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Ecology of fear and its effect on seed dispersal by a neotropical rodent

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Predators exert negative effects on prey, besides the act of killing, generating behavioral and physiological costs, a concept known as the ecology of fear. Studies in scatter-hoarding rodents in temperate zones suggests that prey use habitat structure to perceive predation risk. Less is known about how tropical forest rodents perceive predation risk. Here, we investigated whether the Central American agouti perceive predation risk by ocelots through olfactory cues and whether it influences the foraging behavior for *Attalea butyracea* seeds, one of its main food sources. By monitoring tagged seeds, we found that seed dispersal and pilferage was lower in sites with high density of ocelots, in line with the predictions of ecology of fear proposing that scared animals eat less. We also found that pilferage rates in high ocelot density sites seem to be lower during the rainy—transition period but not during dry season when food availability is generally low. However, we did not find evidence that agoutis adjust their cache spacing behavior in response to ocelot density. In an additional experiment to corroborate that agoutis' responses were caused by ocelots' cues, we found lower dispersal rates for seeds placed next to samples of urine and feces of ocelots as compared to controls, during the first seven days. Moreover, agoutis spent less time handling the seeds with ocelots' cues. Here, we discuss potential cascading effects linked to the behavior of agoutis towards predation risk.

Key words: agouti, ecology of fear, ocelot, seed dispersal.

INTRODUCTION

The ecology of fear refers to the indirect negative effects that predators pose on prey, other than killing, particularly the costs associated to avoiding predation which also impacts populations and ecosystems (Brown et al. 1999; Teckentrup et al. 2018). Such fear may lead for instance to a higher cost for reproduction (Magnhagen 1991; Lamanna and Martin 2016), loss of body mass (Pérez-Tris et al. 2004), reduced growth rates (Beckerman et al. 2007; Lamanna and Martin 2016), costs associated to using new habitats (Brown 1988; Otsuki and Yano 2014) or even physiological stress (Clinchy et al. 2013). Overall, the negative effects on prey populations can be summarized as a reduction in foraging rates: scared animals eat less (Zanette and Clinchy 2019).

Thus, negative effects on prey population can have cascading effects within an ecosystem (Suraci et al. 2016). A particular case is seen in animal–plant interactions, where predation risk can influence

the way in which prey can use their habitat (Laundré et al. 2014). In the case of scatter-hoarder rodents, that disperse and consume seeds, scared animals may respond by avoiding risky habitats or reduce foraging activity in those habitats and consequently reduce the rates of seed dispersal and consumption (Lichti et al. 2017). Experimental work on the effects of predation risk in seed dispersal decisions (e.g., cache locations) comes mainly from studies in temperate regions with evidence showing the role of predators' scents (Sunyer et al. 2013) or even a trade-off by using sites with higher predation risks for lower rates of cache pilferage (Steele et al. 2014).

Overall, the consensus is that perception of risk may be driven by habitat structure in diurnal species and it is higher in open habitats (Verdolin 2006). Moreover, foraging activity in those habitats depends on availability of shelters and quality of the sightline (Lichti et al. 2017). However, perception risk based on habitat structure may be species-specific. For instance, with open habitats being perceived as sites with high predation risk by some species (Verdolin 2006) and as low predation risk by others (Abu Baker and Brown 2010). In some cases, coexisting prey species within the same habitat may perceive

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predation risk differently, suggesting that fine-scale landscape structure can generate contrasting predation risk patterns (Gervasi et al. 2013). It seems unclear whether habitat structure would be a good predictor of predation risk in a tropical forest, where open areas are not frequent and obstacles that block sightline are abundant, providing poor visibility as compared to forests in other regions (Anstey 1964). Therefore, prey in the tropics may use different strategies to estimate predation risk in a spatial context. For instance, odor detection may be one factor, as there is significant evidence of the effect of a predator's odor on a prey's response, including evidence from several tropical predators (Apfelbach et al. 2005; Ferrero et al. 2011).

An excellent system to study the effects of predators' cues on prey–plant interactions in the tropics is the agouti–ocelot relationship (*Dasyprocta punctata*–*Leopardus pardalis*, respectively). Agoutis play an ecological role as seed dispersers and consumers of several large-seeded plant species in neotropical forests (Jansen et al. 2012). They scatter-hoard seeds during the fruiting season and retrieve them during periods of scarcity. A large number of those cached seeds are never recovered, which allows successful dispersal for the plants (Smythe et al. 1982). Moreover, odor is of great importance for communication in agouties (Smythe 1989) and it is expected to be relevant for detection of predators as reported for many prey species (Apfelbach et al. 2005; Ferrero et al. 2011). One of their main predators are ocelots that can actively search for them and help to regulate their population size (Aliaga-Rossel et al. 2006; Moreno et al. 2006; Emsens et al. 2014), indicating that they are a selective force for agoutis.

Suselbeek (et al. 2014) discovered that agouties are more active during the periods of the day with lower predation risk by ocelots, but no work has been done for spatial variation in the risk posed by ocelots and its effect on prey populations. The ocelots' behavior of delimiting their home range through scent marking by urine and feces accumulation (Konecny 1989), besides using long-term latrines (Moreno et al. 2012; Rodgers et al. 2015), should signal agoutis of the ocelot presence and influence their foraging activities. Therefore, even if agoutis cannot visually detect ocelots in the typical dense cover provided by their forest habitat, areas with a high density of ocelots will generate stronger olfactory cues.

Here we investigated the interaction seed–prey–predator to investigate whether predators' cues have an effect on the scatter-hoarding and cache pilferage behavior of a rodent prey. We used as a system the seeds of the palm *Attalea butyracea*—an important diet component of the prey: the Central American agouti (main disperser of *A. butyracea*, Smythe et al. 1982; Gálvez and Jansen 2007)—and the ocelot as the predator. Since agoutis should remain for shorter periods and dedicate more attention to vigilance in risky sites (Brown 1999), we hypothesized that agoutis would show: 1) lower seed dispersal rates as a result of less visits to risky habitats; 2) longer dispersal distances to avoid risky habitats, which would be linked to prediction 1 (longer the distance the less time to visit); 3) for cache density, risky habitats may provide protection from pilfering, which could reduce the investment by agoutis in optimal cache spacing (Gálvez et al. 2009), resulting in higher cache densities as compared to agoutis in safer habitats where pilfering by conspecifics may be higher; and 4) again, since pilferers may face greater predation risk (Lichti et al. 2017) by spending more time searching than cache-owners, agouties should pilfer caches less in sites with high predation risk. Moreover, when we evaluated the effect of season, we predicted that agoutis should remove caches slower during the dry season, since predators' cues may be perceived more easily due to lower wash-off caused by rainfall. Importantly, to the best of our knowledge, there are no studies on

how predation risk may influence seed dispersal and cache pilferage by rodents in a tropical forest.

METHODS

Study site and species

Parque Natural Metropolitano (PNM, 8°59'28"N, 79°32'46"O, Supplementary Figure S1) is located in Panama City with an area of 265 ha, connected to the Camino de Cruces national park (4000 ha). We performed two experiments (i.e., seed dispersal, cache pilferage) in PNM, and an ocelot cues experiment (see details below in experiment 3) in Gamboa (9°06'60.00" N, 79°41'59.99" W), specifically in the trail La Laguna and in the forest surrounding the Gamboa village (Supplementary Figure S2). In the high ocelot density site in PNM, three ocelots were recorded by Rodríguez (2018) and in La Laguna, at least three ocelots were recorded in camera traps in 2020 and there is evidence of ocelots moving from the surrounding forest in and out of the village (Moreno comm. pers.).

In PNM, we chose the area around the trail Momótides as the site with low ocelot density based on an 8-months camera trapping census by Rodríguez (2018), in which no ocelots were registered (Supplementary Figure S1). A two-lane road separates the Momótides site from the rest of the park. For the high ocelot density, we chose the area around the trail Los Caobos, in which records of ocelots were frequent (~ 1 picture per week, Supplementary Figure S1). Both trails are approximately 1 km in length. Moreover, we performed a camera trapping census (SpyPoint Solar, Québec, Canada) to corroborate the density of agoutis and ocelots in the study trails. We placed two cameras per site in fixed locations, at least 500 m apart from each other and five meters from the trail. We quantified monthly capture rates and obtained no records of ocelots in our low ocelot density site, and at least one ocelot in our high-density site. For agoutis, we obtained similar records in both sites (Supplementary Table S1). For the high ocelot density sites, we ran experiments 1 and 2 near places where ocelots were photographed by Rodríguez (2018) or during our own monitoring, which were within the average home range of ocelots (Moreno et al. 2012). Since the amount of environmental food can influence the scatter-hoarding behavior of agoutis (Gálvez et al. 2009), we monitored fruiting *Attalea* and counted only one fruiting tree during the study period in the high ocelot density site. Experiments in this trail were run at least 400 m from this tree, a distance beyond the seed dispersal distance normally performed by agoutis (Jansen et al. 2012). We did not observe fruiting trees of other important seasonal species in agoutis' diet: *Gustavia superba*, *Dipteryx oleifera*, or *Astrocaryum standleyanum* (Smythe et al. 1982; Forget 1992). Given the apparent effect of habitat structure in the perception of predation risk (Verdolin 2006), we estimated habitat structure by comparing visibility in both sites following a modification from Anstey (1964), which consisted of measuring the largest distance over which a cardboard target (40 × 12 cm) can be seen in a horizontal line at the understory level (45 cm), replicated ten times per site. We did not find differences in visibility between sites (Supplementary Table S2).

Seed dispersal

We placed tagged seeds in order to track them in sites with low or high ocelot density. This allowed us to monitor dispersal rates, dispersal distances, and cache spacing. We collected *Attalea butyracea* fruits directly from the ground or on a tree by using a pole saw. We manually removed the exocarp and kept them in water during 48 hours in order to remove the mesocarp. Then we let the seeds

dry under the sun for 48 hours. We then assembled batches of 20 seeds of similar size and each seed was drilled a 1 mm hole in the distal side, to which we attached a 50 cm green nylon thread with a 15 × 2.5 cm pink-colored flagging tape attached to the other end, a standard protocol for quantifying seed dispersal (Jansen et al. 2014). Each seed was identified with a unique identity number which was written on the flagging tape. The batches were placed in grids of 2 × 10 seeds haphazardly and we placed 5 batches per site (low vs high ocelot density) during the rainy (3 October—November 2019) and late rainy season (hereafter: transition, 27 November—26 January 2020, [Supplementary Figure S1](#)). That represents ten replicates per ocelot density treatment (200 seeds per treatment). We monitored the seeds at 1, 2, 3, 4, 7, 9, 18, 28, 38, and 49 days after placement during the rainy season and at 1, 2, 7, 16, 23, 31, 43, 51, 57, and 61 days during the transition. We did not include the dry season since this period is normally out of the fruiting phenology of the species (Adler and Lambert 2008). We searched the surrounding area of the batches for the flagging tape tag up to a distance of 45 m, which revealed the location of the cache and we mapped each cache by using an ultrasonic range-finder (Haglöf DME 201, Haglöf Inc., Madison, WI, U.S.A.) and a precision compass (Suunto KB-14, Suunto Oy, Vantaa, Finland). With the locations of the caches, we estimated cache spacing by calculating the minimum spanning tree (MST), which is the structure that connects all the points (caches) with the minimum total distances without any cycles. We computed MSTs with the function `ComputeMST` (library `emstreeR` in R) and we obtained an averaged nearest-neighbor distance (NND), which was used to compare between sites. Smaller NNDs indicate a higher cache density. As a second estimation of cache spacing, we use a minimum convex polygon (MCP), which encompasses all the mapped caches. Cache density is expressed as the total number of caches divided by the area of the MCP. We and others have used both methods before to estimate caching areas (Gálvez et al. 2009 and references therein).

Cache pilferage

In order to quantify pilferage rates in sites with low or high ocelot density, we mimicked agouti caches by burying seeds approximately 5 cm below the ground surface. Caches in this experiment were placed five meters from batches in experiment 1. We created one 2 × 5 grid of caches per site separated by 2.5 m, similar to previous protocols (Gálvez et al. 2009; Jansen et al. 2014). We attached a 60 cm green nylon thread to the seed as described before but the free end was attached to the nearest sapling or tree. This allowed us to slightly pull the cache to check whether the seed was still present. We monitored the caches during the same times that we checked the seeds in the rainy and transition period (experiment 1, see above); besides we checked them at 1, 2, 3, 8, 17, 23, 32, 45, 52, and 63 days during the dry season (29 January—13 March 2019), a period of food scarcity when agoutis rely more on caches (Gálvez et al. 2009; Emsens et al. 2013). We placed 5 batches per season per ocelot density site, which represents 15 replicates per ocelot density treatment (300 seeds per treatment).

Ocelot cues experiment

To corroborate our seed dispersal and cache pilferage experiments, we carried out a third experiment (9 February until 24 February 2021) in which we placed urine and feces of ocelots near the batch of seeds, to monitor dispersal rates. We collected urine samples from one female ocelot in the Parque Municipal Summit by placing 2 × 25 cm strips of fabric placed inside a flat cage (0.5 × 5 × 30 cm) in the corner of

the enclosure that the ocelot used for urination and defecation. The feces samples were collected manually from the same corner. We used urine and feces samples for the experiment the same day of collection. We marked the seeds as described before and placed the batches haphazardly in grids of 2 × 10 seeds. For the batches with the ocelot cue, we rolled one strip of fabric impregnated with urine around a 15 cm stick that was placed vertically at 5 cm from the seeds. We also placed next to the stick approximately 25 cm³ of ocelot feces. For the control, we only placed the stick without an odor cue at the same distance from the seeds. We added the same amount of feces at day 1, 2, and 3; and urine at day 6 after placement of the seeds. We placed a batch every 150 meters, intercalating the type of batch ([Supplementary Figure S2](#)). Moreover, since rodents can be more likely to move seeds away from risky patches before eating them (Lichti et al. 2017), we monitored the seed handling time of agoutis by placing camera traps in front of the seeds in seven of the replicates from each treatment. For this, we recorded the time at which an agouti took a seed until the time that it took one last seed in a feeding bout. We considered recordings as independent if more than ten minutes passed after the last seed was taken and we averaged those handling times per camera. We did not include spatial analysis of this experiment since agoutis and leafcutter ants removed the thread or flagging tape from a large number of seeds, making it difficult to map them after removal. We only found 36 out of 142 and 35 out of 155 removed seeds for the ocelots' cue and controls, respectively.

Statistical analysis

We performed all analyses in R (R Core Team 2021). We carried out a Kaplan-Meier survival analysis (`survreg`) to compare the dispersal rates or pilferage rates in sites with low or high density of ocelots (experiment 1 and 2, respectively); and to compare dispersal rates in batches with and without ocelots' cues (experiment 3). For experiments 1 and 2, we specified ocelot density and season as fixed factors with full interactions. For both experiments, the best model was the one with full interactions, in terms of Akaike's Information Criteria (AIC). We used the function `pairwise_survdif` (package `surminer`) for pairwise comparisons, specifying a Bonferroni-Holm correction. To compare dispersal distances in experiment 1, we used a linear model with log-transformed distances with ocelot density and season as fixed factors with full interactions. Besides, we used a Wilcoxon test to compare NNDs and cache densities from experiment 1. For experiment 3, we specified the treatment (cue or control) as a fixed factor, and we compared the handling time of agouties in front of the camera by implementing an unpaired Wilcoxon test.

RESULTS

Seed dispersal

Agoutis removed all seeds from just two batches, both located in the low ocelot density site. In total, we traced 100 out of 129 seeds and 44 out of 49 seeds removed in low and high ocelot density sites, respectively. The dispersal distance did not differ between low and high ocelot density sites (5.8 ± 7.1 vs 5.9 ± 6.0 m, respectively; $t = -1.67$, $P = 0.1$). However, an interaction between ocelot density and season ($t = 2.1$, $P = 0.04$) indicates that in low ocelot density sites, agouties dispersed the seeds longer distances in the rainy season as compared to the transition period (7.5 ± 8.2 vs 4.1 ± 3.9 m, respectively). We did not detect differences in cache spacing in sites with low or high ocelot density in terms of NNDs (3.4 ± 3.8 vs 1.5 ± 1.4 m, respectively; $W = 30$, $P = 0.6$, [Supplementary Figure](#)

S3a) or cache density (1.2 ± 3.1 vs 1.4 ± 2.4 seeds/ m², respectively; $W = 18$, $P = 0.8$, Supplementary Figure S3b).

Seeds in sites with low density of ocelots showed lower survival than seeds in sites with high ocelot density ($X^2 = 90.1$, d.f. = 397, $P < 0.0001$, Figure 1A). Agouties took seeds faster during the rainy than during the transition period ($X^2 = 18.2$, d.f. = 396, $P < 0.0001$). There was an interaction between season and density of ocelots ($X^2 = 17.1$, d.f. = 395, $P < 0.0001$), indicating that the survival of seeds in sites with high density of ocelots was not influenced by season (Log-rank test: $P = 0.06$; Dry + Ocelot vs Rainy + Ocelot in Figure 1A) but in sites with low density of ocelots, survival of seeds was lower during the transition period (Log-rank test: $P < 0.0001$; Tran.—Ocelot vs Rainy—Ocelot in Figure 1A).

Pilferage

Survival of caches was lower in sites with low density of ocelots than in sites with high ocelot density ($X^2 = 33.6$, d.f. = 297, $P < 0.0001$). Caches tended to survive longer in the dry season as compared to the transition period (Log-rank test: $P < 0.001$; Dry vs Transition, Figure 1B) and the rainy season (Log-rank test: $P < 0.001$; Dry vs Rainy). There was an interaction between season and density of ocelots ($X^2 = 23.9$, d.f. = 293, $P < 0.0001$), indicating that the survival of caches in the dry season did not vary between sites with low or high ocelot density (Log-rank test: Dry + Ocelot vs Dry—Ocelot, $P > 0.05$, Figure 1B) but it was significantly different during the transition (Log-rank test: Tran. + Ocelot vs Tran.—Ocelot, $P < 0.0001$, Figure 1B) and rainy season (Rainy + Ocelot vs Rainy—Ocelot, $P = 0.02$, Figure 1B).

Ocelot cues

The camera monitoring revealed that only agouties removed seeds from our batches, like previous results from this field site (Gálvez and Jansen 2007). During the first seven days, agouties removed seeds at a faster rate from the control batches as compared to batches with ocelot cues ($X^2 = 6.4$, d.f. = 395, $P = 0.01$, Figure 1C). At day 15, removal rates did not differ between both types of batches ($X^2 = 3.1$, d.f. = 395, $P = 0.08$, Figure 1C). We had recorded sequences of seed removal in five batches with ocelots' cues and in seven control batches. Agouties spent more time in front of the control batches than in batches with ocelot's cues (17 ± 10.0 vs 4 ± 3.1 min, respectively; $W = 31$, $P = 0.03$, Figure 2).

DISCUSSION

Here, we provide evidence from three independent experiments that cues produced by a predator induces a reduction in the foraging behavior of a free-living rodent in a natural setting in the neotropics. The high proportion of seeds cached in the ground, together with the camera monitoring indicates that seed removal was done mainly by agouties. Our results suggest that agouties are under longer periods of hunger in environments with high ocelot densities, in line with the idea that scared animals eat less (Zanette and Clinchy 2019) or perhaps agouties rely on other food sources in risky habitats. The strong chemical communication between ocelots by means of scent marking and the use of communal latrines (Moreno et al. 2012; Rodgers et al. 2015) should generate a warning signal that

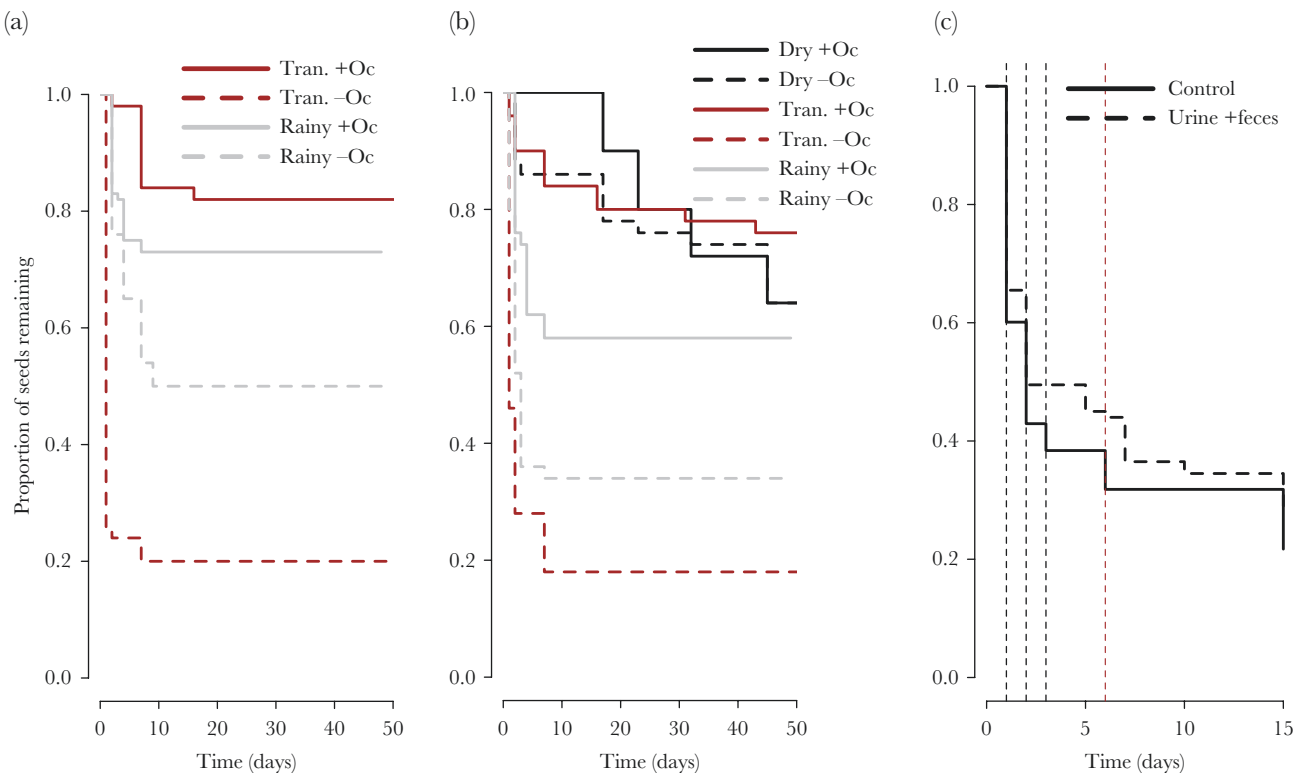


Figure 1

Kaplan-Meier survival curves of seeds in the experiment of dispersal (A), cache pilferage (B) and ocelots' cues (C). For A and B, experiments were carried out at sites with low ocelot density (– Oc) or high ocelot density (+ Oc) during the rainy season (Rainy), transition from the rainy to dry season (Tran.) and dry season (Dry). For C, samples of urine and feces of ocelots were placed next to the batch of seeds (Urine + Feces) or without the samples (Control). Black and brown dashed lines indicate the times for placing urine and feces samples, respectively. See text for statistical details.

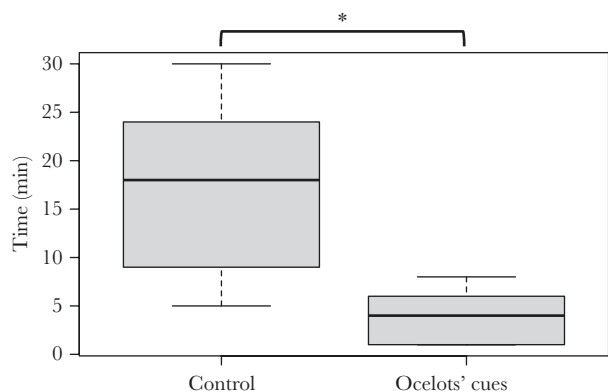


Figure 2

Seed handling time by agoutis in front of the control or ocelot's cues (urine + feces) batches. The * indicates significant differences between batches.

may vary in intensity depending on the frequency of use. During our study, we were able to detect one latrine in the high ocelot density site in PNM, which may be responsible in part of the observed trends in our study. However, we cannot rule out from experiment 1 and 2 other potential causal factors, such as the smaller area of our low-density site or that the closer proximity to the urban zone may induce some unusual seed dispersal behaviors on agoutis.

Our results suggest that agoutis use environmental cues to assess predation risk in a spatial context; even during daytime when they are less likely to encounter ocelots (Suselbeek et al. 2014). Although such adaptive trait would be particularly important against ocelots with unusual daytime activity (Moreno and Giacalone 2006) or in populations in which ocelots' daytime activity is more frequent (Pérez-Irriego and Santos-Moreno 2014; Azevedo et al. 2019). It is possible that ocelot density changes along time (Satter et al. 2019) and we have snapshotted a window of high density; however, for our study site, two independent monitoring in 2017 and 2019–2020 (Rodríguez 2018 and this study) suggests a higher ocelot density for some parts of the park. In places with ocelot population oscillations, this would generate fluctuating cascading effects along time affecting the fitness of the prey and the plant that relies on the prey for its dispersal. For agoutis, who are highly dependent on large-seeded plant species (Silvius and Fragoso 2003; Jorge and Peres 2005; Emsens et al. 2013), reduced access to one of its main food resources (e.g., *A. butyracea*) may impact their reproductive capacity in the long term, as seen in other vertebrate prey (Zanette et al. 2011). However, further work is needed to evaluate whether agoutis use other food sources when access to their preferred food source represents a high risk of predation.

The pulp of this palm is consumed by several species of vertebrates after peeling off the fruit, which facilitates the attack of the seed by the bruchid beetle *Speciomerus giganteus*. Once the seed is buried by an agouti, bruchids are not able to find them (Harms and Dalling 2000). Consequently, in high ocelot density sites, undispersed seeds below the parental tree and remaining for an extended period on the ground after pulp removal would have a higher risk of predation by the bruchid (~ 2 days, pers. obs, Wright 1983), directly affecting the fitness of the palm. A lower proportion of seeds escaping infestation by the bruchids results in a lower proportion of sound seeds that may escape total bruchid and rodent predation and eventually germinate.

Therefore, ocelots may influence the population dynamics of the beetles as well; *S. giganteus* should be more abundant in sites

with high ocelot density given the lower activity of agoutis in those areas. In fact, Peguero et al. (2017) found that the relative abundance of *S. giganteus* was strongly related to the proportion of seeds attacked by rodents, as a result of varying levels of anthropogenic defaunation. These predictions on bruchid abundance will bear if the density of other vertebrates that consume the pulp (e.g., tapirs, monkeys, see Wright et al. 2000)—unaffected by ocelots presence—and the density of the palms remain similar (Visser et al. 2011) across environments with varying densities of ocelots and agoutis.

The longer dispersal distances in the rainy season in low ocelot density sites suggests that *Attalea* seeds are highly valuable during this period (fruiting season, Adler and Lambert 2008) when agoutis are scatter-hoarding food for the dry season (Smythe et al. 1982). However, this value seems to be counterbalanced by the cost of high predation risk, since dispersal distances and dispersal rates were not influenced by season in high ocelot density sites. Dispersal rates did not differ between seasons in the high ocelot density sites.

Few studies have investigated the effect of season on how prey species perceive predators' cues. Hayes et al. (2006) found that three species of Australian rodents avoided predator odor stations more during the dry season. Pilferage was lower during the dry season and if the perception of predation risk is higher during this period (e.g., lower wash-off of cues by rainfall) and pilferers face greater predation risks than the cache-owner—as theoretically predicted (Lichti et al. 2017)—then retrieving their own caches may be a cheaper and safer strategy (e.g., less time spent to find their own caches than the time required for pilfering). Another possibility is that agoutis' surveillance of their own *Attalea* caches (Hirsch et al. 2013) is more frequent during the dry season and they spend less time in pilfering. However, more replicates across years are needed to confirm the interaction between ocelot density and season and its effect on dispersal and pilferage rates.

Additionally, predation risk did not influence cache spacing by agoutis, different from other studies in temperate zones based on habitat structure (Lichti et al. 2017 and references therein). We are not aware of other studies that investigated caching decisions by rodents in response to predators' olfactory cues. Further work may shed some light on whether this relationship occurs, and one prediction would be that rodents under high predation risk would invest less in cache spacing as a response to vigilance for predators, or risky habitats simply provide protection from pilfering, reducing the investment in cache spacing.

Our third experiment using urine and feces of ocelots supports our two initial experiments and strongly indicates that agoutis can in fact detect the odor cues left by ocelots in the forest. We detected a difference in seed removal between treated and control batches during the first seven days, which is within the time frame when agoutis can disperse fresh defleshed seeds (Forget et al. 1994) and make them inaccessible to the bruchid (see discussion above). Therefore, the ocelots' odor cues could extend the time window for successful infestation by the bruchid before an agouti move the seed away. Moreover, agoutis spent less time handling seeds in front of the batches with the olfactory cues implying that this may be a reliable signal for predation risk. The lack of differences in dispersal rates at day 15 may be the result of the dissipation of the olfactory cues, similar to other prey–predator systems (Bytheway et al. 2013), indicating that this chemosensory information for agoutis changes at short temporal scales, making the distribution of risky and safe patches to change with time.

Our results strongly suggests that ocelots' cues generate a landscape of fear increasing the proportion of risky patches. Further work may shed some light about whether such scenario could

influence bottom-up, top-down, and parallel impacts (Laundré et al. 2014) acting on the population dynamics of the agoutis, palms, and bruchids. Why ocelots do not visit certain patches with available prey is intriguing a deserves further evaluation. In our study site, we suspect that the road dividing our low ocelot density site from the rest of the park played a major role and evidence indicates that ocelots can avoid fragmented landscapes created by roads (Schmidt et al. 2020). However, in a more natural setting, ocelots can avoid certain habitats (Wang et al. 2019; Lombardi et al. 2020), which would generate safe patches for prey, in line with the landscape-of-fear model. Finally, it is likely that other wild cats generate a similar effect on seed dispersal dynamics, which highlights the importance of these predators and the potential effect of fear in forest ecosystems, possibly helping to maintain plant diversity, similar to other systems (Schmitz 2003).

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Analyses reported in this article can be reproduced using the data by Gálvez & Hernández (2022).

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