Too much of a good thing? A landscape of fear analysis for peccaries reveals hikers act as a greater deterrent than thorny or bitter food

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Abstract

To study how wildlife perceive recreational users, we studied the habitat selection of a human commensalist, the collared peccary (*Pecari tajacu* (Linnaeus, 1758)). We measured peccary activity patterns in a high-human-activity area (Tumamoc Hill Desert Laboratory in Tucson, Arizona) using a landscape of fear analysis. We examined whether the perception of risk from human activity interacted with the anti-predator mechanisms of local plant species, in both chemical (tannin) and mechanical (thorns). The peccaries avoided food stations near a hiking trail. The population foraged less near houses, i.e. moderate human activity, than in the perceived safety of a small wadi. Plant defense treatments impacted the harvesting of food only in the safe zone, suggesting that risk trumps food selectivity. The strong effect of the hiking trail on habitat selection in this disturbance-loving species is an indicator of a much larger impact on sensitive species in conservation areas.

Key words: Javelina, Giving Up Density; Disturbance; Conservation; Plant-Animal

Interactions; Ocotillo; Creosote; *Pecari tajacu*; Collared Peccary

Introduction

As the earth enters the Anthropocene, truly wild lands have become scarce (Steffen et al. 2011). Globally, public lands are increasingly used for recreation. As a result “nature” is being tailored for car-bound visitors. Bryson (1998) highlights the problems that modern eco-tourism creates: conservation areas are tailored to visitor recreation and not necessarily for the protection of natural resources. Some of the major negative impacts that visitor traffic causes in conservation areas includes habituation (and dependency of wildlife) to the visitor generated resources (Mallick and Driessen 2003), habitat fragmentation by access roads and trails (Ament et al. 2008), reduction in association of humans as risk (Romero and Wikelski 2002), and many more.

Wildlife managers regularly make the assumption that human activity has a negative impact on the wildlife they are managing (e.g. Riley et al. 2003; Ciuti et al. 2012). This remains an assumption until scientists use ecological tools to actually investigate individuals in the managed populations. Here, we address that issue by studying collared peccaries (*Pecari tajacu* (Linnaeus, 1758)) in a US National Historic Landmark. We can expect the impact of the same human activity on rare, shy species (e.g., deer, antelopes, large carnivores) of greater need for conservation, will be much magnified compared to peccaries, which are neither shy nor rare.

The implications of this study can be used to model studies for conservation lands globally. Additionally, the method that this study tests, a landscape-of-fear analysis, can be applied as a regular measure of habitat selection (e.g. Abu Baker and Brown 2013, Coleman

and Hill 2014). Despite using human activity as the variable of disturbance, this study does criticize recreation. Instead, we wish to observe and quantify dispassionately the impacts of human activity as perceived by the wild populations themselves.

The human dominated landscape favors species that are willing to forage on a varied diet, especially rubbish (garbage). This selective pressure has epidemiological consequences on the species (Kruszyk and Ciach 2010, Flint et al. 2016), as well as bringing aggressive and disturbance-loving species into greater contact with humans (Herrero et al. 2011, Barrett et al. 2014).

We studied the population of peccaries on Tumamoc Hill, a natural area, which lies within the city limits of Tucson AZ. The Hill is managed by the University of Arizona for the purpose of long term ecological monitoring and public recreation. On average, 1500 visitors per day visit its single pedestrian trail during the cooler seasons. Most visitors (hikers and joggers) ascent the trail to the observation point 230 m above the city.

Research aims and predictions-

We asked three major questions:

(1) Do the peccaries, known to be bold animals, avoid the high human pedestrian traffic near the trail? (2) How does human activity of hikers compare to human activity in the form of houses? (3) Last, we ask whether environmental risk impacts the choice of food patches based on metabolic costs (risk of injury from thorns, and digestion of tannic foods)?

We predict that the peccaries would rather forage in the safety of the wadi compared to areas that are exposed to human activity (*cf.* Bellantoni, 1991). Additionally, the peccaries should prefer the areas with limited human activity (the houses) compared to the trail, where there is a constant stream of people.

Given that peccaries are known to forage on pricklypear pads (Theimer and Bateman 1992), we expected their foraging to be less affected by our manipulation of tannic acid content (see below) than by our manipulations of thorniness. Despite this expectation, we predict that these patch treatments will be of secondary importance to risk of predation, i.e. be significant only if they perceived low environmental risk.

Methods:

Site-

The Desert Laboratory (aka Tumamoc Hill) in Tucson, AZ (N 32° 13' 13.017", W 111° 0' 14.109") was established in 1903 by Andrew Carnegie with the blessing of President Theodore Roosevelt. It sits on an archeological site of settlements dating back to 500BCE. Severely overgrazed for half a century, its staff wanted to observe its return to a natural state and fenced it away from human exploitation in 1906 (making it a restoration ecology project — the world's first (Jordan and Lubick 2011, p.64) Although apex predators, pumas and jaguars, were sighted at this site historically, the increased human development does not make it prime habitat for them today. Therefore, the major threat to our peccaries is human activity.

We laid out a grid of foraging stations centered on a wadi where a resident herd of peccaries (nine individuals as of October 2016, of which three were under a year old) can be regularly observed bedding. The grid (100 × 100 meters) was located in the area between the hiking trail and a row of houses with two dogs that barked regularly (Figure 1 A and B). We positioned the stations near the houses 50m from the houses (20m from the road that separates the housing development from the landmark). We positioned the stations near the trail 20m meters from the trail, just hidden from the hikers on the trail.

Study Species-

The collared peccary is a common human commensal in the arid zones of the southwest USA. They are found from Arizona, Texas and New Mexico through the neotropical regions of Latin America and throughout Amazonia (Ingmarsson 1999). These social mammals live in herds of 5-15 (usually a family group) where the dominant role is filled by a male. They are primarily herbivorous and in Sonoran Desert and feed on prickly pear cactus pads, bulbs, roots and insects (Bellantoni 1991). Near urban environments in Arizona they prefer the shaded areas of wadis, where they spend the hot hours of the day. They are crepuscular foragers (Ticer et al. 1998, 2001). In the urban environment they are known to come into contact with humans and exhibit aggressive behaviours, as evident by a high number of pet and human casualties as well as property damage (Wright and Ordway 1989).

Experimental Design-

The grid of nine stations was laid at 50m intervals, with slight variation to meet the landscape features.

We used a Giving-Up Density (GUD) approach (*cf.* Bedoya-Perez et al. 2013), using foraging in artificial diminishing-returns food patches to measure the risk associated with the physical location of the patch as it interacts with costs of foraging (injury, ease of finding food etc.) at that location (Brown 1988). The greater the costs at a particular location, the earlier the animals give up foraging at that station, consequently leaving a greater amount of food behind.

Each of GUD stations included three foraging patches. Each built each patch using 1 gallon plastic cylinders. We staked the GUD patches at 1m intervals in a triangular formation secured with 40 cm metal cable to a stake. Each cylinder was drilled with 20 ½” holes that allow the dispersion of corn kernels when rolled.

We filled the cylinders with 2 liters of pink Styrofoam packaging peanuts to create a foraging system that provided diminishing returns: the more a cylinder was foraged, the harder it became to retrieve the remaining food.

To each cylinder three, 20 cm, bars were attached with zip-ties based on the three foraging conditions: control (irrigation piping), tannins (Creosote bush) and thorns (Ocotillo) (Fig. S1). The order of patches was randomized between stations.

The ocotillo (*Fouquieria splendens*) is a common perennial shrub of the Sonoran and Mojave Deserts. It has long woody branches that stem from a common stubby trunk. Each branch is densely covered with 3cm long thorns arrayed at intervals of 1.5cm; these protect the green leaves that usually do not exceed 3cm in length. Individuals may exceed four meters in height.

The creosote (*Larrea tridentata*) is perhaps the most common shrub in the Sonoran and Mojave Deserts. It has yellow sticky resin and it grows in a tangle of branches to a height of 2-3 meters. It is easily identified by its smooth bark, and by small 10 mm resinous dark green leaves. The creosote's resin has high tannic contents that repels herbivorous insects and rodents (Mangione et al. 2000, Medina et al. 2012).

Data Collection-

Each night, an hour before sunset we mixed 300 grams of corn kernels in with the packaging peanuts. In addition, we scattered two fistfuls of kernels in the vicinity of the three patches to attract the peccaries to forage at the stations. To extract the corn, the peccaries rolled and handled the cylinders using the treatment bars for leverage, thus coming in contact with the tannins and thorns. We collected the remaining corn from the patches an hour past sunrise. We weighed the kernels, sifted from the peanuts, in the lab to an accuracy of ± 2 grams using an electronic kitchen scale. The mass of food remaining after the foraging period (combined sunrise and sunset) was the measure of the GUD we used. We logged the daily

high and low temperatures to use as covariates in our analysis. We removed the one day where a precipitation event occurred and extended the experiment by one day to compensate for it.

We set up multiple stations three weeks prior to the experiment to habituate the wild peccaries to their design and to test the efficiency of the systems in recording variation in foraging behaviours. We installed the stations four days prior to the start of the experiment (25/10/2016-28/10/2016) and provided extra food near each station to draw in the peccaries, encouraging them to visit the stations nightly.

Data Collected-

We collected data for 15 nights (29/10/2016-12/11/2016). Each night we recorded whether there foraging activity occurred at each of the GUD stations (see below), we collected the remaining kernels to be weighed for the GUD. In addition, we recorded the daily high and nightly low temperatures using a field thermometer.

Data Analyses-

We analyzed the data in three ways:

(1) A landscape of fear (LOF) analysis. LOFs are maps on which the perceived risk of the peccaries is mapped over the physical features of the landscape.

(2) A log-linear model analyzing the foraging activity compared to the proportion of foraged patches (cylinders).

(3) A spatially-implicit generalized linear model (GLM) testing patch use (average GUD) against human-activity treatments and deterrent type.

We ran a GLM for the three spatial variables of the experiment: (1) zones as longitude (east-west), (2) repetition position for latitude (north-south), and (3) station effect as the

interaction of longitude and latitude. We used the daily high and low temperatures as covariates.

Then we charted the LOF using the protocol from Iribarren and Kotler (2012) and Bleicher (2014) creating a heat map using GUDs as the Z-variable in a three dimensional scatterplot. We generated the raster by applying a distance weighted least squares (DWLS) smoothing function at a tension of 0.5. We then superimposed the LOF heat map on the physical landscape, as represented by an aerial photograph from Google Earth®.

Activity:

We determined whether a patch was foraged by peccaries based on hoof-prints found in the vicinity of each station. We estimated peccary activity by tabulating the number of foraged versus unforaged patches for all combinations of zones (near houses, near trail and in the wadi) and deterrent type (ocotillo, creosote and control) to yield a multi-way contingency table. We used this multi-way contingency table to perform a log-linear analysis that examined direct and interactive effects of predation risk and metabolic costs on the number of patches foraged.

Patch Use:

We analyzed patch use with GUDs. To control for possible pseudo-replication among patches and within a zone, we averaged the GUDs in each deterrent treatment within each zone for each collection day to form the dependent variable. This provided nine GUD means per night (3 zones x 3 deterrents). For these means, we included both food patches, foraged and unforaged, using 300 g as the GUD for unforaged patches. We used another GLM to evaluate whether the GUDs varied with the perception of safety based on the location of the stations (zones), or metabolic costs from anti-herbivore strategies of the local vegetation (deterrents), and from the strong effect of temperature on the foraging patterns. In addition

we tested for the differences observed based between days of the experiment, nesting this variable within the experimental zones. Lastly, we included the interaction of safety and metabolic variables to our model. For significant variables and interactions we performed post-hoc pairwise comparisons using a Tukey's Honestly Significant Difference Test (THSD).

Results

(1) Landscape of Fear

In the analysis of variance for the spatial variables GLM, ($N=378$, $R^2=0.35$), we found significant main effects to the location along the x -axis (correlated with the zone) and to the covariate of daily maximum temperature. The minimum nightly temperature was marginally significant ($P=0.051$) showing a trend of decreased foraging as temperature increased. However, variation along the y -axis (the repetitions) was not significant (Table 1). The station effect (i.e. x by y) was significant, suggesting spatial dependency of the response of peccaries to the risk factors measured.

The lack of variation within zones likely suggests that the physical features which we expect are dividing the land into zones (between the safety of the wadi and the risky flats) are the same demarcations perceived by the peccaries. The overlay of the LOF map on the aerial photograph (Figure 2) shows a clear pattern of safety, i.e. more foraging occurring along the wadi. The deterrent treatments interacted significantly with the y position.

(2) Activity

The peccaries' activity, as measured by the proportion of patches foraged, was clearly influenced by the human activity zones (Table 2; Figure 3). Only 38.8% of the total available patches were foraged near the trail, in comparison with 98% near the houses and 85.8% in the

wadi. The plant foraging deterrents, as metabolic costs, significantly interacted with the human activity zones, as safety related costs.

(3) Patch Use

On average, the peccaries foraged 1/3 of the available corn kernels in the patches, reducing them to a mean GUD of 231.6 ± 4.1 g. The GLM ($N=108$, $R^2=0.935$) testing the environmental risk and metabolic costs found significant impact to the zone in which the patches were located. However, we did not find a significant effect to the plant deterrent treatments (Table 3). The interaction of the metabolic and safety cost variables was statistically significant. However, the THSD showed that the majority of variance was generated between zones and not within them. Nesting the experimental day within zones strengthened the model, predominantly measuring the impact of the temperature on the foraging (Fig. S2).

the post-hoc, pairwise comparison showed that the foraging of the peccaries was greatest (lower GUDs) in the wash then by the houses (THSD p-value =0.05), and greatly diminished near the hiking trail (THSD p-value <0.001 for both) (Figure 4 A).

Two major trends can be observed from the interaction of zones and deterrent:

(1) When exposed to risk from humans the peccaries appear to prefer the patches with the thorny ocotillo (Figure 4 B). This pattern was statistically significant near the houses (THSD p-value=0.05), but only trended near the trail.

(2) In the wadi, with the lowest GUDs we found the strongest evidence that the plant deterrents impact peccary foraging. Here, the peccaries preferred the control to the tannic creosote (THSD p-value= 0.04) or the thorny ocotillo (THSD p-value=0.002).

Discussion

We observed a series of interacting factors that influenced the foraging behaviour of the peccaries. We found strong support for the significance of the physical attributes of landscape; these vary in the degree of safety they provide. On the other hand, patch quality-- in this scenario herbivore deterrent mechanisms-- had a lesser impact, but did interact with the physical structure of the landscape of fear.

We arranged the rest of this discussion to address the implications of this study on two levels: evolutionary interplays within three trophic levels, plants and herbivores and their predators and implications for wildlife conservation.

Evolutionary Constraints and Foraging Ecology

In this subsection we will discuss two major effects: the spatial pattern of risk in response to human activity; and the interaction of that risk with patch quality.

Risk:

As a result of natural selection, many prey species can discern the level of activity shown by their predators and adjust their habitat use appropriately. Our experiment showed that collared peccaries, robust, disturbance-loving herbivores, clearly respond to human activity as a signal of predation risk. We saw a clear correlation between levels of human activity and the level of “fear” exhibited by the peccaries’ foraging patterns.

Predator effects are often not additive but rather exponential (Embar et al. 2014b). As the number of predators increases, the prey response will plateau, as was found with gerbils responding to a titration in numbers of owls in an aviary (St. Juliana et al. 2011). A similar pattern was observed in risk averse desert pocket mice whose landscape of fear only slightly increased in risk elevation when owls were added to a snake dominated vivarium (Bleicher 2014). Our experiment was not suited to finding the rate of change because our zones were

categorical in nature: low human activity near houses and intense human activity near the trail. Replicating this experiment in a site with trails of varying human activity levels should reveal the pattern.

The wadi environment is a preferred bedding habitat for peccaries (Bellantoni 1991), and our experiments suggest that this environment is perceived as safe even close to human activity (70 meters from trail or houses). The wadi provides safety in two major ways: (1) the vegetation density is higher due to the accumulation of water, (2) the wadi is physically hidden as a depression in the landscape below the sightline of most prowling predators.

Although vegetation density is greater in ephemeral wadis compared to their surrounding habitats wadis (Shaw 2015), most food of peccaries comes from plants that grow on the flats above. Notice however that the wadi provides other resources in addition to safety. The temperature at ground level in the sun at the study site can exceed temperatures of 55°C. But the vegetation cover of the wadi provides a cooler environment for the peccaries. Similar patterns of confounding observations can be found in marsupials in central Australia, and other dryland species that migrate long distances daily between the crests of sand dunes where they forage and burrows they occupy in swales (*e.g.* Dickman et al. 1995; Haythornthwaite and Dickman, 2006). In this case, the vegetation stabilizes the ground in the swale allowing the construction of burrows that would collapse on the dune crests. Our experiment shows that given supplementary food in the wadi, the peccaries could avoid the risk associated with foraging on the flats exposed to humans and other predators. This manifested itself in the preference of females and young to remain in the wadi.

Deterrents:

Environmental stochasticity is one of the major drivers of species extinction (Lande 1993, Ovaskainen and Meerson 2010). As a result, when observing the species in environments with large temperature fluctuations, we expect to find high plasticity in foraging behaviours and preferences. When times are dire, animals should be willing to increase the risk they take in foraging to compensate for the low energetic intakes (Embar et al. 2014a). These patterns carry over to risk of injury from handling difficult food items, change to opportunistic foraging and even to consumption of mildly toxic (tannic) foods (Speiser and Rowell-Rahier 1991).

When resources were abundant in the spring, ibex distinguished between thorny and safe food patches. Moreover, they responded with aversion to tannic food presumably because tannins can be mitigated only by water, and water is a limiting resource in the desert (Kieckbusch and Kotler 2016). Aversion to tannic food is logical given that spring in the Negev Desert is the beginning of an eight month dry season.

Notice the important difference between the tannin treatments we used. In the ibex experiments, the tannins have been incorporated into the consumable pellets that the ungulates foraged on. In the present experiment, we relied on fragrant creosote to transmit its cue of high tannic food. If we had used pellets soaked in tannin, perhaps we would have seen a stronger impact than we observed.

In our experiment with peccaries, the primary constraint, given the proximity to humans, was safety. In the wadi the peccaries were more responsive to the dangers of thorns or tannin-rich plants containers. The difference between patches with ocotillo, creosote and the control were smaller under condition of human disturbance, suggesting that counter-human vigilance behaviour makes the peccaries less selective foragers.

Conservation-

Peccaries have expanded, and are expanding, their range from the tropics to desert lands predominantly due to human related habitat manipulations (Taylor 1999, Albert et al. 2004). Ranching practices have favored the range expansion of the pricklypear cactus (Stoddart and Smith 1955, Brement 1968) and following that favored food, so did the collared peccaries (Theimer and Bateman 1992). Despite this commensalistic tendency, we observed a clear abhorrence for the areas where humans were constantly active.

From the strong, visible impact that the hiker activity had on the peccaries, we can infer that shy and more disturbance-susceptible species will be even more heavily influenced. However, in a management experiment, O'Brien et al. (2005) found that fire management reducing food availability had a much greater impact on habitat occupancy of peccaries than did predation risk from coyotes. We suggest a greater complexity than this. At our site, we observed a high coyote activity in prints, scat and on-trail-cameras (Bleicher and Rosenzweig, unpublished). Coyotes pose a low predation risk to the peccaries, as they are a dangerous prey and not worth the risk when easier prey is available.

We found that the peccaries are very aware of predation risk, and in our case, the predator association is human. On the other hand, the availability of limiting resources, unavailable near the shelter (cliffs) drives the ibex to riskier environments in the dry season, *i.e.* water and shade (Hochman and Kotler 2006, Tadesse and Kotler 2011, Kieckbusch and Kotler 2016).

What do the high GUDs near the hiking trail tell us? We observed an inverse foraging trend in the three stations near the trail compared to those in safe habitats (Fig. S2). In the riskier habitat foraging decreased as heat stress (mean high and low temperatures) increased. In safer habitat (wadi and houses), the trend was opposite; the warmer the temperatures, the

more the peccaries foraged. This suggests an effect of intraspecific competition. Observing the terrain surrounding the stations, we saw that the number of foragers was greatest in the wash, whereas only the dominant male would venture out to the trail. This pattern, of males venturing away from safety has been well recorded in many species (*e.g.* Grignolio et al. 2007).

Behavioural (psychological) and neurological studies focusing on post-traumatic stress disorder (PTSD) use models of measuring risk perception under varying conditions by the willingness of rats to respond to novel objects. A few of these studies found that the rats when exposed to environmental stress, or stressed artificially by hormone injections, were less likely to explore novel objects (Rosellini and Widman 1989, Vargas-López et al. 2015). In addition, the longer the exposure to stress, the less the risk-taking behaviour (Saul et al. 2012). Our experiment showed a second inverse trend between safe and risky habitats. The peccaries preferred the resource patches with natural treatments (creosote and ocotillo) in the risky environment compared with the control. Meanwhile peccaries foraged control patches to a greater extent in the safe wadi. Our interpretation here lies in the association of the novel objects with the human activity. Despite all patches being constructed of plastic cylinders, under stressful conditions the patches covered in woody vegetation would appear a more natural source of food.

Following this study we can provide a few conservation-based recommendations to the management of the site. (1) If the bold peccaries perceive the human recreation as ample threat, one that merits avoidance, then the trail is likely perceived as an even greater threat by more sensitive species. As such, it is likely acting as a barrier to movement of both peccaries and other wildlife. Reducing the impact of the recreation on the wildlife, by regulating hours of visitation away from sunrise and sunset could increase the functionality of Tumamoc Hill as a wildlife sanctuary within the city limits. Alternately, providing well camouflaged

culverts beneath the trail could increase habitat connectivity and reduce the impact of the trail. (2) Heat-stress exacerbated the negative-impact of the trail. We suggest that regulating recreation as temperatures increase could help reduce stress on the wildlife. (3) The peccaries associated the houses and trail as low and high risk respectively. This suggests that the rate of human activity may influence the level of stress it causes the wildlife. We suggest a follow-up study titrating the number of hikers on the trail to compare and contrast human activity level with human activity type.

Conclusion-

Management in conservation areas depends on recreation to sustain natural resource management both fiscally and politically. A balance needs to be found between the needs of the wildlife and the needs of the visitors. In this example, we found encouragement in that, only 70m from the trail the collared peccaries found a zone of safety. However, our analysis suggests that species more sensitive to disturbance than peccaries would suffer greatly from intense human activity. We suggest that the correlation between peak human activity and the crucial foraging times for desert species (sunset and sunrise) exacerbates the effects of the humans on wildlife behaviour. We also conclude that human disturbance acts similarly to stressors from diminished resources leading to less selectivity of food patches.

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Table 1.

General Linear Model ($n=324$, $R^2=0.356$) testing for spatial and environmental patterns in peccary (*Pecari tajacu*) foraging. The model shows significance to heat stress, the human activity zones (x) the location of foraging stations ($x \times y$). We find that the plant defense mechanisms (deterrent) impacted the foraging in specific locations along the y -axis (repetition of human activity zone treatments).

Variables	SS	df	MS	F	P-value
Temp Max*	40,598.791	1	40,598.791	10.306	<0.001
Temp Min*	15,154.619	1	15,154.619	3.847	0.051
x-coordinate	380,913.802	2	190,456.901	48.347	<0.01
y-coordinate	15,915.414	2	7,957.707	2.02	0.134
Deterrent	388.784	2	194.392	0.049	0.952
$x \times y$	58,612.068	4	14,653.017	3.72	0.006
$x \times \text{Deterrent}$	27,098.198	4	6,774.549	1.72	0.146
$y \times \text{Deterrent}$	69,223.253	4	17,305.813	4.393	0.002
$x \times y \times \text{Deterrent}$	49,112.432	8	6,139.054	1.558	0.137
Error	1,162,125.351	295	3,939.408		

Abbreviations: SS- Sum of Squares, df- degrees of freedom, MS- mean squares, Temp- temperature, max- maximum, min- minimum, deterrent- patch quality (thorny, tannic, control), *covariate.

Table 2.

Log-linear analysis for peccary activity as measured by the ration of foraged to unforaged patches. This analysis shows that risk from human activity affects the likelihood of patches remaining unforaged. In addition the plant predator-deterrent mechanisms only impact the foraging when combined with predation risk factors.

Variables		G^2	df	P -value
Zone		127.84	2	<0.001
Deterrent		0.28	2	0.8694
Zone	× Deterrent	131.58	12	<0.001

Table 3.

ANOVA Table for GLM using daily averages for human activity zones x plant deterrent treatments ($n=108$, $R^2=0.968$). This spatially explicit model strengthens the findings suggesting that human activity was the major factor influencing peccary foraging. Plant defense mechanisms influenced the peccaries only when examined in interaction with safety variables. The temperature variation (expressed by the experimental day) had a different impact based on the human activity pattern in the station where measured. This suggests that risk taking behaviour is influenced by physical stress from temperature fluctuation.

Variables		<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i> -Value
Zone		135,954.389	2	67,977.194	197.496	<0.001
Deterrents		29.852	2	14.926	0.043	0.958
Zone	× Deterrent	10,057.519	4	2,514.38	7.305	<0.001
Zone	(Day)	183,055.61	33	5,547.140	16.116	<0.001
Error		22,716/926	66	344.196		

Figure Legends:

Figure 1. Study site and set-up. A*. Map of the northern region of Tumamoc Hill Desert Laboratory; Tumamoc Hill Rd (UTM coordinates 12S 499448.91255836 3564167.3684404). is the paved trail on which approximately 1000 visitors hike daily, the black rectangle signifies the location of the experimental array. B*. The triangles represent the location of each of the stations of the experiment; the distance between stations was approximately 50 meters based on terrain conditions. C. the setup of a feeding station (within the wadi) with a Peccary foraging at the station. We positioned each cylinder 1 meter away from other cylinders (with slight variation based on our ability to drive a stake to a secure enough position).

Figure 2. Landscape of fear overlaid on the aerial photo of the study site. The contour lines reflect perceived risk in the peccary population foraging on Tumamoc Hill (UTM coordinates 12S 499448.91255836 3564167.3684404). Warm Colours represent danger: Red (GUD of 300) and Yellow (250). Cold colors represent safety: light green (200) and dark green (<150).

Figure 3. Mean percent of patches foraged as distinguished by the spatially explicit human activity zone $\pm$ SE. The percentage of foraged stations is associated with time allocation: the safer the area the more trays will be foraged.

Figure 4. Mean giving up densities (GUD) measured in grams as collected at (A) different human activity zones (low/wash, intermediate/ houses, high/trail) and (B) as impacted by plant defense treatments (creosote/ tannin, ocotillo/ thorns, control) within each zone $\pm$ SE. Higher GUD suggests higher costs perceived by the peccaries associated with those sites, likely due to (A) risk of predation and (B) where metabolic and predation costs interact.

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18x13mm (300 x 300 DPI)

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280x282mm (300 x 300 DPI)

Figure 3. Mean percent of patches foraged as distinguished by the spatially explicit human activity zone $\pm$ SE. The percentage of foraged stations is associated with time allocation: the safer the area the more trays will be foraged.

176x115mm (144 x 144 DPI)

Figure 4. Mean giving up densities (GUD) measured in grams as collected at (A) different human activity zones (low/wash, intermediate/ houses, high/trail) and (B) as impacted by plant defense treatments (creosote/ tannin, ocotillo/ thorns, control) within each zone $\pm$ SE. Higher GUD suggests higher costs perceived by the peccaries associated with those sites, likely due to (A) risk of predation and (B) where metabolic and predation costs interact.

215x261mm (300 x 300 DPI)