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The effects of human exposure on Galápagos sea lion behavior

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The endangered Galápagos sea lion lives among a rapidly growing human population, and conflicts between humans and sea lions are increasing. Protection of this fragile species requires a better understanding of how anthropogenic activity affects its health and survival. In this study, we engaged a group of local students in a community science project to conduct long-term observations of the effects of human disturbance on sea lion behavior. We compared three types of behavior – reaction to human approach, vocalizations and group size – across four different haul-out sites which varied in their levels of human disturbance. We found that sea lions respond less aggressively to humans on beaches that are more disturbed. This may be because sea lions acclimate to human disturbance or because sea lions with a low tolerance for humans avoid disturbed sites. We also found that aggressive vocalizations between sea lions increase as sea lion group size increases, though group size was not linked to human disturbance. We did not quantify stress levels, but aggressive behavior often indicates elevated stress levels, which are energetically costly and can impair immune function. Our results suggest that conservation efforts should focus on limiting human–sea lion interactions and increasing the number and quality of available haul-out sites.

Keywords: aggression, anthropogenic disturbance, community science, conservation, Galápagos, group size

The endangered Galápagos sea lion *Zalophus wollebaeki* is one of the Galápagos Archipelago's most visible and beloved endemic species. This highly social marine predator uses sandy beaches and rocky outcroppings throughout the Archipelago as haul-out sites, places where individuals rest, breed and care for their young. Often, sea lions choose haul-out sites that overlap with the Galápagos' rapidly growing human settlements, leading to conflict between humans and sea lions. During the day, sea lions compete for space on the beaches with sunbathers, tourists, children and dogs often leading to sea lions chasing humans out of their territory. Sea lions often sleep on fishing boats, creating conflicts with fisherman who see them as threats to their livelihood. At night, sea lions are frequently disturbed by bright lights and music from restaurants and bars.

A crucial question for the conservation and management of this endangered species is: how does living in such close quarters with a rapidly growing human population affect Galápagos sea lions? The species declined from an estimated 40 000 individuals to 16 000 individuals between 1978 and 2001, with little evidence of recovery since 2001 (Trillmich 1979, Trillmich et al. 1991, Alava and Salazar 2006, Riofrío-Lazo et al. 2017). At the same time, the permanent human population of the Galápagos has grown from fewer than 5000 people in 1974 (Epler 2007) to over 25 000 people in 2015 (INEC 2015), and well over 30 000 today. Tourism, too, brings an increasing number of people to the islands each year. In 2015, over 220 000 people visited the Galápagos for cruises or land-based tours (Izurieta 2017), and over 250 000 visited in 2018. Given the fragility of the sea lion population, it is important to understand any threats that humans pose to this species.

Some human threats to sea lions are well-documented. The proportion of recorded sea lion deaths and injuries attributed to humans in one portion of the Archipelago (the island of San Cristóbal) rose dramatically between 2008 and 2012 (Denkinger et al. 2014, 2015). Sea lion pup mortality is also much higher in colonies that live near human settlements than it is in colonies that live on islands uninhabited by humans, perhaps because infectious diseases have been transmitted from domestic animals to sea lions (Denkinger et al. 2017). But such studies only consider deaths and injuries that are directly caused by human activity (e.g. intentional killing of sea lions, injuries caused by

dog attacks or fishing equipment). Much less is known about how exposure to humans may indirectly affect the well-being of sea lions – by altering their behavior, stress levels or reproductive habits.

Researchers have documented such indirect effects of exposure to humans in other sea lion species, usually by observing sea lions' behavioral reactions to being approached by researchers or tourists, either on foot or by boat. Some species, such as the Steller sea lion *Eumetopias jubatus*, react dramatically to human approach. Individuals resting at haul-out sites make agitated calls and often retreat into the water when researchers approach them (Lewis 1987, Kucey 2005). Such disturbances – if they occur frequently – may reduce the amount of time that individual sea lions spend resting on land to recover from hunting, or affect the quality of care that mothers provide to their pups (Kovacs and Innes 1990, Jansen et al. 2015).

Other sea lion species appear more resilient to human presence, at least in the short term. Holcomb et al. (2009) conducted an approach study of California sea lions *Zalophus californianus* hauled-out on an uninhabited island in the Gulf of California and observed little to no behavioral responses (but see French et al. 2011). A study of Australian sea lions *Neophoca cinerea* on two different islands (one that allows public beach access and one that does not) found small but measurable differences in the frequency of aggressive behavioral reactions from sea lions toward tourists across the two sites (Osterrieder et al. 2016). Given this variation in behavioral responses across species, assessments of how sea lions react to humans should be done on a species-by-species basis (Kucey and Trites 2006). Although Galápagos sea lions are generally believed to be less reactive to humans than other sea lion species, this has not been empirically tested. Species-specific assessments are especially important for Galápagos sea lions because many of them they have closer contact with humans than do members of other sea lion species.

Prior attempts at environmental management in the Galápagos have avoided actively involving the local community in designing management protocols, instead often imposing protocols on the community without explanation (Weisberg et al. 2020). As a result, the local community often views environmental management protocols as annoying disturbances in their daily lives and do not take them entirely seriously. Citizen science offers a powerful opportunity to involve the local community conservation efforts. Community Science, a type of citizen science characterized by the local community being involved in data collection with the goal of affecting policy or decision-making (Bonney et al. 2016), is likely to be especially effective in promoting deep engagement with Galapagueños. A potential side benefit of this project is that the participating students may feel more motivated to engage in conservation as a result of learning more about the endangered species.

In order to understand how living alongside humans affects the behavior of Galápagos sea lions, we conducted a Community Science study on one of the largest breeding colonies in the Galápagos – known as El Malecón – which has seven haul-out sites in and around Puerto Baquerizo Moreno, a town of 8000 people on San Cristóbal Island. We and a team of 28 local high school students observed sea lions at four of these haul-out sites. All these sites are in or adjacent to Puerto Baquerizo Moreno's urban zone, but the types and amount of human activity varies from site to site.

We expected that if exposure to humans affects the behavior of Galápagos sea lions, then we would observe variation in sea lion behavior across the four sites. In particular, we expected that if human disturbances are stressful for sea lions, then this stress would manifest itself in more aggressive sea lion behavior, both toward humans and toward one another, at haul-out sites occupied by greater numbers of people. At the same time, mammals living in areas with lots of human visitors often decrease their 'antipredator' responses to humans (Neuhaus and Mainini 1998, Magle et al. 2005), so we also considered the possibility that sea lions would be less reactive to human approach at haul-out sites occupied by more people.

We also recorded sea lion group size (the number of neighboring sea lions resting near any given individual) and predicted that large numbers of people at a site would cause sea lions to crowd together in larger groups than at sites with fewer people. Finally, we observed instances of calling, growling, barking and challenging. Three of these behaviors (growling, barking and challenging) are aggressive behaviors. We predicted that at sites with more people, we would observe more of these aggressive behaviors directed towards both humans and other sea lions.

Methods

Study sites and setup

Twice per week, between June and December of 2017 and 2018, we and a group of Community Scientists conducted observations. These Community Scientists were International Baccalaureate students at the UAE-San Cristóbal school who participated in Project LAVA, an initiative led by the Galápagos Education and Research Alliance (Weisberg et al. 2020). A team of graduate and undergraduate students from the University of Pennsylvania spent six weeks at the beginning of each field season training the community scientists and ensuring their mastery of the observation protocol. The participation of these community scientists (12 students in 2017 and 18 students in 2018) allowed us to observe Galápagos sea lion behavior for six full months each field season. Typically, behavioral observations of this species range from only two weeks to three months per field season (Wolf and Trillmich 2007).

In 2017, we conducted observations on three beaches (Fig. 1): Playa Mann (0°53′44″S, 89°36′33″V ~2350 m^2), Playa de Oro (0°53′59S, 89°36′34″ ~1800 m^2) and Playa Zona Naval (0°54′07′S, 89°36′51″V ~2450 m^2). In 2018, we added a fourth beach, Playa de los Marinos (0°54′09″S, 89°36′47″V, ~3550 m^2). During each of our observations, we counted the number of people at each site. We used the average number of people at each site over the course of both field seasons as a proxy for each site's level of human disturbance. We acknowledge that the sites likely varied in other ways besides the level of human disturbance, but we feel that our approach is a good first step in exploring whether sea lion exhibit behavioral differences across different sites and a similar measure of human disturbance has

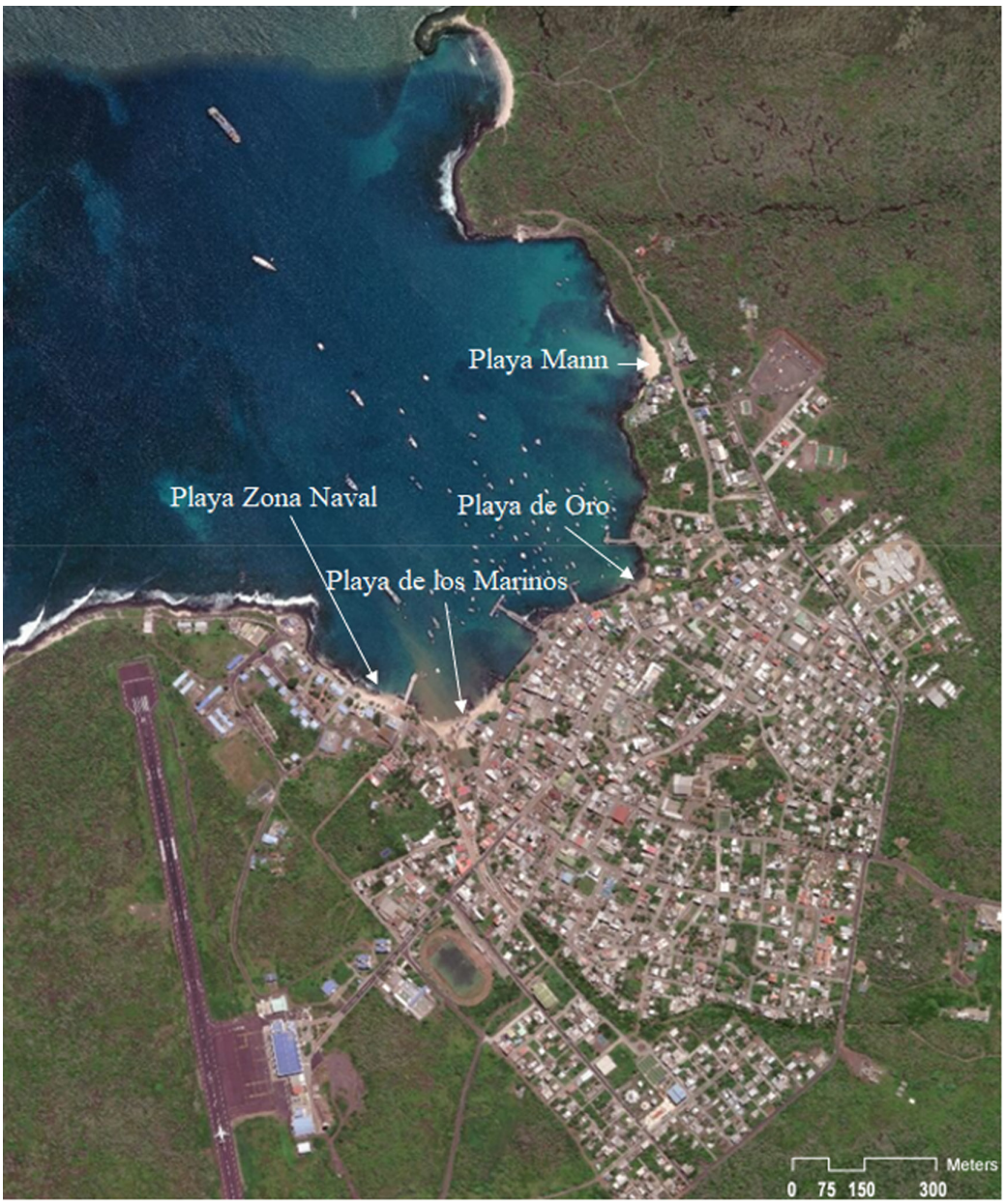

Figure 1. Map of Puerto Baquerizo Moreno showing the four El Malecón colony haul-out sites included in this study.

been used to study Australian sea lions living on Carnac Island (Orsini et al. 2006) and in a comparison of Australian sea lions on Carnac Island and Seal Island (Osterrieder et al. 2016).

Playa Mann is a beach that locals and tourists use for recreation year-round. It is by far the most human-disturbed of all El Malécon's haul-out sites. Naturalist guides bring groups of tourists here for swimming and sunning, and there are multiple food vendors, as well as outdoor showers, on the beach itself. It is common to observe visitors violating Galápagos National Park rules by approaching sea lions to less than 2 m to tease or photograph them. Playa de los Marinos is primarily used by fishermen for repairing boats. It is visited occasionally by tourists and locals, but sea lions hauled out see fewer humans than they do at Playa Mann. Playa de Oro is a launching site for kayaks and paddleboards adjacent to several busy hotels and restaurants. There is frequent foot traffic on a boardwalk running by the beach, but humans rarely spend time working, relaxing or playing on the beach itself. Zona Naval is inside a navy base and is rarely visited by locals or tourists. Due to its proximity to the navy base, this is the colony's least human-disturbed haul-out site. A road runs along the beach, but is set back several meters, and the foot and vehicle traffic along the road is infrequent compared to the traffic along the waterfront outside of the navy base.

We assigned numbers to all sea lions hauled out at a site and then assigned 4–5 of the numbered sea lions to each observer. If there were more sea lions than five times the number of observers (5–10 depending on the site), we preferentially chose to include sea lions that were easiest to approach (e.g. those basking on sand rather than on rocks). Once we had chosen the focal individuals (25–50 per observation, depending on the number of observers)

for the observation and assigned specific sea lions to each observer, the observation protocol proceeded in three parts: an approach assay, a survey of age, sex and group size, and finally, a 15-min behavioral observation period.

Approach assay

Each observer conducted an approach assay on each of their assigned sea lions, one at a time, in order to measure behavioral responses to a direct human approach. This assay is similar to the widely used flight initiation distance test, where an observer approaches an animal to determine the distance at which the animal starts to run away (Ydenberg and Dill 1986), but here the goal was to determine the degree of an individual sea lion's response to human approach. It is similar to the methods used in a previous study on Galápagos sea lions (DeRango et al. 2019) and in other species, such as eastern gray squirrels (Cooper et al. 2008). To conduct this approach assay, an observer stood 6 m away from the focal sea lion and then slowly walked (~1 m s^{-1}) towards its head. If the sea lion's head was obstructed by another sea lion or environmental feature, the observer walked toward the middle of the sea lion's abdomen instead. The approach stopped, either when the sea lion began moving toward the observer, or when the observer came within 2 m of the sea lion – the Galápagos National Park's minimum required distance from wildlife. Finally, the observer rated the sea lion's reaction to their approach on a scale of 0–5, with scores of 4 and 5 representing aggressive reactions:

0: the sea lion's eyes were closed (possibly asleep) and the sea lion did not react
1: the sea lion's eyes were open and the sea lion did not react
2: the sea lion lifted/moved its head to look at the observer
3: the sea lion moved away from the observer
4: the sea lion vocalized (growl or bark)
5: the sea lion moved toward the observer

This 0–5 scale is an adaptation of the scales used to measure behavioral responses to human approach in squirrels (Cooper et al. 2008), polar bears (Dyck and Baydack 2004) and sea lions (Orsini et al. 2006, DeRango et al. 2019).

Group size and characteristics

After the approach assay, observers recorded the age, sex and group size of each of their assigned sea lions. We classified sea lions as either pups (< 6 months old; not yet molted to adult fur), juveniles (6 months to 6 years old; smaller than an adult female; if male, testicles not yet visible and head crest not developed), adults (> 6 years old, no longer suckling; visible testicles if male) or unknown. We recorded the sex of sea lions based on the presence or absence of a penis pocket. If we were not able to see the anterior side of the abdomen, we recorded the sex as unknown, unless the sea lion had an obvious head crest that allowed us to identify it as a male. We recorded group size for each sea lion by recording how many 'neighbors' it had, i.e. how many sea lions were hauled-out within one body length of the focal sea lion. We chose to record group size because it is a proxy for social connectivity in this species (Wolf and Trillmich 2007).

Behavioral observations

Finally, observers recorded all of the following behaviors performed by their assigned sea lions for 15 min:

1) calling: one sea lion audibly calls out to others
2) growling: agitated sound in response to sea lions, other animals or humans
3) barking: short burst of sound, usually by dominant males
4) challenging: running towards or chasing off other sea lions, animals or humans

For interactive behaviors, we recorded the identity of all the sea lions involved. We also noted when any of these behaviors were directed towards humans.

Statistical analyses

We performed all statistical analyses in R ver. 3.4.1 (<www.r-project.org>). Although our sites differed in the number of people and sea lions on the beach, we could not tease apart those differences from other differences between sites (e.g. noise levels, temperature differences) so we included the factor 'site' in our models which is meant to represent all differences between sites. We used the R package 'ordinal' (Christensen 2019) to fit generalized linear mixed models (GLMMs) for sea lion response to the human approach assay. For sea lion group size and each of the recorded behaviors, we first fit Poisson GLMMs and tested if the models were overdispersed. Because all these GLMMS were overdispersed (Supplementary material Appendix l Table A1), we used the quasi-Poisson family option of the R package 'MASS' (Venables and Ripley 2002). The interaction terms between site and age and between site and sex were not significant for any of our GLMMs and therefore are not included in GLMMs. We evaluated the significance of all fixed effects using likelihood ratio tests Finally, because our data were not normally distributed (Shapiro–Wilk tests; Supplementary material Appendix l Table A2), we used non-parametric Dunn's tests with Bonferroni corrections for multiple comparisons to test for significant differences between levels of the non-numeric fixed effects.

Results

Site differences

The average number of people on the beach during our observations differed across our four sites (Playa Mann: people – 73.9, sea lions – 41.2; Playa de los Marinos: people – 7.8, sea lions – 99.0; Playa de Oro: people – 1.9, sea lions – 23.2; Playa Zona Naval: people – 0.05, sea lions – 52.1).

Approach assay

We conducted the approach assay on a total of 3027 sea lions across 2017 and 2018 (Fig. 1). The number of individuals who were assayed more than once is unknown. Only a few sea lions on San Cristóbal are tagged, so it is usually impossible to re-identify individuals. We found that site and the interaction between group size and age were significant (assay

reaction ~ site + group size × age, random = date, ordinal data; Table 1, Fig. 1). Post hoc tests revealed that all pairwise comparisons between the four sites, except between Playa Zona Naval and Playa de Oro, were significant. Sea lions responded least aggressively on Playa Mann (average reaction score = 0.536), followed by Playa Zona Naval (0.734), Playa de Oro (0.768) and Playa de los Marinos (0.948). The relationship between group size and the approach assay reaction was negative, suggesting that sea lions in larger groups responded less aggressively. Adult sea lions (average reaction score = 0.895) responded more aggressively than either juveniles (0.571) or pups (0.521). There was no difference in reaction between juveniles and pups.

Group size

We recorded group size for 3027 sea lions across 2017 and 2018. We found that site and sex were significant, while age was not (group size ~ site + sex, random = date, family = quasi-Poisson; Table 2). Post hoc tests revealed that all pairwise comparisons between sites, except between Playa Mann and Playa Zona Naval, were significant. Group sizes were the largest at Playa Zona Naval (average group size = 1.948), followed by Playa Mann (1.845), Playa de los Marinos (1.621) and Playa de Oro (1.367). Female sea lions (1.85) had larger group sizes than males (1.61).

Behavioral observations

We recorded 422 calls across 2017 and 2018 (Table 3). Site, age and sex were significant, but group size was not (calls ~ site + age + sex, random = date, family = quasi-Poisson; Supplementary material Appendix l Table A3). Post hoc tests revealed that sea lions called significantly fewer times on Playa Zona Naval than Playa de Oro. Females called more often than males. Pups called more than juveniles and there was no difference in the number of calls between pups and adults or juveniles and adults.

We recorded a total of 1311 growls (Table 3). Group size, age and sex were significant, but site was not (growls ~ group size + age + sex, random = date, family = quasi-Poisson; Supplementary material Appendix l Table A3). Post hoc tests revealed that adult sea lions growled significantly more than pups or juveniles. There was no difference in the number of growls between pups and juveniles. Female sea lions growled more than males. The relationship between the number of growls and group size was positive, suggesting that sea lions growled more often when in larger groups.

Table 1. A summary of likelihood ratio tests evaluating the significance of fixed effects in GLMMs on the results for approach assay reactions.

	χ^2	df	p
Age	64.1	3	< 0.001
Group size	13.1	1	< 0.001
Sex	2.0	2	0.367
Site	49.1	3	< 0.001
Age × Group size	12.7	3	0.005
Age × Sex	3.7	9	0.572
Age × Site	8.7	6	0.463
Group size × Sex	4.9	2	0.086
Group size × Site	5.2	3	0.152
Sex × Site	6.4	6	0.655

Table 2. A summary of GLM results on group size.

	χ^2	df	p
Age	1.6	3	0.660
Sex	11.3	2	0.008
Site	84.7	3	< 0.001

We recorded a total of 216 challenges (Table 3). Group size was significant, but site, age and sex were not (challenges ~ group size, random = date, family = quasi-Poisson; Supplementary material Appendix l Table A3). The relationship between group size and the number of challenges was positive, suggesting sea lions challenged more often when in larger groups.

We recorded 203 total barks (Table 3). Because typically only adult male sea lions bark, we did not include age or sex in the GLMs. We found that site and group size were significant (barks ~ site + group size, random = date, family = quasi-Poisson; Supplementary material Appendix l Table A3). Post hoc tests revealed that sea lions barked more often on Playa de Oro than Playa Zona Naval. The relationship between group size and the number of barks was negative, suggesting that sea lions barked more often when in smaller groups.

We observed a total of 226 aggressive behaviors (barks, growls and challenges, Table 3) directed towards humans. Group size, age and sex were significant, but site was not (aggression towards humans ~ group size + age + sex, random = date, family = quasi-Poisson; Supplementary material Appendix l Table A3). Post hoc tests revealed that both male and female sea lions were more aggressive towards humans than sea lions of unknown sex, but there was no difference between male and female sea lions. Adult sea lions were more aggressive towards humans than either juveniles or pups but there was no difference between juveniles and pups. The relationship between the number of aggressive acts towards humans and group size was negative, suggesting that sea lions were more aggressive towards humans when in smaller groups.

We observed a total of 1501 aggressive behaviors directed towards other sea lions (Table 3). We found that age and group size were significant but sex and site were not (aggression towards sea lions ~ group size + age, random = date, family = quasi-Poisson; Supplementary material Appendix l Table A3). Post hoc tests revealed that adult sea lions were more aggressive towards other sea lions than either juveniles or pups but there was no difference between juveniles and pups. The relationship between aggression between sea lions and group size was positive, suggesting that sea lions were more aggressive towards other sea lions when in larger groups.

Discussion

Conservation of endangered animal populations requires an understanding of the effects of anthropogenic activity on health and survival. Here, we used a Community Science approach to compare Galápagos sea lion vocalizations, group size and reaction to human approach across four dif-

Table 3. A summary of recorded behaviors across sites, ages and sexes.

	Calls	Growls	Challenges	Barks	Aggression towards humans	Aggression towards sea lions
Site						
Playa de los Marinos	56	166	55	25	36	206
Playa de Oro	135	239	24	71	49	284
Playa Mann	187	379	47	57	63	419
Playa Zona Naval	198	527	90	50	78	584
Age						
Adults	272	677	110	176	161	794
Juveniles	56	135	27	5	18	148
Pups	27	14	6	0	2	18
Unknown	221	485	73	22	45	533
Sex						
Females	310	603	82	19	101	601
Males	45	226	61	162	80	362
Unknown	221	482	73	22	45	530

ferent haul-out sites which varied in their levels of human disturbance. We found that sea lions were less reactive to human approach on Playa Mann, the beach most disturbed by humans (Table 1, Fig. 2). We also found differences in group size across our study sites, but the differences did not track human disturbance (Table 2). Instead, group sizes were largest on the least disturbed beach and the most disturbed beach. Finally, we did not find variation across sites in the number of aggressive behaviors (growls, barks and challenges) directed towards either humans or other sea lions, but we did find that sea lion aggression towards humans decreased with group size, while aggression towards other sea lions increased with group size (Table 3).

Unlike other pinniped species (Lovasz et al. 2008, Osterrieder et al. 2016), Galápagos sea lions responded least aggressively to human approach at the most disturbed haul-out site. One interpretation of this result is that sea lions who choose haul-out sites where there are large numbers of people become acclimated to the presence of people as a result of their site choice, making them less likely to react in an aggressive or agitated way when directly approached by a human. This study did not identify and track particular individual sea lions, but previous research on site fidelity has found that Galápagos sea lions do consistently return to the same haul-out sites (Wolf and Trillmich 2007), which would provide the occasion for acclimation. This finding is consistent with a recent meta-analysis which found that across mammals, birds and lizards, populations that live among humans are more tolerant of human presence than populations that do not (Samia et al. 2015). If Galápagos sea lions are indeed acclimating to human disturbance, this may have both positive and negative consequences. Acclimation can prevent or lessen stress due to human disturbance. But acclimation can also increase conflicts between humans and sea lions. Sea lions who are very comfortable around humans are more likely to occupy fishing boats, public parks and walkways, and waterfront businesses.

Another possibility is that sea lions with a low tolerance for human presence simply avoid spending time at sites where there are large numbers of people. This is a concern because Galápagos sea lions exhibit long-term and fine-scale site fidelity. Females, in particular, develop preferences for particular spatial areas within haul-out sites. They return to these fine-scale sites year after year, and even appear to transmit preferences for specific sites to their daughters, which may also be a mechanism for transmitting social connections (Wolf and Trillmich 2007). Human disturbance may interfere with this transmission of haul-out site preferences. A daughter who is less tolerant of humans than her mother is, for example, may choose a haul-out site where there are fewer people, even if that means leaving her mother's preferred site and the social connections that come with it.

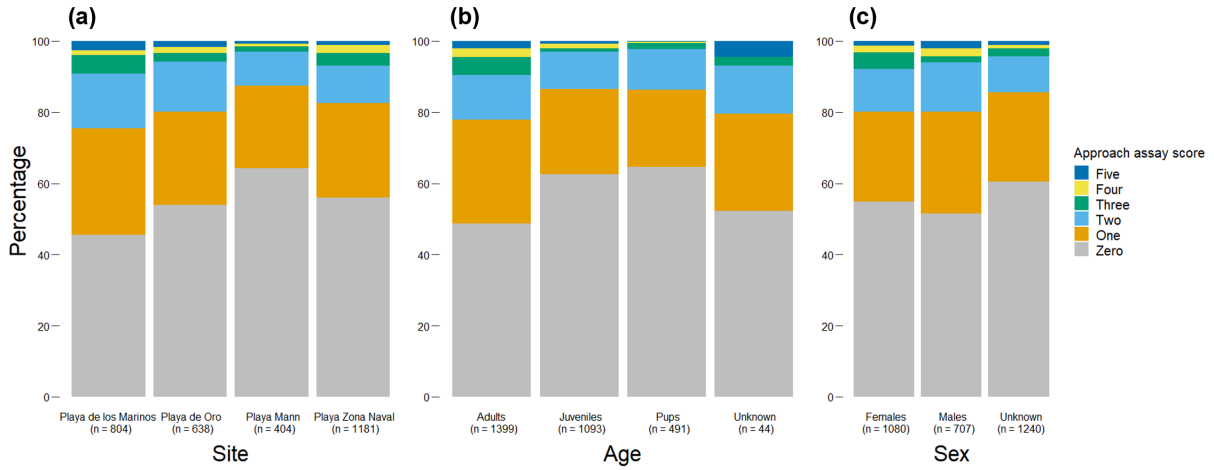

Figure 2. Stacked bar plots showing the percentage of approach assay scores across sites (A), ages (B) and sexes (C).

Our data does not allow us to discriminate between these two explanations – acclimation or low tolerance for human presence. But in a recent study of Galápagos sea lions on the uninhabited islet Caamaño, DeRango et al. (2019) found inter-individual differences in Galápagos sea lion pups' reactions to human approach. Their data suggests that tolerance for human presence varies among individual sea lions, and that these differences in tolerance emerge early in life and remain stable over time. These differences may well affect individual haul-out site choices later in life.

Our second main finding was that aggression towards humans decreases with group size, while aggression between sea lions (the number of growls, barks or challenges) increases with group size. The levels of aggression towards humans or other sea lions were not different across sites and therefore not likely directly linked to human disturbances at the haul-out sites. It is, however, possible that human activity not quantified by this study affects individual haul-out site choices and, by extension, group size at a site.

Although we did not attempt to quantify stress levels, increased aggression, either between sea lions or toward humans, can increase stress levels. Elevated stress levels are energetically taxing and can impair immune function (Eskesen et al. 2009). Aggression related to group size is, therefore, a concern, especially if group size is affected by competition over limited space due to a growing human population. This finding underscores the importance of protecting current haul-out sites and increasing the available space for sea lions to rest so that individuals can avoid crowding together. Indeed, Galápagos sea lions will readily use artificial floating platforms as resting places (Montero-Serra et al. 2014).

These results are relevant for future initiatives aimed at understanding and reducing the effect of anthropogenic activity on Galápagos sea lions. In addition to protecting existing haul-out sites and increasing possible resting areas, we suggest attempting to reduce the interactions between the human and sea lion populations. It is likely that most beach visitors are not aware they are potentially disturbing the sea lions. Signs and other educational material could be mounted near beaches, especially the most crowded areas, to improve awareness. Future studies might track individuals with the goal of determining whether sea lions are actually acclimating to human disturbance, or if sea lions with a low tolerance for humans simply avoid crowded beaches. Additionally, future studies should quantify stress levels across beaches with varying levels of human disturbance and across sea lions resting in groups of varying size. We hope that our Community Science approach will lead to more engagement with the local community, including involvement of Galapagueños in future environmental management decisions. Although the local communities are the biggest source of stress on the islands, they are also positioned to be the most effective protectors.

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Author contributions – J. T. Walsh and Karen Kovaka are joint first authors. All authors conceived and designed the experiments. All authors worked with the high school students to collect the data, though EV took primary responsibility for this. JTW analyzed the data. KK and JTW wrote the manuscript; other authors provided editorial advice. DSW and MW secured funding.

Conflict of interest – The authors declare that they have no conflict of interest.

Ethical approval/permits – This study conformed to the guidelines set out in the 'Plan de Manejo para la Conservación de los Lobos Marinos de la Isla San Cristóbal' and the research protocol was approved by the Galápagos National Park under an agreement between the Dirección del Parque Nacional Galápagos and the Univ. of Pennsylvania.

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