups of tourists observe otter groups from varying distances. In several protected areas, regulation is in place to avoid excessive human pressure and no-entry refuge areas are designated (Staib & Schenck, 1994). While there is limited evidence suggesting that otter groups regularly visited by tourists can habituate and become tolerant of humans, irresponsible tourism, without consideration for the ecological needs of giant otters, can be invasive and negatively influence reproductive success (Duplaix *et al*., 2015). Nonetheless, the effects of consistent human presence on giant otter behavior are not well understood. Extractive activities in neotropical aquatic ecosystems, such as artisanal small-scale gold mining (ASGM) and fishing, can represent a significant threat to giant otters. Giant otters have likely coexisted with indigenous fishermen over several decades. In some cases, otter presence in areas of artisanal fishing can promote conflict with fishermen, due to perceived reduction of fish quantities and damage to fishing equipment (Recharte, Bowler & Bodmer, 2008; Rosas-Ribeiro, Rosas & Zuanon, 2012). On the other hand, extractive activities can damage otter habitat and reduce the availability of fish, on which giant otters rely for nutrition (Noonan, Prout & Hayssen, 2017). Deterioration of suitable bank habitat can reduce the availability of dens and resting areas necessary for giant otters (Palmeirim, Peres & Rosas, 2014). In addition, conflict with fishermen, engine noise and the presence of large dredges and vessels can increase vigilance and escape behaviors. Giant otter in areas with ASGM can also be exposed to mercury, which can accumulate in fish prey and reach toxic levels (Martinez *et al*., 2018). In addition to noise-related disturbance, reduced fish availability in such areas (Barocas *et al*., 2021) may decrease foraging efficiency, augmenting conflicts and the impacts of human presence. Because giant otter populations are not well studied in areas heavily affected by mining and deforestation, little is known about their behavioral responses to these extractive activities.

We examined whether exposure to human activity has impacts on giant otter foraging, avoidance and vigilance, by sampling behaviors of giant otter groups in oxbow lakes subject to a gradient of disturbance intensities. First, we quantified foraging efficiency of groups exposed to ecotourism, fishing and mining. Because the unprotected lakes in the study area showed reduced fish availability (Barocas *et al*., 2021), we predicted that foraging yield would be reduced in fish-poor lakes. We also predicted that because of decreased vigilance, giant otter groups in ecotourism contexts would show higher fish-catching rates. Second, we examined two aspects of giant otter behavioral tolerance, avoidance and vigilance. We hypothesized that giant otter groups in areas more exposed to ecotourism disturbance would be more tolerant to the presence of researchers. Thus, we predicted that such groups would allow researchers to follow and observe them for longer periods of time. In addition, we predicted that, compared to unexposed giant otter groups, groups in lakes with regular ecotourism activity would show decreased rates of defensive behavior. Finally, we predicted that because extractive activities can result in more intense disturbance and human–wildlife conflict (Recharte *et al*., 2008), in oxbow lakes subject to fishing and ASGM, giant otters would show increased vigilance (Blumstein, 2016; Wilson *et al*., 2020).

# Materials and methods

## Research area

We carried out field work in the Madre de Dios province of Peru (Fig. 1). Our study included ten oxbow lakes in the protected areas of Manu National Park (11°41′S, 71°13′W) and the Amarakaeri Communal Reserve (12°25′S, 70°42′W), previously surveyed for giant otter demography (Groenendijk *et al*., 2015*a*,*b*). Three of these lakes were consistently visited by ecotourist groups of up to ten people on unmotorized boats, with tourist activities regulated either by the park authorities or local lodge operators. Another lake, belonging to the Cocha Cashu Biological Station and frequently visited by researchers and students, was included in the same category. One lake, located in the vicinity of a native Matsiguenga community, was subject to traditional fishing practices during a short season (J. Farfan, unpubl. data). The remaining five lakes, which are not accessible to visitors, served as control sites (Table 1). We also sampled four unprotected oxbow lakes in the lower part of the Madre de Dios river (12°40′S, 69°53′W), where significant ASGM activities have been occurring over the last three decades (Caballero-Espejo *et al*., 2018). Three of these lakes were subject to ASGM and fishing during the research period and one, to which access is restricted, was used for ecotourism and fishing (Mendoza *et al*., 2017). The lower Madre de Dios ASGM area contains 11 small-sized communities with a formal population of 2500.

## Behavioral sampling

Between May 2018 and November 2019, we used Grabner XR-Trekking inflatable rubber boats (Grabner, Vienna, Austria) to survey oxbow lakes for giant otter presence during mornings and afternoons (Groenendijk *et al*., 2005). Each team was composed of three members, of which one observed giant otters with a 10 × 42 pair of Nikon Terra binoculars (Nikon, USA) and took notes, and one operated a video camera. When a group of giant otters was identified, we followed it in the open water from a distance of 30–100 m, keeping the minimum distance for which there were no evident changes in giant otter behavior as a result of our presence (Bateman & Fleming, 2017). This distance varied between groups studied, as some were more tolerant to human presence. We maintained a consistent distance from the start to the end of each observation session. We registered all significant behavioral events and performed a scan sample every 5 min (Altmann, 1974). We registered behaviors at the group level because it was not possible to follow individual otters, which constantly surface and dive in the murky water. Giant otter groups typically remain in the same territories, spanning one or two oxbow lakes, over several years and defend territories from individuals outside groups (Groenendijk *et al*., 2014) and thus repeated observations were of the same individuals. Distinct neck markings suggested that each sampled oxbow lake contained different individuals. In each scan, we counted the number of visible otters and registered their activity. When giant otters forage, each individual that captures a fish emerges from the water in a visible manner to feed. Thus, this behavior can be quantified in detail (Staib, 2005; Davenport, 2010). In case of a perceived threat, giant otters also move as a group towards it, raising their forequarters perpendicularly out of the water while remaining stationary. In the process they reveal their throat pattern and vocalize (Mumm & Knörnschild, 2017), a visible behavior termed periscoping (Carter & Rosas, 1997), used here to quantify group defense. We registered each fish capture and periscoping event. We also registered the starting time of each observation session and took note when giant otter groups were no longer in sight for over 5 min. As a measure of behavioral avoidance, we recorded the duration that we spent following a group, reasoning that groups more tolerant of human presence could be followed for longer periods of time. Because we were able to approach less behaviorally reactive groups more closely, this provides a conservative measure of avoidance, as close approach by humans could, in theory, shorten the duration of a follow.

## Lake conditions

We surveyed each lake for the availability of medium-sized and large fish (over 100 g) using custom-made gillnets (Araújo Flores, 2015). Giant otter diet is mostly composed of

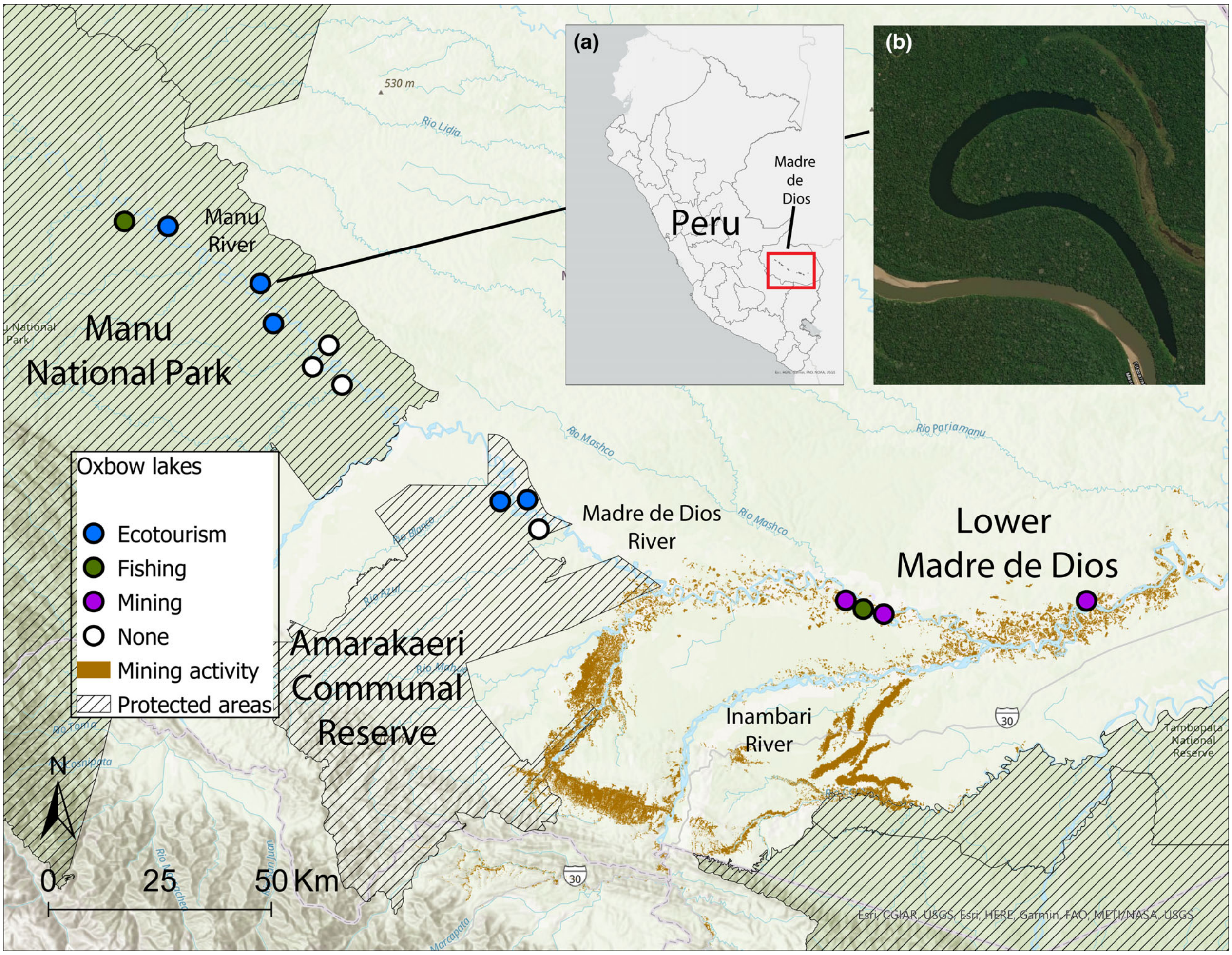

**Figure 1** Maps of the giant otter research area, including oxbow lakes in protected areas and areas with human activity. Insets show the area relative to Peru (a) and the oxbow lake Salvador, where regular ecotourism activities occur (b).

large and medium-sized fish (AB, unpubl. data). For each lake, we calculated effort-corrected fish abundance as the total catch divided by the number of hours spent surveying. Methods and sampling hours, including at least two 4-h sessions, were consistent among lakes to ensure comparability (Barocas *et al*., 2021). Fish species composition was consistent with previous studies (Rosas, Zuanon & Carter, 1999). We used field observations from at least 15 visits per lake between 2017 and 2019 to develop a human activity index for each lake. A score of 0 indicated no activity except limited access of researchers; 1 indicated limited, irregular activity including fishing and sporadic ecotourism; 2 indicated consistent human activity without motorized vessels or fishing nets; and 3 indicated consistent extractive activity, including fishing or mining, and the use of motorized boats and engines (Table 1). For further analyses, we divided lakes by the predominant type of human activity. The categories were no activity (control), ecotourism, mining and fishing.

## Statistical analysis

We used generalized linear mixed models (GLMM; Harrison *et al*., 2018) to examine the effects of fish abundance and human activity index on the total number of fish caught by giant otter groups within each 5-min interval. We built a full model with a Poisson error structure and a log link function including these variables as fixed covariates. Because giant otter activity can vary during daytime hours (Leuchtenberger *et al*., 2014), we specified time elapsed since sunrise with a quadratic term as an additional fixed factor. To account for possible satiation or depletion of local fish abundance during a foraging session, we added a linear term that describes the order of each observation within the session. The logarithm of the number of otters observed in each scan was specified as an offset term and lake identity was specified as a random covariate. All fixed covariates were standardized to improve convergence and examined for correlations. We compared the fit of the full model with all possible covariate

**Table 1** Location of lakes, types of human activity, covariates examined and descriptive sampling and behavioral data of lakes where giant otter groups were sampled for behavior. Data were collected in the Madre de Dios province, Peru during 2018–2019

| Lake | Area | Main human activity type | Human activity index | Fish abundance | Mean group size | No. sessions | Hours observed | Total fish caught | Total follows | Total periscoping events |
|---|---|---|---|---|---|---|---|---|---|---|
| Maisal | Manu NP | Fishing | 1 | 2.8 | 5.4 | 5 | 10.3 | 31 | 12 | 17 |
| Cashu | Manu NP | Tourism | 2 | 13.0 | 6.1 | 8 | 39.3 | 1278 | 19 | 79 |
| Salvador | Manu NP | Tourism | 2 | 23.6 | 5.4 | 8 | 56.4 | 1043 | 19 | 68 |
| Otorongo | Manu NP | Tourism | 1 | 33.1 | 3 | 2 | 2 | 0 | 2 | 0 |
| Juarez | Manu NP | None | 0 | 29.6 | 3.3 | 2 | 3.9 | 7 | 4 | 15 |
| Garza | Manu NP | None | 0 | 28.1 | 4.4 | 3 | 3 | 64 | 5 | 0 |
| Lagarto | Manu NP | None | 0 | 30.6 | 5.6 | 11 | 68.2 | 1172 | 32 | 172 |
| Blanco | Manu NP buffer zone | Tourism | 2 | 8.8 | 3.6 | 5 | 7.7 | 58 | 15 | 26 |
| Camungo | Manu NP buffer zone | Tourism | 2 | 14.4 | 4.7 | 6 | 5.5 | 26 | 10 | 8 |
| Aguajal | Manu NP buffer zone | None | 0 | 7.0 | 1.7 | 4 | 2 | 1 | 5 | 6 |
| Bajo11 | Lower Madre de Dios | Mining | 3 | 5.0 | 4.3 | 6 | 4.4 | 18 | 11 | 11 |
| Bajo10 | Lower Madre de Dios | Mining | 3 | 2.9 | 4.9 | 3 | 3 | 4 | 4 | 0 |
| Huitoto | Lower Madre de Dios | Fishing/tourism[a] | 2 | 2.2 | 5.6 | 13 | 26.8 | 278 | 27 | 65 |
| Bajo04 | Lower Madre de Dios | Mining | 3 | 2.6 | 3.8 | 5 | 4.5 | 1 | 10 | 5 |

[a] Considered as ‘Fishing’ for categorical analyses.

combinations using Akaike information criteria (AICc; Burnham & Anderson, 2002). We examined $\beta$ coefficients and $P$-values for each covariate to determine significance. We used conditional $R^2$ (Nakagawa & Schielzeth, 2013) to estimate the proportion of variance explained by the data and performed diagnostics of overdispersion and residual plots for the best-supported model (Hartig, 2019). For all mixed model analyses, we used the package lme4 (Bates *et al.*, 2014) in the R computational environment (R Core Team, 2019). Because sampling time was reduced in some of the oxbow lakes (Table 1), we repeated this and subsequent analyses including only groups that were sampled for more than 4 h.

Fish resources that giant otters depend on are considerably reduced outside protected areas (Barocas *et al.*, 2021). This pattern may mask the effects of human activity on giant otter foraging. To directly test whether ecotourism influences foraging, we performed the same analysis on a dataset including only oxbow lakes within protected areas, where fish abundance was higher (Table 1). Ecotourism, coded as a binary variable (i.e. none in control lakes and present in exposed lakes), was added as predictor. We used the same procedures mentioned above to find the best-supported model.

Within each lake, we measured the total time over which a group was followed since first contact as a metric of giant otter avoidance of humans. We only considered time periods in which we were certain that the giant otter group was aware of our presence in the lake. We inferred this through directional movement, vocalization or periscoping by group individuals. To examine whether otters in lakes with different types of human activities were more tolerant, we used two approaches. The first was a GLMM where activity index was specified as the main fixed covariate, lake identity was specified as a random covariate and length of follow was the response variable. This approach enabled us to examine whether avoidance response was proportional to the degree of human activity and to account for replication in observations using lake as a random covariate. The second was a Kruskal–Wallis nonparametric test (McDonald, 2009), where the predominant human activity in each lake was a categorical covariate. This approach enabled us to examine response to a category of human activity in a more qualitative manner (i.e. whether otters were previously exposed or unexposed to human activity). Because follow duration differed statistically among human activity categories, to further understand which categories differ, we subsequently performed the Dunn's test for multiple comparisons of rank sums (Dunn, 1964). To avoid Type I error, we used the Benjamini–Hochberg correction for multiple comparisons (Thissen, Steinberg & Kuang, 2002).

We examined whether giant otters exposed to human activities were more tolerant to the presence of researchers by quantifying their tendency to perform defensive periscoping behavior. We divided observation sessions into 1 h units and registered periscoping occasions, defined as events in which at least one individual swam towards the observers, revealed their throat pattern, and emitted harsh vocalizations. We summarized the number of periscoping events for each hour or part of it. In case the observation period did not amount to an hour, we adjusted the number of periscoping events proportionally. We specified the number of periscoping events per hour as a response variable in a GLMM with a Poisson error structure and a log link function. The intensity of human activity was specified as a fixed factor and lake identity was specified as a random covariate. We examined $\beta$ coefficients and *P*-values for the human activity covariate to determine significance. We subsequently compared the fit of the full model to a null model using AICc. To determine whether giant otter group defense behavior differed between specific types of human activities, we used a non-parametric Kruskal–Wallis test (McDonald, 2009), where the category of the predominant human activity in each lake was the covariate. We subsequently performed the Dunn's test of between-group rank sums and the Benjamini–Hochberg correction for multiple comparisons.

# Results

We sampled 14 giant otter groups, for a total duration of 237 h. Mean group size varied between 1.7 and 6.1 individuals (Table 1). The analysis of foraging success included 2299 behavioral group scans. We discarded all models which included both fish abundance and human activity because these variables were significantly correlated ($r = -0.78$). The model including the time, satiation and fish abundance covariates was the best-supported model (AICc weight = 0.63, Table S2). The additional model with support included the quadratic time term (AICc weight = 0.33). The human activity variable was present in models which received 2% of the support out of all examined models. There was strong support for a negative trend in fish capture rate as sessions advanced (total AICc weight = 0.99; top model $\beta \pm \text{SE} = -0.11 \pm 0.02$; $P < 0.001$). As expected, group size had a strong positive effect on overall fish capture rate ($\Delta$AICc = 243.7). Support for the time since sunrise term ($\beta \pm \text{SE} = -0.08 \pm 0.02$) indicated that fish capture peaked after sunrise (Fig. 2). Fish abundance ($\beta \pm \text{SE} = 0.52 \pm 0.17$) had a strong positive influence on fish capture rate (Table S3). The best-supported model explained most of the variance in fish capture (conditional $R^2 = 0.57$). Results with the reduced dataset were similar, except there was more relative support for the model with the quadratic time term (total weight of two top models = 0.99, Fish abundance $\beta \pm \text{SE} = 3.51 \pm 0.66$) which explained a higher proportion of the variance (conditional $R^2 = 0.96$; Tables S4 and S5). When testing the influence of ecotourism with the reduced dataset, the best-supported model (AICc weight = 0.65) did not include the ecotourism covariate. This model confirmed that group size ($\beta \pm \text{SE} = 0.12 \pm 0.01$), time after sunrise ($\beta \pm \text{SE} = -0.06 \pm 0.01$) and satiation ($\beta \pm \text{SE} = -0.05 \pm 0.01$) were significant predictors of foraging success. When present in the full model (AICc weight = 0.35), ecotourism was not a significant predictor ($\beta \pm \text{SE} = 0.55 \pm 0.64$). We recorded 175 follows of giant otter groups from 14 oxbow lakes. Otter groups were followed for a mean (±SE) of 64.1 ± 5.7 min. The model with intensity of human activity as a fixed covariate was not better supported

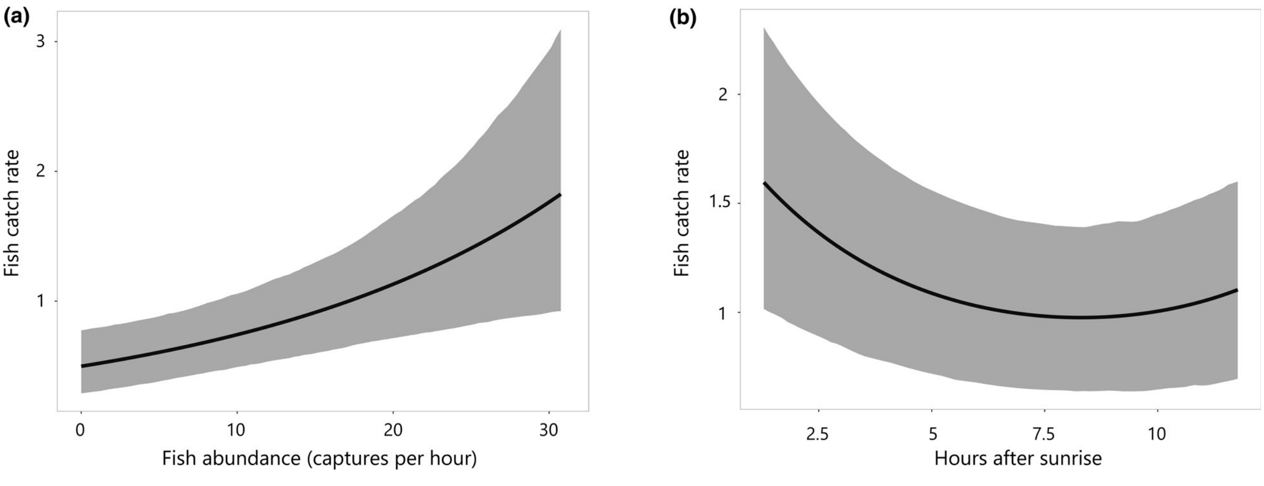

**Figure 2** Mean and 95% confidence interval predictions of a generalized linear mixed model with numbers of fish caught by giant otters per 5 min as the response variable. Giant otter behavioral data were collected in Madre de Dios province, Peru, during 2018–2019.

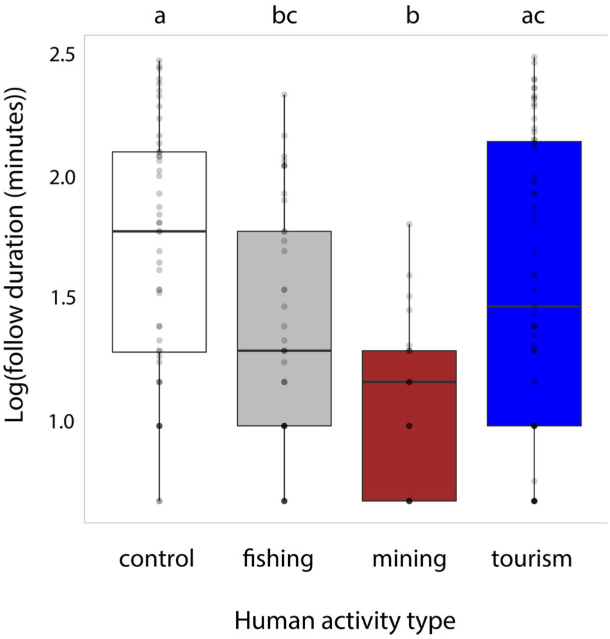

**Figure 3** Boxplots representing the distribution of follow durations divided into four classes of human activity. Lower and upper hinges represent the 25th and 75th percentiles and the hinge between them is the median. Letters denote statistical differences using Dunn's post hoc test. Data represent 175 giant otter behavioral follows conducted in 14 oxbow lakes during 2018–2019.

than the null model ($\Delta$AICc = 1.1), and the continuous human activity coefficient did not differ from 0 ($\beta \pm \text{SE} = -0.17 \pm 0.18$; $P = 0.33$). The categorical Kruskal–Wallis test, which did not account for replication, suggested that follow duration differed among types of human activity ($\chi^2 = 22.5$; $P < 0.001$). Pairwise tests among the four different categories indicated that follow duration was higher in giant otter groups in areas without human activity compared to mined ($Z = -4.44$; $P_{\text{adj}} < 0.001$) and fished ($Z = -2.74$; $P_{\text{adj}} = 0.01$) lakes, and that groups in lakes with ecotourism had higher follow duration compared to mined lakes ($Z = -3.56$; $P_{\text{adj}} = 0.001$; Fig. 3). The results were similar with the reduced dataset (GLMM activity $\beta \pm \text{SE} = -0.25 \pm 0.26$; $P = 0.32$; Kruskal–Wallis $\chi^2 = 24.1$; $P < 0.001$).

Giant otter periscoping events were analyzed for 253 observation periods in 11 oxbow lakes. Otter groups performed a mean of 1.76 ± 0.13 periscoping bouts per hour. The model that included human activity was better supported than the null model ($\Delta$AICc = 3.0). Human activity intensity negatively affected periscoping rate ($\beta \pm \text{SE} = -0.23 \pm 0.1$; $P = 0.02$; Fig. 4). Kruskal–Wallis test results indicated that observations of periscoping rates differed significantly among classes of human activity that animals were exposed to ($\chi^2_3 = 12.1$, $P = 0.007$). The Dunn's post hoc test revealed that periscoping rates did not differ among control lakes and lakes with mining and fishing but was higher in control lakes compared to lakes with ecotourism ($Z = 3.22$; $P_{\text{adj}} = 0.007$; Fig. 4). Results were similar with the reduced dataset (GLMM activity $\beta \pm \text{SE} = -0.21 \pm 0.1$; $P = 0.04$; Kruskal–Wallis $\chi^2 = 11.0$; $P = 0.01$).

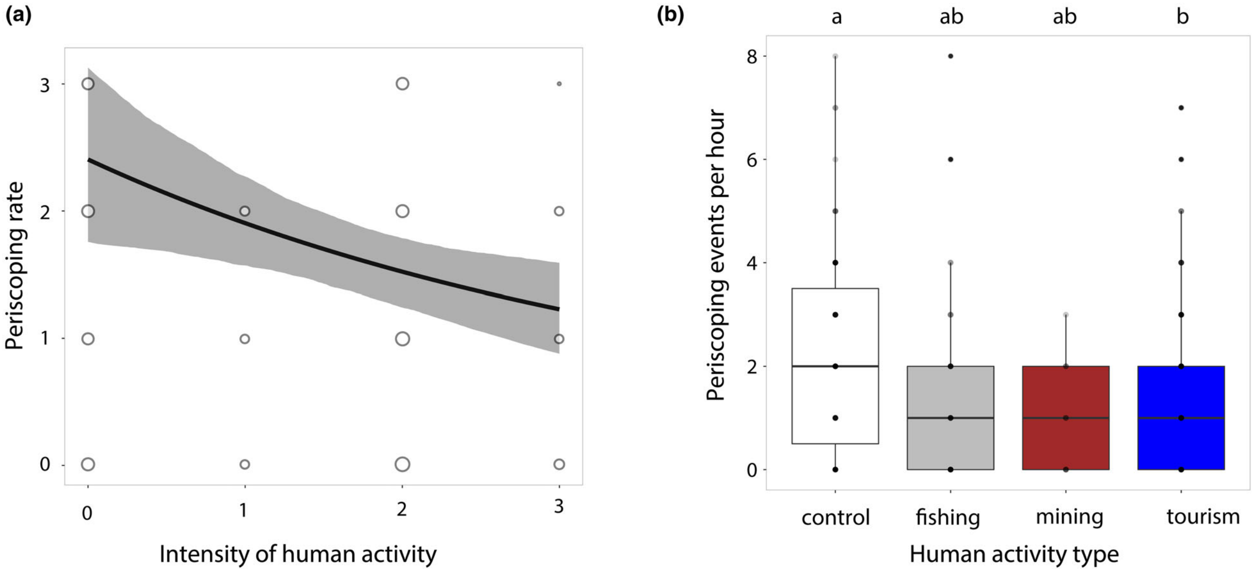

**Figure 4** Effects of human activity on periscoping behavior in giant otters. Prediction of mean and 95% confidence interval from a generalized linear mixed model with giant otter periscoping rate as the response variable and observed data points (a). Circle sizes are scaled to the number of points for each value. Boxplots representing the distribution of periscoping events divided to four classes of human activity (b). Lower and upper hinges represent the 25th and 75th percentiles and the hinge between them is the median. Letters denote statistical differences using Dunn's post hoc test. Data represent 253 giant otter periscoping events collected in 11 oxbow lakes during 2018–2019.

## Discussion

We used three behavioral metrics, reflecting foraging success, avoidance and vigilance, to examine the responses of giant otter groups to exposure to human activity. Fish availability but not human activity influenced giant otter foraging success. Our findings also indicate that giant otters were more tolerant of human presence – as measured by duration of follows by researchers – when there was no previous exposure to humans or human activity involved ecotourism than when lakes were used for mining and fishing, suggesting that giant otters exposed to such activities may subsequently be more likely to avoid humans. Levels of periscoping behavior, reflecting vigilance, were lower in lakes with ecotourism activities compared to control lakes, suggesting that giant otters may have become tolerant to the presence of nonmotorized vessels and additional mild disturbances which characterize such activities.

One documented effect of disturbance on the behavior of animals is an increase in foraging effort necessary to meet their nutritional needs (Rode, Farley & Robbins, 2006). However, none of the human activities we evaluated were statistically associated with fish capture rates. Instead, per-capita foraging success appeared driven by ecological factors. As we expected, there was support for the relationship between giant otter group size and foraging success. After accounting for this relationship, fish capture rates in oxbow lakes were positively associated with high fish availability and varied among activity hours, with peaks in early morning. Decreased giant otter foraging efficiency may be linked to significantly reduced fish biomass in unprotected oxbow lakes subject to mining and fishing (Barocas *et al*., 2021). Besides the reduction in fish biomass, a possible consequence of shifts in hydrological processes driven by gold mining in aquatic ecosystems (Sonter, Ali & Watson, 2018; Dethier, Sartain & Lutz, 2019), lower foraging success could also be explained by reduced per-capita yield when foraging in smaller groups. It is unclear whether giant otters cooperatively forage on schools of fish. However, foraging in groups may facilitate fish predation and increase individual nutritional yield (Rosas *et al*., 1999; Duplaix *et al*., 2015). Also, previous research suggests that giant otter groups in higher quality territories typically have increased survival and reproductive success (Groenendijk *et al*., 2014, 2015*a*,*b*). Thus, extractive human activities may have effects on giant otters both by reducing the amount of fish available (causing an increase in time spent performing this activity) and by reducing territory quality, leading to longer-term demographic effects such as smaller family groups with fewer helping individuals.

Giant otter groups in mined and fished oxbow lakes were followed for shorter periods, suggesting that these otters more actively avoid research vessels and have reduced tolerance to human activity. This finding suggests that otters may alter their spatial foraging patterns following extractive activities, a possible outcome of sensitization to more aversive human activity (Blumstein, 2016). Elsewhere, giant otters are perceived as damaging to fishing efforts and thus become involved in conflicts with fishermen (Recharte *et al*., 2008; Rosas-Ribeiro *et al*., 2012). Thus, interactions with humans in such areas may result in harassment or harm to giant otters, explaining their increased caution. This effect, however, may not be general, as giant otters have coexisted with humans in neotropical aquatic ecosystems for several centuries. Giant otters living in oxbow lakes with regular ecotourism activities did not show similar evidence of sensitization. Frequent encounters with ecotourists may have promoted long-term tolerance (Bejder *et al*., 2009). Such findings suggest that current visit patterns by tour groups are not perceived as an immediate threat for giant otters and have reduced effects on their behaviors and time budgets. Although poorly managed ecotourism can have negative impacts on giant otters (Groenendijk *et al*., 2015*a*,*b*), regulations within Manu National Park and the adoption of similar best practices outside the park likely to reduce any aversive reaction by giant otters. These include guidelines on maintaining distance from giant otters, efforts to reduce noise disturbance and tour operators that are sensitive to otter behavior and move away when they show signs indicating disturbance (J. Mendoza, pers. obs.).

Further support for relatively benign effects of ecotourism comes from the analysis of periscoping patterns, where otters demonstrated a reduction in this territorial behavior in oxbow lakes with ecotourism compared to lakes with no human activities. Giant otter groups that are 'naïve' (i.e. visited only for a few occasions each year for research purposes) may perceive human research vessels as more of a threat compared to groups that experience such encounters daily or weekly. This finding is consistent with the hypothesis that animals can habituate to repeated exposure to nonthreatening human activity (Blumstein, 2016). Interestingly, this effect was observed for periscoping behavior and not for follow duration, highlighting the importance of assessing impacts of human activities on multiple dimensions of animal behavior, and further indicating that avoidance of human activity in space and time could mask behavioral responses (Bateman & Fleming, 2017). Exposure to increased disturbance from human activity may not necessarily impact vital rates, as animals may be able to compensate for immediate behavioral responses (New *et al*., 2013). In the case of giant otter groups, further studies are needed to examine whether disturbance regimes have longer-term demographic consequences.

Because the goals of our study included the quantification of giant otter behavior and collection of giant otter demographic data, we did not implement an experimental approach. Thus, our results should be interpreted with caution. However, our presence and distance from giant otter groups likely constituted a suitable simulation of the conditions during tourist group lake visits and possibly additional human activities. Further understanding of responses by the giant otter groups in question would benefit from control treatment approaches, including observation from a distance during tourist viewing, as is common in marine mammal studies (Lusseau, 2003; Christiansen, Rasmussen & Lusseau, 2013), approach experiments where it is possible to quantify flight initiation distance (Stankowich & Blumstein, 2005), and playback experiments which specifically assess anthropogenic noise effects (Wale, Simpson & Radford, 2013; Eastcott *et al*., 2020).

Our results suggest that, under current conditions, giant otter individuals and groups vary in their responses to human activity. Maintaining such behavioral variability could be crucial to ensure the survival of animal populations, especially of endangered species (Wong & Candolin, 2015). Thus, the maintenance of portions of giant otter populations unhabituated to humans may promote their ability to survive under scenarios of environmental change and increases in human activities (Saltz *et al*., 2019). This implies that current regulations by Peruvian park authorities, including keeping several lakes off limits for tourists and the strict timing of visits and tour group sizes within lakes, should continue. In addition, our findings suggest that there are certain periods in the day when foraging yield is higher. Decisions on the timing of tourist group visits should be based on these findings to avoid excessive impacts to foraging success that may have cumulative effects on health, reproduction and survival. Finally, oxbow lakes that have larger, more stable giant otter groups are also the ones that are most popular among tour operators because they are more likely to guarantee a rich observation experience. Such lakes have a disproportionate importance as prime otter territories and sources for dispersing individuals (Groenendijk *et al*., 2018). Thus, giant otters in these lakes should be more carefully monitored.

## Conclusions

Our findings suggest that giant otter responses to human activity are diverse, depending on the intensity and type of activity to which they are exposed. In resource-poor unprotected areas, giant otters may experience prey depletion and more acute disturbance characterized by boat and engine noise and interactions with miners and fishermen. Current ecotourism management practices in protected areas appear to be adequate to ensure the behavioral flexibility and viability of the studied giant otter population. However, further research is necessary to understand whether the behavioral responses observed result in longer-term demographic patterns, especially in aquatic ecosystems subject to fishing and gold mining. Our approach underscores the value of studying multiple behavioral metrics under distinct disturbance scenarios, in collaboration with management authorities, to ensure that ecological behavioral studies can inform the management and conservation of species and ecosystems (Greggor *et al*., 2016).

Our findings further support the contention that ecotourism, when managed appropriately, can be pursued with minimal concern for negative impacts on giant otters, thus potentially providing economic incentives for protection of the species and its habitat. To be effective, revenues generated must support the local, largely indigenous, human communities (Shepard *et al*., 2010) and/or the capacity of managers of protected areas. Ecotourism will remain an important component of conservation, but studies such as ours are required to ensure that they are more panacea than Pandora's box (Krüger, 2005).

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## Supporting information

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

**Table S1.** Locations, catch total and species richness estimates of Oxbow lakes sampled for fish.

**Table S2.** Generalized linear mixed model results, showing model structure, number of parameters and Akaike information criteria metrics for covariates predicting giant otter foraging efficiency.

**Table S3.** Output of best-supported Generalized linear mixed model giant otter foraging efficiency.

**Table S4.** Generalized linear mixed model results, showing model structure, number of parameters and Akaike information criteria metrics for covariates predicting giant otter foraging efficiency.

**Table S5.** Output of best-supported generalized linear mixed model giant otter foraging efficiency.