



Research article

Daily activity patterns in agoutis (*Dasyprocta* spp) in response to relaxed predation

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ABSTRACT

Animals' fitness is determined in a large proportion by the balance in energetic requirements maintained during daily activities, in response to environmental factors. Predation is a major environmental factor influencing the activity patterns of prey, and the deployment of adaptive responses to predation represents a significant cost to prey populations and communities. Experimental removal of predators to study the effect on activity patterns of prey is impractical for vertebrate species. However, islands are often deprived of predators and provide an excellent arena to study prey's responses in the absence of any cue related to predation risk. Here, we investigated whether natural absence of predators in islands has influenced the activity patterns of diurnal agoutis in Panama, by monitoring activity in three sites in each habitat type (predator-free vs predator). We predicted that agoutis in predator-free sites can expand their activity patterns towards the night, which is the period of highest predation risk, in sites with predators. One of our predator-free sites showed relative high activity at night, with no evidence of nocturnality in sites with predators. A clear pattern across our three predator-free sites was that agoutis started their daily activity earlier, before sunrise, which is a period with significant predation risk as well. Our study highlights the role that felids play in regulating agoutis' daily activity patterns and we discuss the implications of our finding. Finally, we also offer a review on agoutis' activity pattern in the Neotropics.

1. Introduction

Daily activity patterns are of significant relevance for animals' fitness because they may balance energetic requirements in response to biotic and abiotic variables [1]. Daily activity patterns of physiology and behavior are controlled by cell-autonomous rhythms of gene transcription, popularly known as circadian clocks [2]. In that line, daily activity patterns are adaptive sequences of daily routines fit into the time frame of a particular environment, as a result of evolution, but sufficiently plastic to be able to adapt to changes in the state of the environment [3]. Some elements that may generate variation in the environment and consequently act on daily activity patterns include abiotic factors such light conditions, ambient temperature, relative humidity, precipitation, and wind speed, while biotic factors include conspecifics, competitors, parasites, prey, and predators [1].

Predation risk is a significant environmental cue that can influence the activity patterns of prey and avoiding predators represents a

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behavioral, physiological, and neurobiological cost on prey populations and communities, which ultimately affects prey fecundity and survival [4]. For instance, prey respond to spatial variation in predation risk in heterogeneous landscapes ('landscape of fear' [5]), which is strongly linked to the ability of the prey to perceive and respond to that risk [6]. In that line, habitat structure seems to drive the perception of risk in diurnal prey [7]. Moreover, prey can respond to temporal variation in predation risk and evidence shows for example temporal shifts of activity by prey after predator introductions to reduce activity overlap with nocturnally active predators [8]. But the perception of risk is likely to be regulated by an interaction of spatial and temporal variation in risk, generating a dynamic landscape of fear where spots of high risk vary across temporal cycles [9].

Habitats without mammalian predators – like islands [10] – offer the possibility to investigate prey's responses in the absence of the spatial – temporal dynamic that drives the perception of predation risk. It is expected that the lack of predators would lead to a loss or relaxation of anti-predator adaptive behaviors. For instance, by investing less in vigilance [11] or showing reduced flight initiation distance [12,13] as compared to populations in sites with predators. In that line, we could expect that prey species in islands isolated from predators may expand their daily activity patterns to increase foraging success, possibly as a plastic response to short-term isolation [14] or as a hard-wired adaptation in response to long-term isolation [15,16].

Here, we investigated whether natural absence of predators in islands has influenced the daily activity patterns of a prey species. Panama possesses a large number of islands deprived of native mammalian predators, which offers the possibility to study prey's behavior in the absence of predators, as compared to mainland sites with predators. The agouti – felid relationship (particularly ocelots) offers an excellent system to study predator – prey interactions. Depending on the agouti species and location, ocelots can be their main predator and help to regulate their population size [17–22], indicating that they are a selective force for agoutis. In the case of agoutis, daily activity patterns of agoutis and whether they adjust it to avoid predators has been studied in several agouti species [23–30]. These studies revealed the agouti – ocelot mismatch in activity patterns: agouties are diurnal while ocelots are mainly nocturnal. In previous work, we demonstrated that *Dasyprocta punctata* in Central Panama follows predictions of the ecology of fear by reducing foraging in sites with high density of ocelots or in response to odor cues [31] and other studies demonstrated temporal avoidance of ocelots [25,30]. Therefore, we wondered if long-term isolation from predators has allowed agouties to expand their temporal niche by increasing nocturnal foraging. In other mammals and rodents, relaxed predation can generate a loss of recognition of predators' cues as soon as after five to eight generations [32,33], which is an important anti-predator behavior. Therefore, a shift in daily activity timing could be an expected response to relaxed predation, occupying at least partially the time periods in which predators would be active if present. The literature shows that agoutis can become more nocturnal as a response of external factors, like disturbance [34] and food abundance [23]; indicating that they are physiologically and behaviorally capable of such plasticity in activity. Since, predation is a strong factor that constrains daily activity to daytime in agoutis, we expected that sites in habitat with predators should have higher overlap in their activity distributions. For predator-free habitats, each site should have inherent conditions (e.g. availability of resources) that generate variation in the frequency of individuals being active at night, therefore resulting in less overlap in their distribution. Furthermore, our study provides a literature review to evaluate whether agouti species and populations deprived of predators tend to show more nocturnal activity patterns.

2. Materials and methods

2.1. Literature review

On June 13, 2023, we used Web of Science's Core Collection to search for scientific articles on activity patterns of agouti species. We performed a basic search by topic using the term 'dasyprocta' and then we refined the search with the term 'activity'. This search

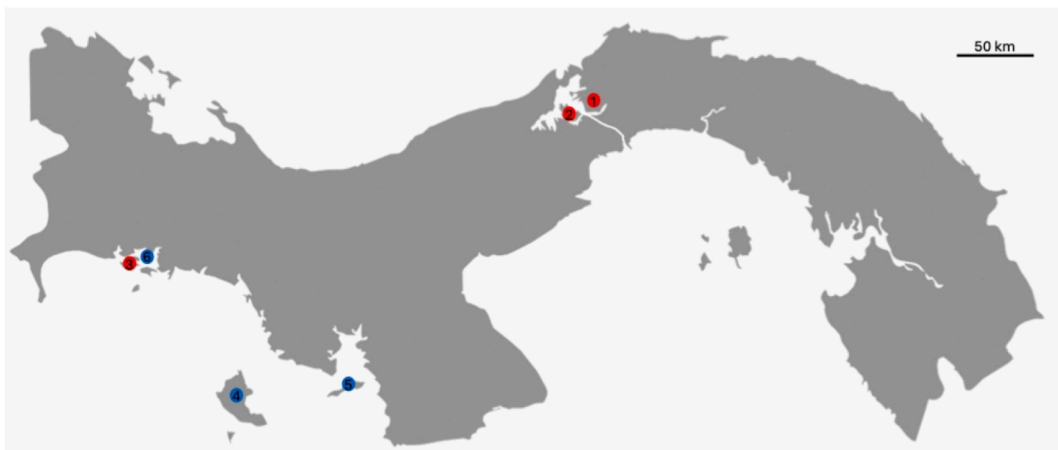


Fig. 1. Location of study sites in Panama, showing the predator (red) and predator-free sites (blue). Gamboa = 1, Gigante = 2 and Chalapa Island = 3, Coiba Island = 4, Cebaco Island = 5 and Muertos Island = 6.

generated 49 articles, and we examined each article and kept only those that studied daily activity patterns of agoutis. Moreover, we performed an independent search (November 2023–March 2024) for each species in Google Scholar that consisted of the sentence ‘daily activity of Dasyprocta’ completed with the specific epithet of the species, together with the name of the country in which the species is known to occur [35,36]. For example, ‘daily activity of Dasyprocta punctata in Panama’. Most of the articles found in this search were already included in the WoS search; however, this search found studies that covered activity patterns of an assemblage of various mammal species, that included agouti species.

We extracted the peaks of daily activity from each article. If not explicitly mentioned, the peaks were extracted from the figures by using ImageJ [37]. In case that a study provided more than one figure, we used the figure summarizing the results [38,39]. Some articles provided intervals of activity that did not allow a precise estimation [40,41]. Moreover, we particularly evaluated whether some level of nocturnal activity occurred per study. Nocturnal activity defined as occurring from 20:00 h - 6:00 h [42,43].

2.2. Camera monitoring

In order to evaluate whether agoutis in predator-free sites have expanded their temporal niche towards the night, we placed trail cameras (Winghome, Camerabird 630M, China) in three sites with predators and three sites without predators (Fig. 1). Our predator-free sites are naturally deprived of wild felids or any other carnivores reported in the literature as potential predators of agoutis (e.g. tayra, bush dogs, coatis [44–46]). We placed cameras in both type of sites around the same dates and we paired these sites in terms of

Table 1

Studies that recorded daily activity patterns of agoutis. Night indicates evidence (yes), partial (yes/no) or no evidence of nocturnal activity. Peaks: approximate peaks of activity. Felid: study site contains felid predators or not, obtained from the study or references. Superscripts: 1. <https://faunamanabi.github.io>, 2. Pers. comm. (T. Lee), d: dry, r: rainy, n-pa: non-protected area and pa: protected area. Country: BO = Bolivia, Br = Brazil, CO = Colombia, CR = Costa Rica, EC = Ecuador, GF = French Guiana, GY = Guyana, HN = Honduras, MX = Mexico, PA= Panama, PE = Peru, SR: Suriname, VE = Venezuela. Studies with two sets of peaks separated by a comma represent values for different sites or years.

Species	Reference	Peaks	Night	Felid	Country
<i>D. azarae</i>	[56]	8:00/16:00	no	yes	BR
<i>D. azarae</i>	[72]	18:00	no	yes	BR
<i>D. azarae</i>	[26]	7:00/16:00 ^d /17:00 ^r	no	yes	BR
<i>D. azarae</i>	[59]	7:00/17:00 ^{n-pa} , 7:00/17:00/18:00 ^{pa}	no	yes	BR
<i>D. azarae</i>	[34]	7:00/17:00	yes	yes	BR
<i>D. coibae</i>	[48]	7:00	yes	no	PA
<i>D. fuliginosa</i>	[73]	9:00/17:00	no	yes	EC
<i>D. fuliginosa</i>	[74]	8:00/16:00	no	yes	PE
<i>D. fuliginosa</i>	[75]	6:00–15:00/6:00–16:00	yes	yes	CO
<i>D. guamara</i>	no studies				VE
<i>D. iacki</i>	[60]	6:00/14:00, 7:00/18:00	no	yes	BR
<i>D. kalinowskii</i>	no studies				PE
<i>D. leporina</i>	[76]	6:00–7:00/16:00–17:00	no	yes	VE
<i>D. leporina</i>	[77]	7:00/16:00	yes/no	yes [78]	BR
<i>D. leporina</i>	[39]	6:00/17:00	no	yes	BR
<i>D. leporina</i>	[79]	9:00	no	yes	VE
<i>D. leporina</i>	[38]	5:00/8:00	no	yes [80]	BR
<i>D. leporina</i>	[58]	7:00/16:00	no	yes	SR
<i>D. leporina</i>	[27]	16:00	yes	no	BR
<i>D. mexicana</i>	[81]	NA	no	yes	MX
<i>D. mexicana</i>	[82]	6:00/16:00	yes/no	yes	MX
<i>D. mexicana</i>	[57]	8:00/17:00 ^d , 7:00/16:00 ^r	no	yes	MX
<i>D. prymnolopha</i>	[28]	6:00/14:00	no	yes	BR
<i>D. prymnolopha</i>	[83]	7:00/17:00	no	yes	BR
<i>D. punctata</i>	[46]	16:00–17:00	no	yes	PA
<i>D. punctata</i>	[84]	8:00/17:00	no	yes [85]	CO
<i>D. punctata</i>	[41]	6:00–8:00/16:00–18:00	no	yes	CR
<i>D. punctata</i>	[86]	7:00/17:00	no	yes	MX
<i>D. punctata</i>	[29]	8:00/16:00	no	yes	CO
<i>D. punctata</i>	[87]	7:00/17:00	no	yes	CO
<i>D. punctata</i>	[88]	17:00	no	yes	CO
<i>D. punctata</i>	[23]	NA	yes	yes	PA
<i>D. punctata</i>	[89]	12:00–15:00	no	yes [90]	CR
<i>D. punctata</i>	[25]	8:00/17:00	no	yes	PA
<i>D. punctata</i>	[30]	6:00/17:00	no	yes	PA
<i>D. punctata</i>	[91]	7:00/17:00	yes/no	yes	CO
<i>D. punctata</i>	[92]	7:00/5:00	no	yes ¹	EC
<i>D. punctata</i>	[93]	7:00/18:00	yes/no	yes	CR
<i>D. punctata</i>	[40]	8:00/16:00	yes	yes	CR
<i>D. punctata</i>	[94]	6:00/18:00	yes	yes	CR/PA
<i>D. ruatanica</i>	[95]	NA	yes ⁶	no	HN
<i>D. variegata</i>	[96]	7:00/18:00	no	yes	BO

the number of days of monitoring, for the analysis, that varied from 7 to 50 days. The sites with predators, in which we have recorded ocelots (*Leopardus pardalis*), included Pipeline Road/Gamboa (hereafter Gamboa, N9.143, W79.726/N9.120, 79.701), Gigante peninsula in the Barro Colorado Natural Monument (N9.126, W79.859) and Chalapa island in the Chiriqui Gulf (N8.239, W82.361). The predator-free sites included Cebaco island (N7.499, W81.223), Coiba island (N7.599, W81.724) and Muertos island in the Chiriqui Gulf (N8.262, W82.296). In summary, Coiba, Cebaco, Gamboa and Gigante had the highest camera trapping efforts, and the lowest efforts were in Chalapa and Muertos (Table S1). In all sites, secondary forest is dominant with similar temperature and humidity (lowest: $\sim 20^\circ\text{C}$, maximum: $\sim 32^\circ\text{C}$) [47–49]. The Central American agouti (*D. punctata*) is present in the three predator sites and in two of the non-predator sites (Muertos and Cebaco) [50]. Coiba Island is thought to contain its own endemic species *D. coibae*; however, a recent molecular study [35] suggests that agoutis in islands, with relatively short times of isolation, may not differ genetically from mainland population. We used independent detections at each site to evaluate activity patterns and we considered independent records to be those with at least 15 min between detections. We placed cameras at a minimum distance of 250 m between cameras.

2.3. Statistical analysis

We performed all analyses in R [51]. For the camera monitoring, we performed a multivariate analysis of variance (MANOVA) for circular data, following [52]. This procedure uses the sin and cosin of the response variable for the MANOVA. We built a model which included the time data transformed to radians as the response variable. We used type of habitat (predator vs -predator-free) and site as fixed factors, while camera placement date as the error term. As a post hoc analysis, we compared the distributions of time activity by performing pairwise comparison between sites by means of the compareCkern function in the package activity. This randomization test calculates the degree of overlap (Δ) between two activity kernels [53]. We plotted kernel density estimations of activity for each site and habitat by using the function densityPlot and we built a rose diagram to visualize activity patterns in each site with the function ggplot (package ggplot2). We used a Wilcoxon test to evaluate the number of observation in habitat with and without predators. Finally, we used a Wilcoxon test to evaluate whether the overlap values across sites from the same habitat type was higher for sites with predators as compared to predator-free sites.

3. Results

3.1. Literature review

We obtained 40 studies that investigated daily activity patterns of agoutis, which included ten out of 12 described species (Table 1). Only three of the agouti populations were not under felid predation pressure and they showed some level of activity during the night. However, six populations with felid predation pressure also showed evidence of night activity. The other 26 populations had presence of felid predators without evidence of night activity. Overall, for all populations, the main peaks of activity occur during the daytime.

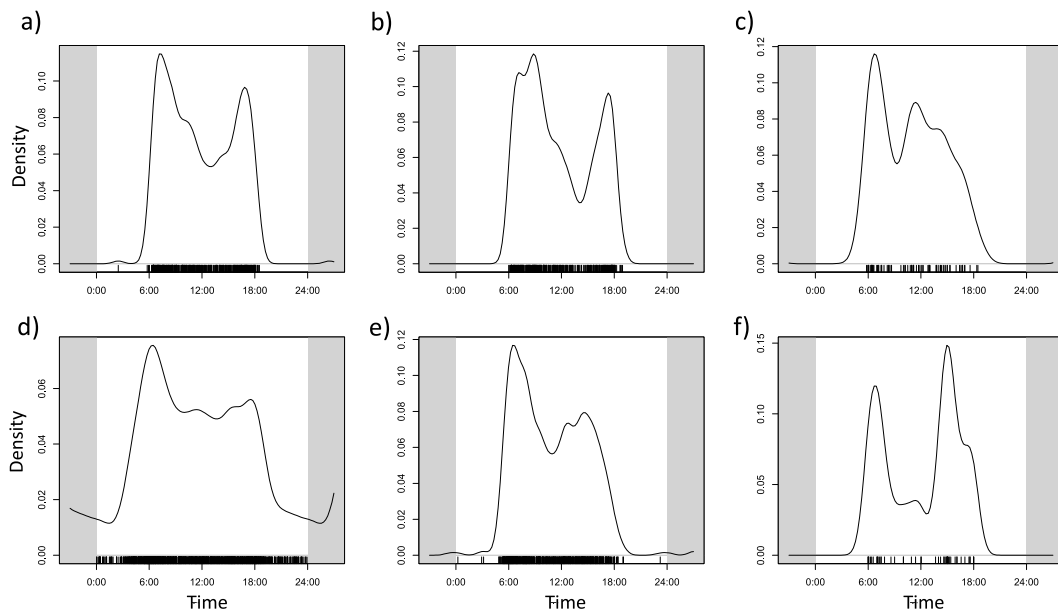


Fig. 2. Kernel density estimates of daily activity patterns of agoutis in sites with felid predators (a–c) and predator-free (d–f). Sites with predators included Gamboa (a), Gigante peninsula (b) and Chalapa island (c); while sites without predators included Cebaco island (d), Coiba island (e) and Muertos island (f). Independent observations are shown as tick marks along the x-axis.

3.2. Camera monitoring

Over the six study sites, we monitored for 2167 trap days (24 h period) and obtained 2752 agouti observations (Table S1). Although, sites without predators tended to have a higher number of observations, this difference was not significantly different (mean \pm standard deviation, 625 ± 525 and 305 ± 194 observations, respectively; $W = 7$, $p = 0.4$).

Daily activity pattern distributions differed across the six sites (Pillai's trace value = 0.03, $F = 49.5$, d.f. = 2, $P < 0.0001$; Fig. 2, Table 2). Whether predators were present or not was also influential (Pillai's trace value = 0.06, $F = 20.4$, d.f. = 8, $P < 0.0001$; Fig. 3). The highest frequency of night activity in sites without predators is generated by the observations from Cebaco island (Fig. 2d, Fig. S1d). Removal of Cebaco from the analysis still generates a significant difference between sites with and without predators (Pillai's trace value = 0.004, $F = 3.4$, d.f. = 8, $P = 0.03$, Fig. S2).

We found a bimodal pattern of activity for all the predator sites (Fig. 2a–c), and only one of the predator-free sites (Fig. 2d–f) had a clear bimodal pattern (Fig. 2f). Overlap in daily activity patterns between sites with predators was higher (0.85 ± 0.07) than between sites without predators (0.74 ± 0.05 , $W = 9$, $P = 0.05$, Fig. S3).

4. Discussion

Here, we explored whether agoutis in Panama show plasticity in their daily activity patterns in response to natural absence of predators. We expected activity patterns in predator sites to be constrained to daytime, and in predator-free sites, agoutis would expand their activity towards the night. We found a difference in activity, supporting our predicted pattern, which was particularly strong for one of the predator-free sites (Cebaco). For the other two sites, the difference with predator sites was mostly during sunrise and the peaks of activity during daytime. Agoutis from predator-free sites started activity earlier than those from predator sites, a time period of high predation risk and avoided by agoutis [25,28,30], suggesting a relaxation of predation constrains on activity in our predator-free sites. This is also supported by the fact that agoutis in the three predator sites did not show any nocturnal activity, and this is corroborated by the higher overlap in daily activity between predator sites than between sites in predator-free sites.

We found partial evidence from the literature, due to low number studies, that agoutis from predator-free populations become more nocturnal. However, several populations with predators also showed some degree of nocturnality, which suggests that predator absence is not the only cause of a shift towards nocturnality. For instance, agouties in sites with predators may become more nocturnal as day temperature increases and food availability decreases [23]. Most agouti species and populations show a bimodal pattern of activity with peaks shortly after sunrise and before sunset. Nearly all the agouti populations showed lower activity at midday when temperature reaches a maximum. Agoutis can gain heat by radiation [54]; therefore, they are expected to avoid periods of high sun exposure and temperature. Related to this is the fact that trapping and capturing agoutis near midday increases the risk of hyperthermia (DG pers. obs., [55]).

The data distribution from our predator site Gigante is corroborated by the bimodal distribution from Barro Colorado Island, a site with predators and approximately 490 m apart [25,30] and this distribution was observed in 32 out of 37 sites with predators in the literature. Also supporting our results is the fact that the activity pattern for our predator-free site Coiba matches previous results from the same site [48], suggesting a trend towards a unimodal distribution. Moreover, two out of three predator-free populations from the literature and two of our predator-free sites seemed to show a unimodal distribution, suggesting that relaxed predation is a potential trigger for this activity pattern. However, some populations with predators also show one peak of activity, which indicates that other factors that may interact with predation risk also generate this pattern. For instance, Suselbeek et al. (2014) found that activity of

Table 2

Pairwise comparisons of activity distributions of all sites based on 100 bootstrap iterations, evaluating the probability that two sets of observations come from the same distribution. Overlap (Δ) between sites and 95 % confidence intervals (CI). In bold are shown the comparisons used for comparing overlap values across sites within habitat type (see text for details). The first three on top are predator sites and the three at the bottom are predator-free sites comparisons.

Comparison	compareCkern test	overlap (Δ) 95 % CI
Cebaco vs Coiba	P < 0.0001	0.76 (0.72–0.79)
Cebaco vs Muertos	P < 0.0001	0.69 (0.58–0.79)
Cebaco vs Gamboa	P < 0.0001	0.73 (0.70–0.76)
Cebaco vs Gigante	P < 0.0001	0.73 (0.69–0.76)
Cebaco vs Chalapa	P < 0.0001	0.77 (0.66–0.80)
Coiba vs Muertos	P < 0.0001	0.78 (0.66–0.89)
Coiba vs Gamboa	P < 0.0001	0.84 (0.80–0.88)
Coiba vs Gigante	P < 0.0001	0.80 (0.75–0.85)
Coiba vs Chalapa	P = 0.99	0.92 (0.86–0.98)
Muertos vs Gamboa	P < 0.0001	0.77 (0.66–0.88)
Muertos vs Gigante	P < 0.0001	0.72 (0.60–0.84)
Muertos vs Chalapa	P = 0.06	0.77 (0.63–0.89)
Gamboa vs Gigante	P = 0.36	0.93 (0.86–0.97)
Gamboa vs Chalapa	P = 0.08	0.83 (0.66–0.83)
Gigante vs Chalapa	P < 0.0001	0.80 (0.67–0.83)

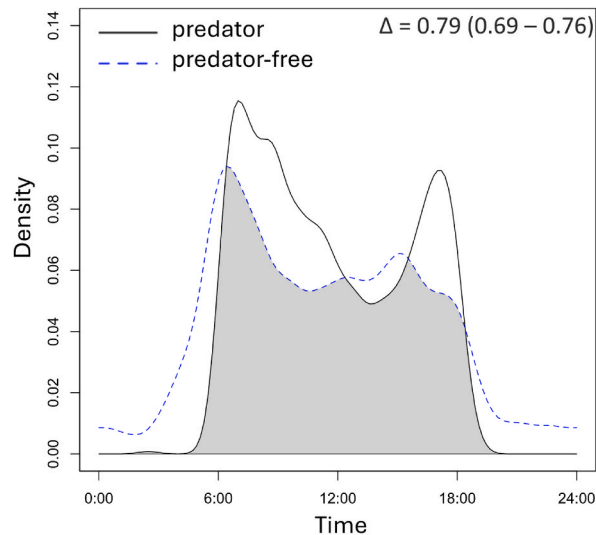


Fig. 3. Kernel density estimates and overlap (Δ) between agoutis from sites with predators and predator-free. The overlap coefficient shows between brackets the 95 % confidence intervals.

D. punctata during the period of elevated predation risk declined with food abundance. Whether other factors interact with predation risk and influence agouti activity patterns requires further work. For example, high temperatures generate bimodal distributions in *D. azarae* [56], while season [26], habitat patch size [38] and disturbance [34] are also reported to cause shifts in activity patterns of agoutis. Nevertheless, some of these factors like temperature and disturbance have been reported to have no effects on activity patterns of agoutis [38,57]. Surprisingly, some populations seem to show a trimodal distribution [58,59] which also calls for further work to better understand the mechanisms regulating daily activity patterns of agoutis.

It is important noticing that any potential selection towards nocturnality could be confused with a parallel effect caused by poaching. In Brazil, illegal poaching seems to trigger nocturnality in agoutis (*D. azarae*) and other mammals [34]. We did not quantify disturbance estimates and therefore it remains unclear how much poaching influenced our results, but we suspect it to be low or null in at least two of our predator-free sites: Coiba and Cebaco, the first a protected area and the second site was in private land. However, we saw poachers in our third site (Muertos), which could perhaps explain the dissimilarity of this site with the other two predator-free sites. Overall, sites with varying levels of human disturbance and predator abundance can provide a better picture on these interacting factors.

Cebaco showed the clearest pattern of nocturnal activity, between 20:00–5:00, and we also witnessed agoutis in Coiba being active from 19:00–21:00 near the facilities of the station. A possible explanation for Coiba is habituation of agoutis to human presence near the station and we have observed agoutis in lighted areas around buildings in the canal area in Panama City, indicating that caution should be considered when studying agouties near human settlements. For Cebaco, the lack of dogs and lack of evidence of poaching in our study area, both causes of nocturnality in agoutis [27,34,60], makes us to consider that this is a natural shift in activity timing towards nocturnality. Interestingly, in our three predator-free sites, agoutis spotted in the forest during daytime often flee and performed alarm barks [46], similar to agoutis in sites with predators, as evidence of ghosts of predators past [16] to explain the maintenance of this behavior. Further physiological work can help to elucidate whether agoutis in predator-free sites, like Cebaco, are reducing the use of anti-predator strategies or becoming adapted to nocturnality. Similarly, whether sporadic non-felid predators (e.g. boas, Duquette et al., 2017) in predator-free sites are a significant driving force in activity time shifting merits more work as well.

Our study made use of islands naturally deprived of predators, however, anthropogenic predator extinctions could provide a deeper insight into the plasticity of daily activity patterns in agoutis, ecological effects of predator removal [61,62] and ecological effects of shifting daily activity timing [63]. Moreover, something that seems to require more attention in the literature is how agouti predators adapt to changes in activity patterns of their prey [64,65] and factors impacting their own activity patterns [66,67]. For instance, some populations of jaguars, pumas and ocelots show significant levels of diurnal activity [68,69] but sometimes it is unclear whether this is a response to changes in prey activity [69]. Moreover, diurnal activity of large felids is often tied to activity of large prey like ungulates [70] rather than agoutis. Furthermore, it also remains unclear how potential diurnal predators like tayras [44], bush dogs [45], jaguarundis or coatis [46] may influence activity patterns of agoutis.

Finally, our review provides some insight into the most studied (*D. azarae*, *D. leporina* and *D. punctata*) and less studied species (e.g. *D. guamara*, *D. kalinowskii*, *D. ruatanica*), including an estimation of which countries in the region are carrying out research on agoutis' ecology and behavior (e.g. Brazil, Colombia, Costa Rica and Panama) and which ones are lacking this line of research, similar to reviews in agouti – plant interaction [71]. Given the ecological services provided by agoutis, beyond seed predation and dispersal, helping to maintain forest dynamics [71], it is imperative to understand basic elements of the biology of all the extant species in the Neotropics.

CRediT authorship contribution statement

Dumas Gálvez: Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Emilio Romero:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Conceptualization. **Daniel Murcia-Moreno:** Writing – review & editing, Supervision, Methodology, Investigation. **Braulio Bonilla:** Writing – review & editing, Supervision, Methodology, Investigation, Data curation. **Roderick Valdés:** Writing – review & editing, Supervision, Methodology, Investigation.

Data availability statement

The data supporting this manuscript is available as supplementary material.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Dumas Galvez reports financial support was provided by SENACYT. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.heliyon.2024.e39986>.

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