Different types of anthropogenic disturbance affect tropical animals

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Table of Contents

Thesis Abstract

These two distinct but interconnected studies aim to provide a comprehensive understanding of how anthropogenic disturbances, specifically noise pollution and human activities, affect both invertebrate and large carnivore behaviour. The integration of these studies allows for a holistic examination of how human-induced changes impact different taxonomic groups within tropical ecosystems, offering valuable insights for conservation strategies and ecosystem management.

Anthropogenic disturbances, such as noise pollution and human activities, pose significant threats to the environment and wildlife. This thesis investigates the effects of anthropogenic noise on the behaviour of *Acromyrmex octospinosus*, a species of leaf-cutter ants, and explores the coexistence and behavioural adaptations of jaguars and pumas in human-dominated habitats.

In Chapter 1, we examine the impact of noise disturbance on the foraging behaviour of *Acromyrmex octospinosus* in a laboratory setting. By subjecting ants to varying levels of noise -- Low (83 dB), Medium (97 dB), and High (101 dB) -- we observe a consistent decrease in ant movement speed across all noise treatments compared to the control group. Ant colony activity, measured by ant count, is not significantly affected by noise disturbance. Additionally, the size of leaf fragments varies across different noise levels. These findings provide robust evidence of how noise disturbance alters the foraging behaviour of leaf-cutter ants.

In Chapter 2, we focus on the coexistence and behavioural adaptations of jaguars and pumas in human-dominated habitats. Tropical forests, which house a significant portion of the world's biodiversity, are increasingly threatened by human activities. By analysing camera trap data from Manu National Park in Southeastern Peru, we observe that jaguars and pumas employ strategies, such as spatiotemporal segregation and fine-scale changes in activity peaks, to coexist in areas with varying levels of human disturbance. We find a negative association between pumas and the human disturbance index (HII) and correlations between pumas and factors such as distance to water sources and prey composition. These findings shed light on the

behaviour and coexistence mechanisms of these big cat species in human-dominated habitats and pristine rainforests.

Chapter 1 – Thesis Introduction

Anthropogenic disturbance has resulted in the loss of 239 million hectares of rainforest worldwide since 1990 (Staeck, 2022). The loss of rainforests is a global tragedy with far-reaching consequences for all life on Earth. The rainforests are home to an estimated 50% of the world's plants and animals. In addition, they play a vital role in regulating the Earth's climate and are an important source of food and medicine for many of the world's poorest people (Bierregaard, et al., 1992). Thus, deforestation is not only an environmental disaster, but also a social and economic one.

Threats to Tropical Rainforests and Wildlife

There are four main types of human-related disturbance that impact rainforests: logging, agriculture, mining, and oil extraction (Schroth, 2004; Kumar et al., 2022). Each of these activities can have serious consequences for the rainforest ecosystem. Logging can lead to soil erosion, as well as to the loss of valuable trees and other plant life (Ananda and Herath, 2003). Agriculture can lead to deforestation, as well as to the loss of biodiversity (Law et al., 2021). Mining can pollute the air and water, as well as damage the landscape (Chauhan, 2010). Oil extraction can contaminate the soil and water, as well as cause air pollution (Ossai et al., 2020). All of these activities can have a negative impact on the rainforest environment and contribute to climate change.

The anthropogenic disturbance of rainforests can have a profound impact on the behaviour of the animals that inhabit them. For example, logging can create soil instability and erode the forest floor, making it difficult for animals to find food and water. Furthermore, the noise disturbance caused by these activities can have a negative impact on rainforest wildlife, as it can interfere with their communication and make it difficult for them to find mates or identify predators. In some cases, noise disturbance can also lead to behavioural changes in animals, such as increased stress levels. Furthermore, the loss of trees can create open areas in the forest that are hotter and drier, leading to changes in the microclimate that can affect the behaviour of animals. Finally, the introduction of non-native species into the forest can disturb the natural balance, leading to competition for resources and a reduction in the overall quality of the habitat.

Anthropogenic disturbance can have a significant impact on predator - prey dynamics in tropical rainforests. For example, logging activities can lead to the loss of trees and other vegetation that provide cover and habitat for prey species (Schwab et al., 2021). This can make prey more vulnerable to predation and can also reduce the availability of food and other resources for predators. Additionally, human-caused fires can also alter the structure of the forest, making it more difficult for predators to ambush and stalk their prey (Doherty et al., 2022). Jaguars *(Panthera onca)* and pumas *(Puma concolor)* are two of the most iconic predators in the Americas. Despite their different hunting strategies, these big cats often share the same habitat and prey (Foster et al., 2010, 2013). Understanding how human disturbance affects jaguars and pumas can help conservationists develop management plans that allow these species to co-exist and provide insight into how other large predators might respond to similar pressures.

Anthropogenic disturbance can also have a direct impact on insect behaviour. For example, forest fragmentation may result in a decrease in native pollinator species visiting flowers (Aizen and Feinsinger, 1994; Schüepp et al., 2014). Furthermore, urbanisation of areas has been shown to alter predator-prey interactions, alter the abundance of insects, and host plant quality due to roads and a reduction in “green space” (Rocha and Fellowes, 2020). This can change the landscape of the forest and the types of plants and animals that live there, which can in turn affect the foraging patterns of insects (Wong and Candolin, 2015; Classen-Rodríguez et al., 2021). Leafcutter ants (Atta and Acromyrmex) are social insects and one of the most well-known ant species in tropical rainforests. Studying the impact of noise on ants can help us better understand how this type of pollution affects other social species.

Objectives and Aims

The primary goal of this thesis is to consider the behavioural changes of these animals (jaguars, pumas, and leaf cutter ants) under different types of human-generated disturbance regimes (noise disturbance, habitat destruction). It addresses knowledge gaps in the response of eusocial insects (ants) to different noise treatments and if different types of habitat destruction affect jaguar-puma behaviour.

Aim 1: *Investigate how different levels of noise disturbance affect the foraging behaviour of the leaf-cutter ant Acromyrmex octospinosus in a lab setting*

Acoustic noise from anthropogenic disturbance is a well-known problem that causes changes in the environment. However, there are limited studies on eusocial insects and how it affects their behaviour. I used ants *(Acromyrmex octospinosus)* as our model species and played different levels of white noise to determine how increased sound impacts foraging behaviour. I find that ant movement speed in control treatment was consistently greater than any of the noise treatments. Ant colony activity (ant count) was not affected by noise disturbance, leaf fragments were smaller compared to control, but leaf size was inconsistent across the different noise levels. This means that noise disturbance can negatively alter ant foraging behaviour.

Aim 2: *Examine the activity cycles of jaguars and pumas in three different types of secondary forest that are differentially affected by anthropogenic disturbance and compare these to patterns in primary forest*

Anthropogenic disturbance and the impact on the coexistence of jaguars and pumas has been studied in varying environments. However, previous studies have not examined how different levels of disturbance could affect their ability to coexist. I used existing camera trap data from three disturbed sites and one primary forest in the Peruvian Rainforest. I tested whether temporal and spatio-temporal separation exists, their habitat requirements and how their activity patterns coincide with that of their prey. I find that both species coexist through spatiotemporal separation and fine-scale activity peaks. This provides critical information to ensure that we can effectively conserve both species in the face of anthropogenic change.

Background

Covid-19 pandemic made the original study impossible, as a result I had to switch to a desk-based project and a lab study. I had to learn new research methods and adapt to the change. It has been a lot of work, but I have remained positive and determined to finish my research projects.

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CHAPTER 2 - Leaf cutter ants move slower under noise disturbance: A laboratory experiment

Abstract

Noise from anthropogenic disturbances is a well-known problem that causes changes in the environment. Anthropogenic noise, originating from sources such as construction, transportation, and gas extraction, disrupts natural acoustics, undermining essential ecological functions and has been shown to alter the behaviour and distribution of marine mammals, fish, and birds. However, invertebrates are one taxon where there are few studies relating to the impact of noise disturbance. In this study, we investigate how different levels of noise disturbance affect the behaviour of *Acromyrmex octospinosus* in a laboratory setting. Ants were subjected to a variety of noise levels, that is, Low (83db), Medium (97db) and High (101db). The control treatment exhibited consistently higher ant movement speeds compared to any of the noise treatments. Interestingly, noise disturbance did not have any significant effect on ant colony activity, as indicated by ant count. However, leaf fragments were found to be smaller in the noise treatments compared to the control treatment, although leaf size varied inconsistently across the different noise levels. These findings provide compelling evidence that noise disturbance can influence the foraging behaviour of ants. It is worth noting that this is the second study to demonstrate the impact of noise disturbance on leaf-cutter ant foraging. These results underscore the need for further research, considering factors such as the duration of noise exposure and the use of similar sound profiles. Our results illustrate that additional research is needed, taking into account the length of time colonies are exposed to noise and the use of similar sound profiles. Furthermore, research should be carried out to determine whether different colonies of the same species that are strongly affected by one stimulus (e.g., noise) respond differently to another stimulus (e.g., predation), in order to determine whether personality is driving the changes.

Introduction

Worldwide, anthropogenic disturbance is having a destructive impact on the environment and subsequently causing declines in populations or species of animals (Murphy and Romanuk, 2014). Acoustic noise from anthropogenic disturbance is a well-known problem that causes changes in the environment. Anthropogenic noise is different from typical sounds found in the environment (wind, rain, other animals etc) and can come from many sources e.g., construction, transportation, gas extraction (Raboin and Elias, 2019). Studies have shown that increased noise in the environment can reduce foraging, communication, predator avoidance, and affect distribution in marine mammals, fish, and birds (Weilgart, 2007; Francis et al., 2012; Sabet et al., 2016). For example, Luo et al., (2015), found that traffic noise decreased the effectiveness of foraging in Daubenton's bats, causing them to feed less than without noise traffic (in silence). Simpson et al., (2016) discovered when motorboat noise was played to Ambon Damselfish, it reduced their response to predatory attacks when compared to ambient noise conditions. Both studies concluded that disturbance of noise should be included in management plans when considering species conservation.

However, one taxon in which there are limited but increasing number of studies on the impact of noise (but ever increasing) are invertebrates. Invertebrates are mega diverse and make up a large proportion of species on Earth (Wilson, 1987). They play critical roles in shaping our ecosystems and provide important services like pollination, decomposition, and prey for other animals (Lavelle et al., 2006). Most of these functions are critical for food security and climate change (Prather et al., 2013). Given the critical importance of invertebrates and the increasing anthropogenic disturbance, understanding how noise can affect them is essential to maintain ecosystem health. Vertebrates require a specialised organ to detect and process sound; this has evolved over millions of years (Fay and Popper, 2000; Albert and Kozlov, 2016). Whereas the methods invertebrates use to detect sound are various and complex (Albert and Kozlov, 2016; Raboin and Elias, 2019), leading to potentially more ways that sound could impact this diverse taxon.

Eusocial insects are those that live in a colony and (amongst other things) have a division of labour and care for the brood (Schultner et al., 2017; Psalti et al., 2021). To facilitate information exchange, which can be crucial to colony survival as a whole, they communicate through different modalities - chemical, visual, tactile, and mechanical signals (Masoni et al., 2021). Mechanical signals correspond to airborne sounds and substrate-borne vibrations (Golden and Hill, 2016). Chemical, visual and tactile communication signals have been studied in eusocial insects, whereas studies on the impact of anthropogenic sound on mechanical signals are few.

There are more than 250 fungus growing ant species that make up the attini tribe, including leafcutter ants (Meirelles et al., 2015). They inhabit Neotropical rainforests and are dominant herbivores, removing leaf fragments from trees and transporting them back to the nest, where they are used as a substrate for growing a fungus *(Leucoagaricus gongylophorus)* which is then harvested to feed the larvae (Swanson et al., 2019).

Leafcutter ants have been extensively studied, and it is well known that they use chemical pathways (pheromone paths) to communicate the location of foraging material (Jackson and Ratnieks, 2006). Leafcutters also use ‘tandem running’, a behaviour in which a recruit or recruits are led to foraging material, with the leader moving faster than the ants following (Jackson and Ratnieks, 2006). Another communication mechanism used by ants is stridulation which is produced from the stridulatory organ and causes vibrations that deliver encoded messages (Oberst et al., 2014; Hager et al., 2017). Studies have shown that ants use these stridulations when excavating nests, locating food, during conflicts (attack from predators or coordinating attacks against prey) and relocation of the colony (Markl, 1965; Roces et al., 1993; Hager et al., 2017). A recent study by Masoni et al., (2021) revealed that stridulation is modulated depending on behavioural context and can be considered as a real vibro-acoustical signal, informing conspecifics of information relating to foraging and different colony related activities. One little-studied area is how introduced vibratory noise can affect ant behaviour. Byrne et al., (2022) tested whether noise disturbance at 80db impacted ant activity (abundance), leaf fragment size, and speed when compared to a control. They found that ants (*Acromyrmex octospinosus)* increased speed and cut smaller fragments, but colony level activity stayed the same, suggesting that over time colony level fitness could be reduced. However, what is still unknown is at what level noise may begin to impact foraging behaviour and fitness.

In this study, we aimed to Investigate how different levels of noise disturbance affect the foraging behaviour of the leaf-cutter ant *Acromyrmex octospinosus* in a lab setting We used the same species as Byrne et al., (2022) and the same laboratory set-up. Specifically, we answer the following objectives: (Obj1) is straight-line movement speed reduced under different noise levels? (Obj2) is colony activity reduced under different noise levels?, and finally (Obj3) is leaf fragment size and weight reduced under different noise levels?

Methods

(a) Experimental setup

We used leafcutter ants *(Acromyrmex octospinosus)* from a single colony. These ants are commercially available in the UK; however, in the wild they range from southern Mexico to northern South America. A froilabo climate chamber (model SP-BVEHF) was used to house the nest at a controlled temperature of 25°C at 80% humidity. The chamber was connected to three glass boxes (one 29x20x6cm, two 30x20x20cm) by 4 m of transparent plastic tubing, which was 2.8 cm in diameter (Figure 1). The three boxes were connected by 50 cm transparent plastic tubing; this allowed ants to move in the direction of food sources and return to the nest using the same path. Box 1 contained forage (35g privet - *Ligustrum* spp), which was placed at the beginning of each experiment. Box 2 had a raised floor and contained Fluon ® around the edges to prevent ants from escaping. This box was empty and used to film ants passing through. One GoPro Hero 7 camera was placed above Box 2 to film/assess movement speed. Camera two was placed between box 1 and box 2 to record the number of ants moving towards Box 1 and returning to the nest. Box 3 had a removable lid and contained a gravel floor where the leaf fragments were extracted from passing ants (Figure 1).

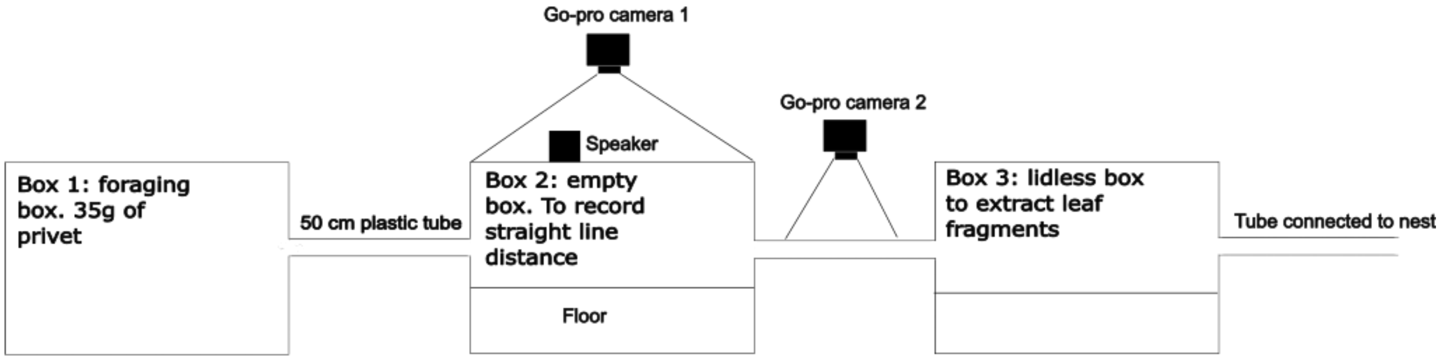

Figure 1: Setup of lab experiment

(b) Behavioural recording

Experimental replicates were carried out between June and December 2021. We conducted five replicates of each of the three sound profiles and a set of control treatments. A vibration speaker was placed on top of Box 2, the speaker converts electrical energy into mechanical energy, making the surface they are attached to vibrate. This vibration is then emitted into the environment. A 60 second white-noise WAV file was used to produce the vibration, with 63 instantaneous, intermittent white noise bursts that all had the same peak amplitude was used throughout the noise treatments. To avoid habituation, white noise bursts varied in duration from 0.01-2 seconds. For control replicates, the speaker was turned on and in place, but did not emit noise. Ambient noise during the control trials was recorded at 41dB. Noise treatments were broken down into three categories: Low, Medium, and High. To categorise sound profiles inside and outside the box (measured 10 cm from the box), a Casella CEL-24X sound level meter was used. Low disturbance outside the box was classified as LAF_{max}=63.1db, inside LAFmax = 83db, medium outside LAF_{max}=73.4db, inside LAF_{max}=97db, and finally, high disturbance outside the box was recorded as LAFmax = 80.5 and inside the box LAF_{max} =101db.

The recording of ant activity started when the first ant returning to the colony with a leaf fragment entered Box 2. The GoPro was turned on for 10 minutes, then off for 10 minutes. This cycle continued for a duration of 2 hours. At the end of the replicate, six ten-minute videos were obtained. To count the number of ants performing certain behaviours, i.e. moving in the direction of the nest carrying a leaf, towards the forage without a leaf, or towards the nest without a leaf, the videos were analysed using BORIS software (Friard and Gamba, 2016).

The straight-line movement speed was assessed using the videos from Box 2. Two lines were placed 24 cm apart in the BORIS software and the time taken for ants to move between the two lines was recorded. This was conducted for each behaviour (towards nest with leaf, towards forage, towards nest without leaf). If the ant stopped for longer than five seconds or changed direction more than 90°, the data were excluded from the analysis.

(c) Leaf measurements

To sample leaf fragments (dry weight, wet weight, and surface area), leaves were removed from ants in Box 3 when returning to the nest, in-between the ten-minute video recordings. The leaf fragments were extracted with tweezers and a paintbrush to free the ant from the leaf. Sixty leaf fragments were scanned, and the surface area was calculated with ImageJ (Schneider et al., 2012) for each replicate. Each fragment was weighed to obtain wet weight, then all fragments from a ten-minute time period were placed on a metal tray and oven dried at 45 ° C for 48 hours to obtain six pooled dry weights per day.

(d) Statistical analysis

Movement speed, ant activity counts, fragment surface area and wet weight were nonnormally distributed; as such, the Kruskal-Wallis test was conducted to test if there were differences between control and noise treatments. If differences were detected, Pairwise-Wilcoxon tests were used to detect differences between control and individual noise treatments. Dry weight was normally distributed, and ANOVA was used to test for differences between control and noise, if there was a significant difference, a TukeyHSD post-hoc test was used to find individual differences. Data analyses were performed using R (v4.1.1) (R Core Team, 2022).

Results

Ant-speed

The straight-line speed was significantly different between control and all noise treatments for each behaviour, toward forage, toward the nest, toward the nest with the leaf (all p-values <0.001, Figure 2, see Appendix Table 1 for statistical output). There was a general trend of decreasing straight-line speed with increasing noise disturbance. However, certain pairings of noise treatments were not significantly different, that is, medium to high disturbance when ants moved toward forage (Figure 2A), low to medium when moving towards the nest (Figure 2B) and carrying leaves (Figure 2C).

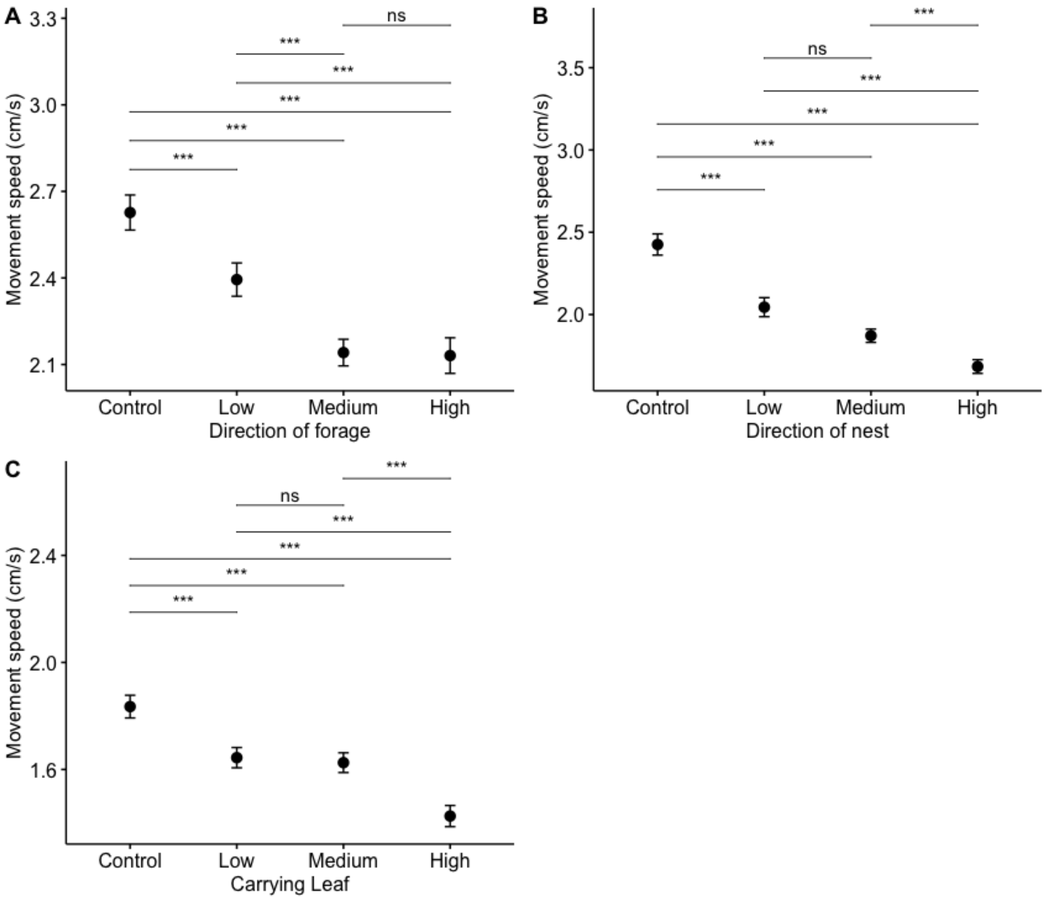

Figure 2: Mean (+/-se) movement speed of ants A) toward forage, B) toward nest, C) carrying leaves between differing noise treatments. *** indicates P < 0.05, ns. indicates no significant difference. See Appendix Table 1 for test statistics.

Ant activity counts

While the activity counts of the ants were not significantly different for any behaviour, a downward trend was evident for both the direction toward the forage and the direction toward the nest (all p-values >0.05, Figure 3, see Appendix Table 1 for test statistics).

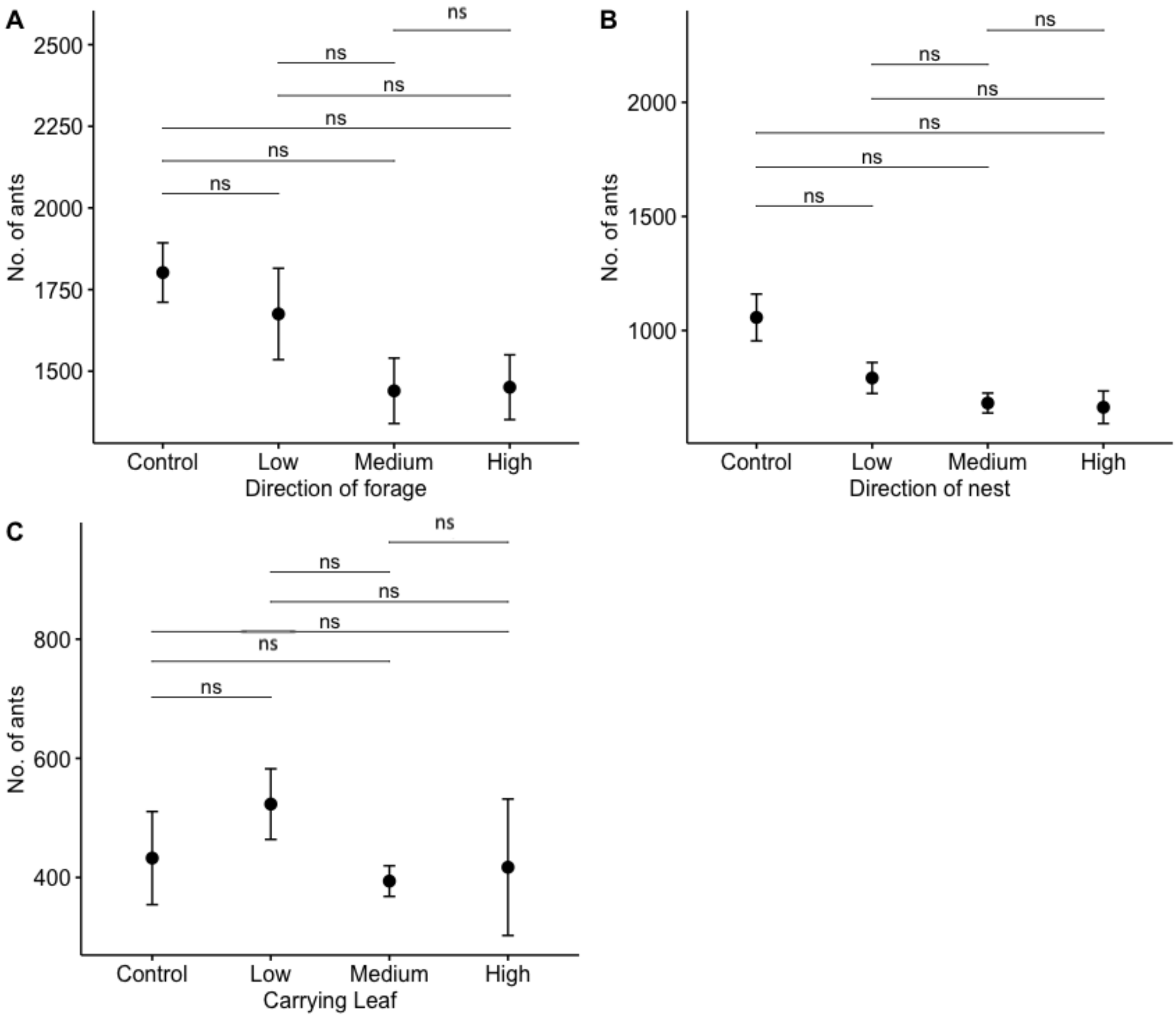

Figure 3: Mean (+/-se) of colony activity counts A) towards forage, B) toward nest, and C) carrying leaves. All results were not significant. See Appendix Table 1 for test statistics.

Leaf Measurements

The leaf fragment measurements were somewhat inconsistent between the noise treatment levels (Figure 4). Control had greater weights (dry and wet), and surface area than low disturbance and greater dry weight and surface area from high disturbance (Figure 4 - see Appendix Table 1 for pairwise comparison and test statistics). Low noise disturbance had a smaller wet weight and surface area compared to medium disturbance, but not significantly different from high disturbance for any leaf measurement. Medium noise disturbance was greater than low and high disturbances for surface area and wet weight, but not dry weight.

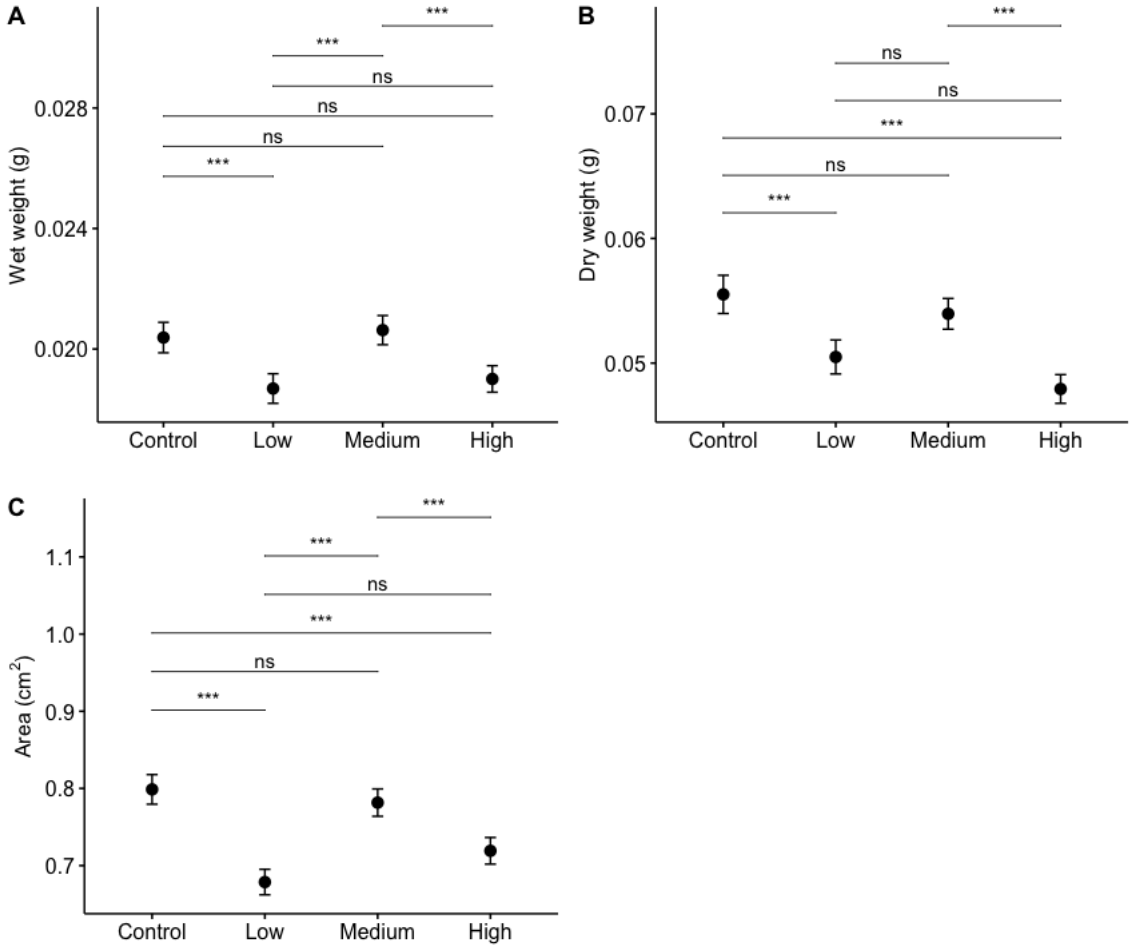

Figure 4: Mean (+/-se) leaf fragment metrics A) wet weight, B) dry weight C) and surface area between noise treatments levels. *** indicates P < 0.05, ns. indicates no significant difference. See Appendix Table 1 for test statistics.

Discussion

The results of this study provide robust evidence that noise disturbance can alter the foraging behaviour of ants. In particular, our key findings are; (Obj1) the straight-line speed decreased with increasing noise levels, (Obj2) colony activity (ant count) was not affected by noise disturbance, (Obj3) leaf fragments were smaller compared to control, but leaf size was inconsistent between the different noise treatments.

This is the second study to directly investigate noise disturbance in foraging social insects. Byrne et al., (2022) found that leaf-cutter ants increased speed when white noise was played through a vibrational speaker at 80db. In addition, the count of the ants did not change between the noise and control treatments. These results are partially supported by our study. We expanded the noise profiles used to understand whether there is a minimum threshold that still impacts ant behaviour. At low, medium, and high noise levels, our results showed variation from Byrne et al (2022), revealing in our study that ant speed decreased, but abundance (ant count) was similar across treatments. The 50db low noise level used in our study is classified as 'quiet' and is reported to be the same noise profile as rain. For example, Farji-Brener et al., (2018) tested the effects of rainfall and humidity on leaf-cutter ants and found that foragers increased their speed by 30% due to rain noise and dropped fragments due to increased load. These results indicate a potential association between noise and an increase in foraging speed.

The increase in speed under disturbance supports the notion that ants adapt behaviour, but ant counts did not change, affecting overall foraging. A similar behaviour has been reported by Sujimoto et al., (2020). They found that *Atta sexdens,* when exposed to low barometric pressure, returned two times more leaves than when the pressure was normal or high. However, the total number of foragers did not change between treatments. Suggesting individual ants adapting to noise, or disturbance rather than a colony-wide response. Although our study supports these previous studies with respect to colony activity remaining similar under different disturbance regimes, we found that speed decreased rather than increased. The reason for this is not clear, however, a possible explanation could be colony personality. Colony personality is described by Kolay et al. (2020) as “consistent interindividual differences in behavioural traits across time and/or context”, with personality traits reported in a broad scope of taxa. In social insects, these have been reported at the colony and individual level. For example, Cole et al., (2010) showed that the thermal range and temporal foraging activity pattern of the *Pogonomyrmex occidentalis* colonies differed. Previous studies have also found instances where the colony has similar responses to environmental changes, but different behaviours between colonies. By way of illustration, Pinter-Wollman et al., (2012) found the black harvester ant *(Messor andrei)* colonies differed in speed and responsiveness to different foraging and disturbance situations (debris removal, response to alarm etc), however, their speed was similar in dry conditions. Furthermore, MacLean et al., (2017) found that acorn ant colonies *(Temnothorax curvispinosus)* responded similarly to increased temperature with an increase in foraging rate, whereas at colder temperatures the colonies had a lower foraging rate. This highlights that under different conditions ant colonies of the same species can have similar responses to environmental cues but also exhibit different behaviours. Byrne et al., (2022) and the current study showed similar responses to sound disturbance (no reduction or increase in ant activity counts and reduced leaf fragment size), however, speed was significantly reduced in our study. This could be attributed to differences in colony personality.

These differences in personality could also affect communication pathways when responding to noise disturbances. We tested one part of the communication arsenal that ants use to navigate their daily lives in response to noise disturbances. Stridulation has been shown to provide information to near-by ants when cutting leaves, recruitment to battle, and when a nest is buried. The pheromone trails provide information to other ants on the direction of the foraging material. We found that ants reduced straight line speed, which could have been derived from interrupted pheromone trails due to disturbance. In Byrne et al (2022), they suggested the ants deduced the noise as a threat and responded by increasing speed to retrieve foraging material quicker, continuing the task, but returning with smaller leaf fragments. In our experiment, we found the inverse, ants reduced speed. This could be due to ants, who instead of perceiving a threat, spent more time investigating the disturbance. However, further work should be undertaken to understand the impact of noise disturbance on other communication modalities in ants. One way could be to investigate the spatial patterns of paths under different noise disturbance regimes to understand if ants move around more or less in different directions, other than towards forage material.

Another important factor which could drive differences between the colonies used in Byrne et al., (2022) and the current study is the different noise treatment regimes. In our experiment, we played white noise over 15 replicates (five for each sound profile - low, medium, or high) and five controls, hence 75% of the time the ants were exposed to noise treatments. Whereas Byrne et al., (2022) played 10 noise treatments and 10 controls, with ants being exposed to noise 50% of the time. Therefore, the ants in our study were under the influence of noise disturbance for a greater proportion of time, which could have caused the differences in behavioural response between the two studies. This combination of findings could provide support for the premise of differences in colony personality; however, due to the experimental treatments being different, further studies are warranted to examine the response of the aforementioned colony under identical sound treatments, thereby elucidating whether the colony exhibits divergent or analogous reactions to prolonged exposure to noise.

In summary, we demonstrated that vibration and subsequently noise disturbance can strongly limit leaf-cutting ants foraging ability through the reduction of speed and collection of smaller leaf fragments, which could impact the long-term fitness of the colony. Our results illustrate the need to conduct more experiments on the impact of sound on social insects, including a prey-predator dynamic and other sound profiles.

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Appendix

Table 1: Comparison of wet, dry, and leaf area between control and noise treatments was performed. The Kruskal-Wallis test statistic has been calculated to assess the differences. An asterisk (*) indicates the result of the ANOVA statistic. In addition, a Tukey post-hoc test was conducted to compare the means.

		Replicate					
Experiment	**Treatment**	**Control**	**Low**	**Medium**	**High**	**Test statistic**	**P-value**
Ant speed	Direction towards forage	1.160^{a}	1.057^{c}	0.945^{b}	0.941^{b}	52.617	<0.001
	Direction towards the nest	1.071^{a}	0.826^{b}	0.903^{b}	0.743^{c}	85.676	<0.001
	Carrying leaf	0.810^{a}	0.725^{b}	0.717^{b}	0.629^{c}	52.665	<0.001
Ant abundance	Direction toward forage	1802.2^{a}	1675.4^{a}	1440.0^{a}	1451.0^{a}	1.5354	>0.05
	Direction towards the nest	1057.0^{a}	791.8^{a}	681.8^{a}	663.4^{a}	6.36	>0.05
	Carrying a leaf	432.6^{a}	523.2^{a}	394.0^{a}	417.2^{a}	9.1869	>0.05
Leaf Fragments	Wet	0.020^{ab}	0.019^{c}	0.021^{a}	0.019^{bc}	11.203	<0.05
	Dry	0.056^{a}	0.050^{b}	0.054^{a}	0.048^{c}	6.619*	<0.001*
	Area	0.798^{a}	0.678^{b}	0.781^{a}	0.719^{c}	26.029	<0.001

Chapter 3 - Coexistence of Jaguars and Pumas in human disturbed rainforests, south-eastern Peru

Abstract

Tropical forests are hotspots for biodiversity, covering less than 10% of the earth’s surface but contain more than 50% of the world’s species of flora and fauna. These natural refuges are under increasing pressure due to human expansion and can modify animal behaviour. For instance, in areas with high human disturbance, jaguars and pumas may alter their usual hunting grounds and shift their activity patterns to avoid encounters with humans. This behavioural response can result in changes in their home range size, resource selection, and even interspecies interactions. Similarly, the availability of prey species may decline in areas with intense human activity, leading to shifts in the dietary habits and foraging strategies of these big cats. In this study, I examined the coexistence of jaguar and puma in three human dominated habitats and one primary rainforest in Manu National Park, Southeastern Peru using camera trap data. My findings demonstrate that jaguars and pumas coexist within the study area by employing strategies such as spatiotemporal segregation and fine-scale changes in activity peaks. Furthermore, my analysis revealed a negative association between pumas and the human disturbance index (HII), as well as a similar negative correlation between pumas and factors such as distance to water sources and prey composition. These results shed light on the behaviour of these two species in areas with varying levels of historical human disturbance. Overall, through the utilisation of camera trap data, this study provides valuable insights into the behavioural patterns and coexistence mechanisms of jaguars and pumas in human-dominated habitats and pristine rainforests. By understanding how these predators adapt to changing environments, we can develop effective conservation strategies to mitigate the impacts of human activities on tropical forest ecosystems.

Introduction

Tropical forests are hotspots for biodiversity, covering less than 10% of the earth's surface but contain more than 50% of the world's flora and wildlife (Wilson and Peter, 1988; Marsh, 2003). However, the pressure on these natural havens is growing as a result of human population growth. Forest fires, agricultural expansion, tree extraction, and infrastructure development are among the main drivers of the decline in tropical biodiversity, with a staggering 12.2 million hectares of tree cover lost in 2020 alone (Hansen et al., 2013). As a result, two thirds of the world's global forest cover is classified as secondary (Wright, 2005; Pain et al., 2020). Anthropogenic modification of habitats can also cause modifications to the behaviour of resident animals and subsequently the critical ecosystem functions and services they provide (Wies et al., 2021). For instance, in areas with high human disturbance, jaguars and pumas may alter their usual hunting grounds and shift their activity patterns to avoid encounters with humans (Cruz et al., 2018). This behavioural response can result in changes in their home range size, resource selection, and even interspecies interactions (Morato et al., 2016). Similarly, the availability of prey species may decline in areas with intense human activity, leading to shifts in the dietary habits and foraging strategies of these big cats (Parsons et al., 2022). Therefore, understanding how secondary forest impacts animal activity can help determine how competing species coexist and provide important information to implement effective conservation strategies.

When natural habitats are disturbed through anthropogenic activities, large carnivores are often the first to be impacted (Cuaron, 2000; Tucker et al., 2021). These disturbances can occur rapidly and lead to changes in microclimatic conditions and habitat structure, which can in turn impact food availability, animal behaviour and may lead to changes in animal interactions (Dias et al., 2019). For example, Tucker *et al.*, (2021) showed that in human disturbed forests in Asia, seed dispersal by mammals was reduced by 25%, in Central and South America by 16%, and in Africa by 15%. Furthermore, Patten, Burger, and Mitrovich (2019) found that human activity impacted the diel cycle of two predators and one prey, bringing the activity of species into a greater overlap which could increase encounter rate of predation and thus cause trophic cascades. Figel et al (2021) examined the reactions of pumas and jaguars to human disturbance in fragmented landscapes in the Colombian Magdalena River basin which is currently unprotected. According to various studies, the research findings on spatial and temporal interaction between pumas and jaguars have been inconsistent. While some studies have shown similarities in the activity patterns of the two felids (Harmsen et al. 2011; Foster et al. 2013; Astete et al. 2017; Herrera et al. 2018), others have highlighted habitat partitioning between them (Sollmann et al. 2012; de la Torre et al. 2017; Palomares et al. 2017; Alvarenga et al. 2018). Additionally, there is evidence of temporal segregation (Harmsen et al. 2009; Romero-Muñoz et al. 2010; Santos et al. 2019), while some reports also indicate spatial overlap (Harmsen et al. 2009; Di Bitetti et al. 2010; Astete et al. 2017; Santos et al. 2019). Furthermore, a recent study by Figel et al (2021) demonstrated that both jaguars and pumas avoid areas with high human disturbance, resulting in altered activity patterns. Likewise, Ouboter et al (2021) found that jaguars and pumas exhibited more nocturnal behaviour in response to ecotourism in a protected area in Suriname. However, it is important to note that the methodologies used in these studies differ, with Figel et al (2021) focusing on general human disturbance and Ouboter et al (2021) specifically examining the impact of ecotourism. Overall, these studies collectively conclude that changes in the behaviour of pumas and jaguars, caused by human disturbance or ecotourism, could negatively affect their ability to forage for diurnal prey and subsequently impact the survival of these large predators.

The two largest terrestrial predators in the Neotropics are jaguars and pumas, which are near threatened on the National Red List of Peru (SERFOR, 2018). The two species are often referred to as umbrella species (Thornton et al., 2016), and as such conservation of both will likely greatly benefit the whole ecosystem (Hernández-SaintMartín et al., 2013). However, due to human disturbance and habitat conversion, their ranges have contracted in certain areas (Sanderson et al., 2002). Jaguars overlap entirely with the range of pumas, and they are of similar size and can feed on the same prey. Regardless of these similarities, it has been proposed that competition is not great because they are spatially segregated (Emmons, 1987; de la Torre et al., 2017), have different diel activity (Monroy-Vilchis et al., 2009; Harmsen et al. 2009, Romero-Muñoz et al. 2010, Hatakeyama et al., 2020), and prey selection (Aranda and Sánchez-Cordero 1996, Núñez et al. 2000, Novack et al. 2005, Cascelli de Azevedo and Murray 2007, Flores-Turdera et al. 2021). However, it should be noted that these strategies are not always obvious in different studies. For instance, Ayala et al. (2020) discovered that in Peru and Bolivia, there was no temporal segregation, while Hatakeyama et al., (2020) found that this was the main mechanism in Brazil. Romero-Muñoz *et al.*, (2010) also found temporal segregation was a key factor in explaining the coexistence of jaguars and pumas in Bolivia. To date, research on the coexistence of these large felid species focuses separately on temporal, prey, or spatial (spatio-temporal) strategies. Furthermore, previous studies do not examine coexistence under varying histories of anthropogenic disturbances.

We studied the coexistence of jaguars and pumas in Manu National Park, Peru. The park is a priority region in WWF Global 200 and recognised as a global epicentre of biodiversity (Rodriguez and Young, 2000; Olson and Dinerstein, 2009). The park has been protected as a UNESCO World Heritage site since 1970 (Salazar Moreira and Palomino-Schalscha, 2020) but the inter-oceanic highway connecting Peru and Brazil (completed in 2010) has resulted in an increase in secondary roads and immigration into the Manu area (Oliveira et al., 2019). Subsequently, agricultural practices, cattle ranching, illegal mining, and urban development have increased (Nicolau et al., 2019) leaving the area with socioeconomic issues, ecosystem degradation, and areas of poverty (Sánchez-Cuervo et al., 2020). This region provides an ideal situation in which to study the impact of anthropogenic disturbance on the coexistence of large predators.

In this study, we examined the activity patterns of jaguars and pumas in three different types of secondary forest that are differentially affected by anthropogenic disturbance and compared these to patterns in a primary forest. We investigated (1) whether there is temporal and spatio-temporal division between these two species, (2) if predator activity patterns consistently coincide with those of the dominant medium-to-large-sized prey across the forest types and (3) if the study area's habitat requirements for jaguars and pumas are the same or dissimilar. We explored the potential conservation implications of our findings and contrast them with those of earlier studies.

Methods

Site Description

The study was carried out within the Manu Biosphere Reserve, southeastern Peru. Four survey locations were chosen that represent varying land use gradients in the region and have different past and present human disturbances (Figure 1). The Manu Learning Centre (MLC) has undergone >40 years of regeneration after different levels of human disturbance (71°23'28"W 12°47'21"S), including cattle ranching, selective logging, and agricultural clearance (Figure 1A). MLC has been protected since 2002 and is primarily a research facility with ecotourism. The Shintuya native community (71°13'18"W 12°39’26"S) has been colonized by people from the Andes region. The research was conducted on private land, which is used mostly for tourism, but also for hunting and logging (Figure 1B). The area has an elevation of 1200m and a similar topography to the MLC. The Diamante community (70°50'34"W 12°16’11"S) is the largest in Manu and has been selectively logged. The study was carried out on the same land, which contains a small air strip used to access Manu. Previous survey trails were used as vehicle access points for timber extraction (Figure 1C). The primary forest of Romero rainforest lodge (70°58'54"W 12°13'28"S) is located in the Manu National Park and is used for tourism activities. The lodge is ~300m a.s.l and is strictly protected from logging, hunting and any farming practices.

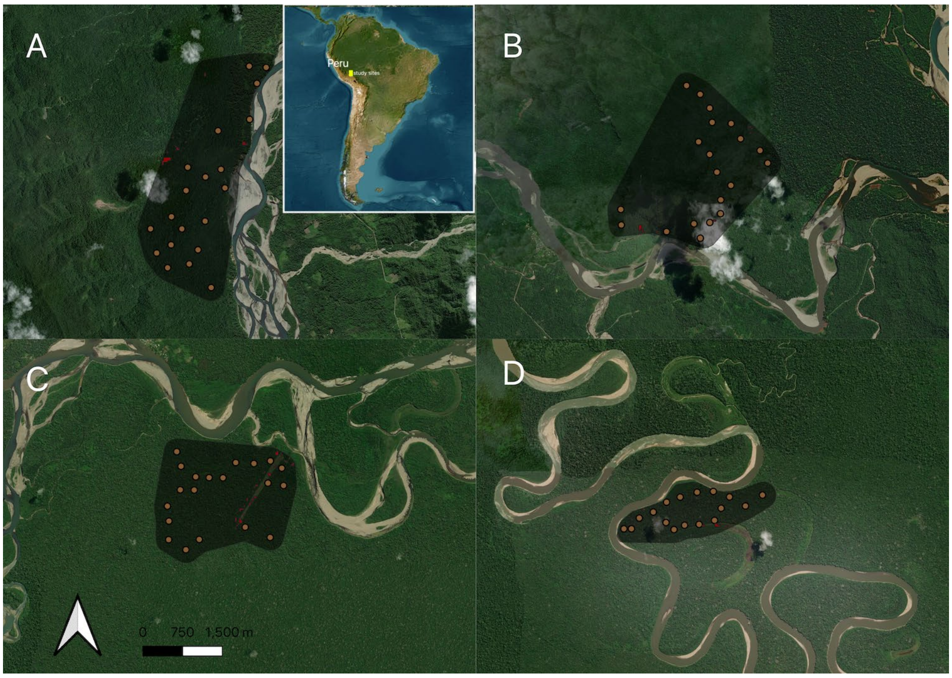

Figure 1: Map of study locations in Manu National Park, Peru. A = Manu Learning Centre, B = Shintuya, C = Diamante, D = Romero. Circles denote camera trap locations, red colour = Hansen Forest loss 2000-2016 v1.4 (Hansen et al 2013).

Data collection

The raw camera trap and vegetation data in the current study were used with permission from Whitworth et al. (2019). Here, we used a subset of the original dataset which includes only terrestrial camera trapping and therefore excludes arboreal sampling. A total of 248 (80 camera stations had terrestrial and arboreal, and 88 had just arboreal cameras) camera traps were installed in April and May and removed in September – October in both the 2015 and 2016 dry seasons. Two study locations from the original study of Whitworth et al. (2019) were removed because they had less than 12 jaguar and puma records required for analysis. This resulted in a total of 50 terrestrial camera trap stations (Table 1 for breakdown of cameras at each site). The camera traps were placed >500m apart and set to take 14s of video with a 30 second interval between the recordings. All videos were examined, and where it was possible, the species of the mammals and birds were determined. Data were extracted from camera trap images using exiftool (Harvey 2005, ver 11.25) and organised into csv files for analysis using the R statistical environment R (*R Core Team*, 2020). For full details of study design and detailed site descriptions, see Whitworth et al. (2019).

Jaguar and puma prey species were defined from the literature and identified from camera trap images: nine-banded armadillo *(Dasypus novemcinctus)*, common opossum *(Didelphis marsupialis),* collared peccary *(Pecari tajacu)*, white-lipped peccary *(Tayassu pecari)*, paca (*Cuniculus paca*), red brocket deer (*Mazama americana*), agouti *(Dasyprocta punctuata)*, lowland tapir *(Tapirus terrestris)*. Five bird species, pale-winged trumpeter *(Psophia leucoptera)*, razor-billed curassow *(Mitu tuberosum)*, grey tinamou *(Tinamus tao)*, great tinamou *(Tinamus major)*, and little tinamou *(Crypturellus soui)* thought to be potential prey of a similar body size and predominantly terrestrial were grouped into the category 'avian prey' (Emmons, 1987; Weckel et al., 2006). In the lowland Neotropics, these species collectively account for the much of the avian and mammalian biomass and relative abundance in the jaguar and puma diets (Novack et al. 2005; Foster et al. 2010; Miranda et al. 2018).

Table 1: Number of camera traps per site used in the analysis of the total terrestrial cameras available due to no detections of jaguars or pumas in brackets.

Site	Camera traps
Shintuya	9 (19)
Diamante	16 (19)
MLC	16 (20)
Romero	10 (10)

Data Analysis

(a) Temporal overlap

We eliminated photos of the same species captured fewer than 60 minutes apart from the same camera trap in order to obtain independent records (following Tobler et al., 2008). The timestamp that was registered on each photograph was used to categorise the images. The activity patterns of each species were calculated using the 'overlap' package in R version 4.0.4 (R Core Team, 2020). The generation of activity patterns for each species and the identification of predator and prey overlap were done using kernel density estimation. We calculated the overlap coefficient (Δ) for each pair of species and compared these between each sampling location. The overlap coefficient ranges from 1 (complete activity overlap) to 0 (no overlap). We used an Δ1 estimator, which was recommended for small sample sizes (<75 camera record) as recommended by Meredith and Ridout, (2014). Following Marcos-Ayala *et al*. (2020), coefficients were designated low ($\leq$ 0.5), medium (0.5-0.75) and high overlap ($\geq$0.75). To determine whether the two species had significantly different activity patterns, we performed a Watson two-sample test used for circular data (Botts et al., 2020). Species were divided into four categories: mostly nocturnal (between 90 and 70 percent of observations in the dark), mostly diurnal (between 10 and 30 percent of observations in the dark), and crepuscular (10 percent of observations in the dark and 50 percent of observations during the crepuscular phase – between and crepuscular between 06:00–07:00h and 18:00–19:00h), the rest of the species were classified as cathemeral.

(b) Spatiotemporal Segregation

To estimate spatiotemporal segregation for jaguar and puma, we used two methods. First, we estimated the time-to-encounter based on consecutive jaguar-puma and puma-jaguar camera trap records. To do this, we created a matrix of survey location, trap identity, date, timestamp of each independent camera trap image. From this we determined the time between consecutive recordings for each individual trap identity. We then took the mean of these times for each sampling location and all locations combined. Secondly, in accordance with Karanth et al., (2017), we generated a matrix for each species in which the rows corresponded to camera trap stations and the columns to the hourly intervals of the diel cycle as a whole. Each cell contained a total number of species detections. We determined the percentage of cameras and hourly intervals where each species overlapped by dividing the total number of cameras where a species was recorded in pairs and alone by the total number of stations where it was identified.

(c) Environmental variables affecting predator distribution

To identify explanatory environmental variables that may influence predator distribution in the study locations, we implemented a generalised linear model using jaguar and puma presence and absence at the individual camera trap level as the response. To quantify anthropogenic disturbance, we collected known variables that have previously been shown to have an impact on forest health and animal populations. A global dataset called the Human Impact Index (HII) takes into account how humans are affecting habitat decline (Sanderson et al., 2002; Kennedy et al., 2019, 2020). It contains the eight human stresses listed below, with a scale from 0 (least disturbed) to 50 (most disturbed): built environments; human population density; electrical infrastructure; croplands; pasturelands; highways; railroads; and navigable rivers (Venter et al., 2016). Distance to nearest community was used as a proxy for hunting (Whitworth et al. 2019) and calculated in QGIS using local knowledge of the area. Forest loss and locations of rivers were extracted from Google Earth Engine (Hansen et al., 2013; Pekel et al., 2016) and then distances from camera traps to each environmental variable were calculated in QGIS. As prey densities are likely to be related to predator presence, we reduced presence / absence of prey composition at each site using Nonmetric Multidimensional Scaling (NMDS) to two ordination axes and used these as compound variables. These axes represent prey biodiversity at each site, which can provide insights into predator-prey dynamics. Canopy cover, canopy height, shrub density, tree density, leaf litter cover and depth relate to forest structure and can have a large impact on how animals are distributed. They were also used as explanatory variables in the models and were recorded as part of the Whitworth et al., (2019) study (see paper for details of their metrics).

To further reduce the number of separate variables used in the models, we created a single human disturbance index by combining HII, distance to the nearest community, the number of photos of the camera trap with humans per site, and distance to the nearest area of forest loss using Principal Component Analysis (PCA). Using PCA we reduce the disturbance related variables to two components/axes. The first two axes contained the highest percentage (35% and 30%, respectively) of variance explained and as such were included in the regression analysis. To assess redundancy between explanatory variables, we conducted a nonparametric spearman correlation using the ‘cor’ function in R. None of the variables showed high correlation ($r>0.7$), and as such all were included in the model. Finally, a generalised binomial linear model was run to assess the impact of the above variables on the jaguar and puma distribution. Final models were chosen using a stepwise model selection, variables were removed based on a significance criterion of $p<0.05$ until all variables in the model were considered significant. NMDS and PCA analysis was performed in R using the package ‘vegan’ (Oksanen et al., 2016).

Results

In total, we found 119 independent records of jaguars, 152 records of pumas, and 2918 records of their nine main prey species or groups in the four sampled habitats. The highest capture rate for our focal predatory species was in the least disturbed location in Romero (jaguar n = 23, puma n = 26, Table 2).

Table 2: The quantity of independent records and the catch rate (per 1000 camera trap days) for jaguars, pumas, and their primary prey in four forest areas.

Species	Shintuya	Romero	MLC	Diamante
Jaguar	24 (18)	33 (23)	29 (9)	33 (12)
Puma	25 (19)	37 (26)	35 (11)	55 (20)
Collared peccary	34 (26)	112 (78)	67 (22)	104 (38)
Armadillo	20 (15)	3 (2)	49 (16)	12 (4)
Paca	138 (106)	69 (48)	72 (23)	95 (34)
Red brocket deer	50 (38)	37 (26)	36 (12)	68 (25)
Tapir	46 (35)	52 (36)	45 (15)	73 (27)
Agouti	1 (1)	228 (159)	12 (4)	524 (191)
Common opossum	1 (1)	16 (11)	13 (4)	66 (24)
White-lipped peccary	0	9 (6)	16 (5)	14 (5)
Avian prey	63 (47)	207 (145)	354 (115)	212 (77)

(a) Conspecific temporal activity between locations

Jaguars varied in their temporal activity patterns in each of the four study locations, with an average overlap coefficient 0.65 between pairs of study locations (Table 2). Activity patterns were more similar between Romero and Diamante (Δ1 = 0.75).

Although predominantly nocturnal in Romero, jaguars showed a peak of activity diurnally (See Appendix Figure A1 for kernel density overlap plots). Whereas in Diamante activity is reduced around mid-morning. The lowest overlap coefficient was between MLC and Diamante (Δ1 = 0.61). Jaguars were mostly nocturnal in Diamante, but MLC activity increased midday and decreased during the evening. See Appendix Table A2 for all diel activity classifications.

Puma activity was more similar between study sites with an average overlap coefficient of 0.73 (Table 3, Appendix Figure A1). The highest overlap was between Shintuya and Diamante (Δ1 = 0.81), with both species showing cathermal activity. The lowest overlap coefficient was between MLC and Romero (Δ1 = 0.65) where Romero puma activity was mostly nocturnal and MLC activity peaks midday and early evening, but activity decreased at night.

Table 3: Jaguar and puma daily activity pattern overlap coefficients (Δ1) at four study sites in the Peruvian rainforest (95 percent bootstrap confidence intervals are in parenthesis).

Species	**Location**	**Romero**	**MLC**	**Diamante**
Jaguar	Shintuya	0.63 (0.46 - 0.78)	0.66 (0.49 - 0.82)	0.62 (0.46 – 0.79)
	Romero	-	0.67 (0.50 - 0.83)	0.75 (0.58 – 0.91)
	MLC	-	-	0.61 (0.44 – 0.77)
Puma	Shintuya	0.71 (0.54 - 0.87)	0.76 (0.60 - 0.90)	0.81 (0.67 – 0.94)
	Romero	-	0.65 (0.48 - 0.81)	0.71 (0.58 – 0.85)
	MLC	-	-	0.72 (0.57 – 0.84)

Temporal activity patterns between sympatric predators

Activity patterns of jaguar and puma had a high overall coefficient of overlap (Δ1 - 0.88, Appendix Figure A1) and were not significantly different (p-value > 0.05, Appendix Table A3 for test results). However, jaguar and puma activity patterns varied between sites. At Shintuya, the overlap in activity between the two species was high (Δ1 = 0.79, p-value > 0.05) while in MLC, Diamante and Romero, medium overlap coefficients were observed (Δ1 = 0.65 – 0.72, p-value < 0.05, see Figure 2 for density overlap plots). In MLC jaguar activity peaked around noon, whereas puma activity peaked around 18:00. These patterns were reversed in Diamante, where puma activity peaked around midday and jaguar peaked around 18:00. Jaguar activity in Romero peaked around midday and early evening, whereas puma peaked at 12:00.

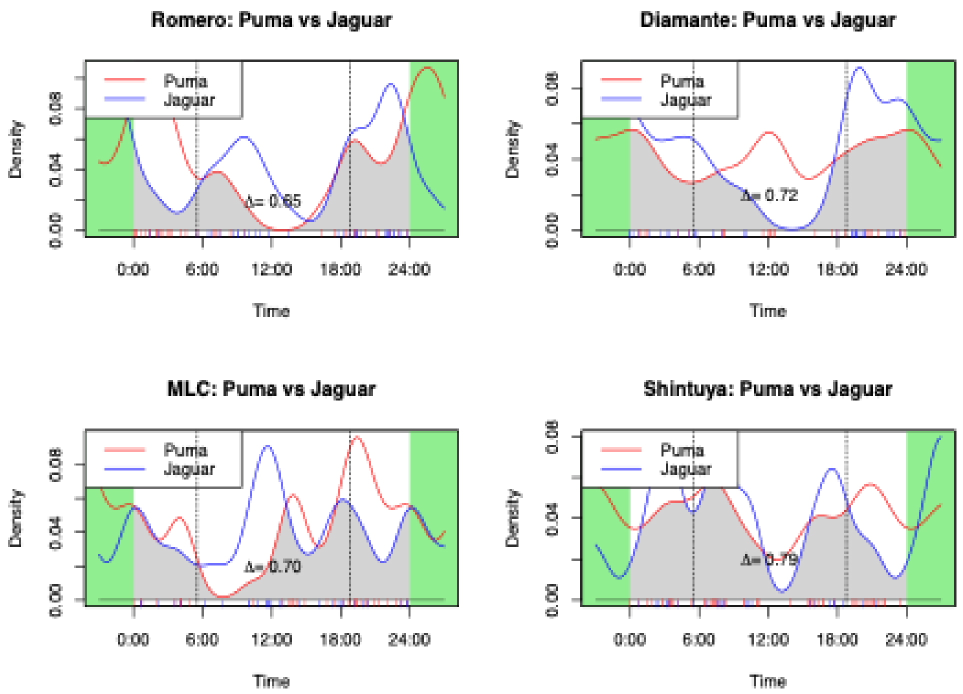

Figure 2: Density plot showing overlap of jaguar and puma for all locations.

Predator-prey activity between locations

Jaguar and puma did not have high temporal overlaps with the same prey at a study site, indicating potential targeting of different prey. However, the jaguar and puma shared a medium overlap with seven prey species (Table 4). The activity patterns of the jaguar had a high overlap, with no significant differences in activity with the armadillo (Δ1 = 0.79), opossum (Δ1 = 0.82), and tapir (Δ1 = 0.91) in Diamante (Table 3, Appendix Table A2 for the test results). Low overlap activity without significant differences in activity with agouti (Δ1 = 0.25), avian prey (Δ1 = 0.27), and peccary (0.28) in Diamante. All other jaguar-prey overlaps had medium coefficients (Δ1 = 0.5-0.75). Most of the prey species were nocturnal or mostly nocturnal, and this was largely consistent between sites (Appendix Table A2). Only peccary species were diurnal, while red-brocket deer was cathermal in all sites except MLC where it was mostly nocturnal. There was very little consistency in the strength of predator-prey overlaps between locations (Table 3, Appendix Table A3).

Puma had high overlap coefficients with no significant differences with red-brocket deer (Δ1 = 0.84, p-value > 0.05) and tapir (Δ1 = 0.78, p-value > 0.05) in Shintuya, Opossum (Δ1 = 0.79, p-value > 0.05) and paca (Δ1 = 0.85, p-value > 0.05) in MLC, tapir (Δ1 = 0.81, p-value > 0.05) and paca in Romero (Δ1 = 0.77, p-value > 0.05). In Diamante puma, it had a high overlap with red-brocket deer (Δ1 = 0.84, p-value > 0.05). Low overlaps were only recorded in Romero with avian spp (Δ1 = 0.27, p-value < 0.05), agouti (Δ1 = 0.26, p-value < 0.05), and collared peccary (Δ1 = 0.28, p-value < 0.05). All other prey species had medium overlap coefficients (Δ1 = 0.5-0.75). See Table 3 for all overlap coefficients.

Table 4: Overlap coefficients between predator and prey in each location. NA = data deficient records. * = high overlaps (Δ1>0.75), bold = low overlaps (Δ1<0.50), no format = medium overlap (Δ1 = 0.50-0.75).

Species	Location	Agouti	Armadillo	Avian_spp	Deer	Opossum	Paca	Peccary	Tapir	W_peccary
Jaguar	Shintuya	NA	0.60	0.71	0.73	NA	0.50	0.74	0.62	NA
	Romero	**0.44**	NA	**0.46**	0.68	0.66	0.62	**0.47**	0.66	NA
	MLC	0.63	0.50	0.67	0.61	0.66	0.65	0.60	0.57	0.55
	Diamante	**0.25**	0.79*	**0.27**	0.71	0.82*	0.80*	0.28	0.91*	**0.22**

Puma	Shintuya	NA	0.65	0.67	0.84*	NA	0.68	0.62	0.78*	NA
	Romero	**0.26**	NA	**0.27**	0.64	0.74	0.77*	**0.28**	0.81*	NA
	MLC	0.54	0.67	**0.47**	0.65	0.79*	0.85*	**0.46**	0.72	**0.42**
	Diamante	0.50	0.61	0.52	0.84*	0.59	0.58	0.52	0.72	**0.45**

(b) Spatio-temporal activity

The time-to-capture results showed an average of 24.09 days (95% CI: 19.96–29.22) from the time a jaguar was captured on camera to the time a puma was captured on the same camera at all sites. The converse, the jaguar captured after puma, was an average of 28.48 days (95% CI: 24.85–32.11). The lowest capture interval for a jaguar detected after a puma was 1.66 days and 1.06 days for a puma detected after a jaguar. Moreover, mean times to detect in forest types were between 28 and 40 days (Appendix Table A1), but lower mean times were recorded for jaguar – puma in Diamante (13 days, 95% CI: 10.14–16.69) and jaguar – puma (11.58 days, 95 % CI: 8.95–14.25) and puma – jaguar (21.25 days, 95% CI: 15.32 – 27.18) in Shintuya.

The results related to the proportion of cross-over visitation (i.e., when both species were observed the same camera trap station and hourly interval) revealed 31% of the total jaguar visits and 27% of the total puma visits crossed (Table 5). These proportions are low when compared to the purely temporal overlap patterns, which revealed high overlap coefficients.

Table 5: Averaged across hourly intervals, the percentage of camera stations where (i) one species was found by itself, without the presence of the other species, or (ii) both species were active

Location	Species	Cameras Visited	Detected together	Percent at same camera
Shintuya	Jaguar	7	2	29%
	Puma	4	2	50%
Romero	Jaguar	9	2	22%
	Puma	10	2	20%
MLC	Jaguar	6	3	50%
	Puma	10	3	30%
Diamante	Jaguar	11	3	27%
	Puma	13	3	23%
Combined	Jaguar	32	10	31%
	Puma	37	10	27%

(c) Habitat preferences

To test which environmental variables influenced predator distribution we used a generalised linear model with stepwise removal of nonsignificant variables. Presence of Jaguar was positively associated with canopy height and negatively associated with distance to water, and prey composition – prey species decrease with increase of jaguar presence (Table 6). Puma was negatively associated with the human disturbance index, suggesting they are not found where there is high disturbance, and similarly negatively associated with distance to water.

Table 6: Generalised linear model output.

Species	Effects	Estimate	Standard error	df	z-value	p-value
Puma	Distance to water	-2.3724	0.8883	35	-2.671	<0.01
	Human disturbance (PC1)	-1.1882	0.5654	35	-2.102	<0.05
Jaguar	Canopy height	0.1543	0.0699	34	2.207	<0.05
	Distance to water	-2.1704	0.8099	34	-2.680	<0.01
	Prey composition (NMDS1)	-2.6196	1.2619	34	-2.076	<0.05

Discussion

Our study explored the temporal and spatial coexistence of pumas and jaguars, and their main prey, in habitats with varying degrees of historical human disturbance in Peru. Our findings suggest that the observed spatio-temporal segregation and fine-scale changes in activity peaks may contribute to their coexistence. However, there is the possibility of abundant prey availability, pointing towards a potential mechanism that could also enable their coexistence. Furthermore, our study revealed distinct behavioural differences in both felid species at sites with higher levels of human activity.

(a) Activity patterns of felids

The results of this study revealed that jaguar activity varied between habitats and was not consistent. Diel activity patterns were mostly cathermal for jaguars in three of four sites, which is consistent with other study regions, Brazil (Porfirio et al., 2016), Belize (Monette et al., 2020), Mexico (Hernández-Saint Martín et al. 2013) and other areas of Peru (Emmons 1987). However, in Diamante, jaguars were mostly nocturnal (76% of observations at night). There are several possible explanations for this change in activity pattern. One possibility has been suggested by Cavalcanti and Gese, (2010) and Foster et al (2013) who reported diurnal habits in different Brazilian biomes, citing behavioural changes in connection to activity patterns of the main prey e.g. increased abundance of the crepuscular Capybara. Therefore, in Diamante, the change in diel activity at our site could be related to tracking a main prey item, the lowland tapir, with whom the jaguar shared a strong overlap coefficient ($\Delta1 = 0.91$). Alternatively, previous studies have also reported a change in behaviour where increased anthropogenic disturbance or habitat alterations have occurred (Brazil, Astete, 2008); southern Belize, Dobbins et al., 2017). Diamante is subject to selective logging and contains a small air strip, altering the surrounding habitat. However, exploiting the cathermerality niche gives animals flexible strategies to adapt to selective pressures (Hill, 2006). This could be a reason why overall overlap coefficients were not high for jaguars at different sites.

The cathermal activity pattern of pumas in Shintuya and Diamante was consistent with previous studies (Bitetti et al., 2010; Negrões Soares et al., 2011; Ayala et al., 2020). However, in MLC and Romero, pumas were mostly nocturnal, corresponding to patterns of lowland tropical forests in Belize (Harmsen et al., 2009). Although uncommon in the literature, we found a significant difference between the temporal activity of pumas and jaguars (Harmsen et al., 2009; Romero-Muñoz et al., 2010; Santos et al., 2019) at the Romero location, which may indicate an evasion strategy. However, our data cannot discern whether that was mutual between the two species or if different factors were the cause. For example, pumas shared a high overlap with the nocturnal paca in MLC and Romero, while in Shintuya and Diamante they followed a similar activity pattern with deer and tapir, suggesting that prey selection could be a driver of changing activity patterns. The nocturnal change in diel activity in MLC could also be a result of increased human activity at this site, as it is an active centre of research and ecotourism. Chávez Tovar, (2010); Foster et al., (2013); Rodríguez-Soto et al., (2013) have reported that pumas respond negatively to increased human activity. Additionally, we observed large mean detection intervals between jaguar and puma (30-40 days at MLC) so it is unlikely that jaguars were the cause of puma-altered activity. Puma temporal activity between all sites were largely consistent, with the largest overlap between Shintuya and Diamante ($\Delta1 = 0.81$). This coincided with two main preys (tapir and deer). While the lowest overlap observed was between Romero and MLC ($\Delta1 = 0.65$), likely due to increased human activity in MLC. Romero, located inside Manu National Park, is strictly protected, with few tourists visiting, whereas the MLC has visitors throughout the year.

(b) Spatial and temporal overlap of felids

Our results did not show temporal partitioning between felids at three of our four study sites, consistent with similar studies in the literature (Scognamillo et al., 2003; Harmsen et al., 2010; Herrera et al., 2018; Foster et al., 2013; Porfirio et al., 2016). However, fine-scale activity peaks potentially facilitate co-existence. For example, in Diamante, puma activity peaks around noon, whereas jaguar activity peaks around 6:00 pm. At MLC, jaguar activity peaks at 12:00 p.m. and puma peaks at 6:00 p.m. Finally, in Shintuya, where the overlap was highest (0.79), jaguar and puma still showed fine-scale changes in activity peaks. Similarly, habitat partitioning has been reported in other studies (Sollmann et al. 2012; de la Torre et al. 2017; Palomares et al. 2017; Alvarenga et al. 2018, Figel et al. 2021). We found on average 24.10 days (Jaguar-puma) and 28.48 days (Puma-jaguar) between when a different predator species was recorded at the same camera trap location. This highlights that if these sympatric predators are active at similar times of day, they can co-exist by hunting in different areas, potentially supporting co-existence in our study areas. However, evidence of spatial overlap of jaguar and puma has also been reported in other studies, adopting other avoidance techniques to allow co-existence, for example, food resources or/and partitioning of their activity period (Bitetti et al., 2010; Astete et al., 2017; Boron et al., 2018; Santos et al., 2019).

Prey activity

Prey availability or main prey activity may be more important determinants of both felids' activity patterns than avoidance of one another, according to earlier research (Carrillo et al. 2009; Foster et al. 2013; Mendes Pontes and Chivers 2007; Rabinowitz and Nottingham 1986; Schaller and Crawshaw 1980; Sunquist and Sunquist 2002). In our sites, jaguars and pumas significantly overlapped with some of their main prey species, as noted by other studies (Foster et al. 2013; Hernández-Saintmartín et al. 2013). Interestingly, neither jaguar nor puma strongly overlapped with that of the same prey species at any of our study locations, which indicates the targeting of different prey. Furthermore, neither predator had strong overlaps with peccaries, which has extensively been recorded elsewhere (Harmsen et al 2009; Hernández-Saintmartín et al. 2013; Foster et al,. 2013). A question arising from these results is whether they targeted different prey or whether it was by chance. Both felids showed cathemeral activity (active throughout day and night), increasing the probability of encountering more prey. Therefore, they could target prey during their inactive periods (Hernández-Saintmartín et al. 2013), which may explain their medium/low overlap with peccaries. It is likely that the activity schedules of jaguars and pumas were influenced by those of their prey, as there was little time separation between them at most sites.

(c) Habitat preferences

Puma presence across our study sites was negatively correlated with human presence, in agreement with other studies (Emmons 1987; Chávez, 2010; Foster et al., 2010; Rodríguez–Soto et al., 2013). However, other studies have shown that puma are more adaptable to human disturbances (Knopff et al., 2014; Figel et al., 2021). Our measure of human disturbance incorporates different aspects of human activity which could be a reason for differences from the aforementioned studies. Jaguars and pumas were negatively correlated with distance to water which is contrary to other studies (Crawshaw & Quigley 1991; De Angelo et al,. 2011; Matos Dias et al,. 2019). A possible explanation is that all sites are located off the main tributary where boats frequently pass by, causing noise disturbance. Another reason could be the availability of alternative water sources/streams at each site. The presence of jaguars was positively correlated with the height of the canopy, as Davis et al. (2010) and Sunquist & Sunquist (2002) noted. Canopy height is associated with undisturbed dense forests, species diversity, and other ecosystem functions (Tao et al., 2016), whereas loss of canopy has been associated with decrease in vertebrate biomass (Thoisy et al., 2016), This obviously highlights the importance of safeguarding tropical rainforests (Wright & Muller-Landau 2006). Although jaguars and pumas share habitats, it is improbable that any of our tested covariates facilitated the coexistence of these sympatric predators.

Conclusions

Our study provides information on the behaviour of jaguars and pumas in areas with different levels of human disturbance. Spatiotemporal differences and prey activity seem to be the primary factors enabling the co-existence of these sympatric predators in the study locations. Our results largely correspond with the literature; however, interestingly there were some sites which revealed different behaviours. For instance, the research station MLC, which is primarily inhabited by humans, experienced changes in puma behaviour. However, the activities of jaguars remained unaffected. Similarly, at the site of Romero located in the National Park with comparatively lower human disturbance, similar patterns were observed. This highlights that another factor could be driving the changes in behaviour. As noted by the gamut of other studies, prey selection is the likely driver in the behavioural patterns of these predators. We also showed that both were adaptable to different study sites and changes in behaviour could be driven by prey rather than the habitat per se. As although jaguars and pumas share habitats, it is improbable that any of our tested covariates facilitated the coexistence of these sympatric predators.

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Appendix

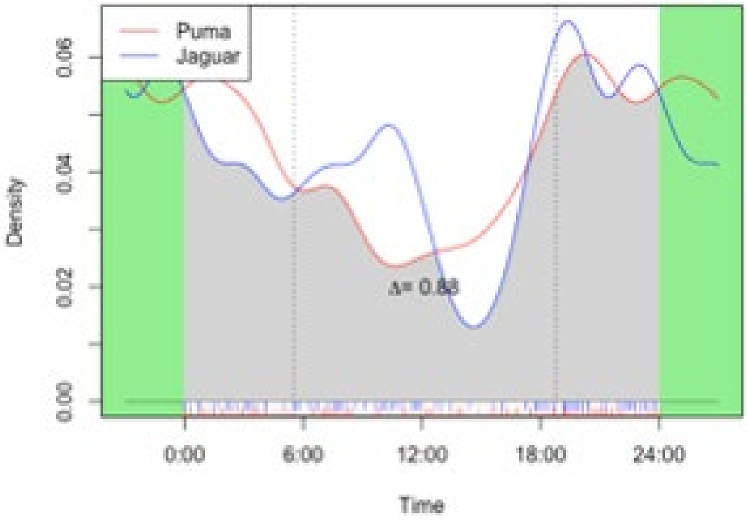

Figure A1: Density plots showing overlap of puma vs jaguar at each site

Table A1: Mean time (days) to detect across each camera trap location for jaguars and pumas.

Combination	Location	n	Mean detect (days)	**CI lower**	**CI upper**
Jaguar – Puma	Shintuya	25	11.58	8.41	14.75
Puma – Jaguar	Shintuya	25	21.25	14.52	27.97
Jaguar – Puma	Romero	37	34.24	21.22	47.26
Puma – Jaguar	Romero	37	28.78	18.40	39.17
Jaguar – Puma	MLC	34	40.44	23.37	57.52
Puma – Jaguar	MLC	34	31.04	9.42	52.65
Jaguar – Puma	Diamante	55	13.41	8.62	18.21
Puma – Jaguar	Diamante	55	32.31	24.48	40.14
Jaguar – Puma	All	151	24.10	18.52	29.67
Puma – Jaguar	All	151	28.48	23.55	33.41

Table A2: Numbers of independent photographs (>60mins apart) of mammals recorded along trails (total) and percentage of photographs that were nocturnal (N%; 18:30-05:30 h), diurnal (D%; 06:30-17:30 h), or crepuscular (C%; 05:30-06:30 h and 17:30-18:30 h).

Location	Common name	Scientific name	Total	C (%)	D (%)	N (%)	Classification
Shintuya	Jaguar	*Panthera onca*	24	17	46	38	Cathermal
	Puma	*Puma concolor*	25	8	40	52	Cathermal
	Agouti	*Dasyprocta punctata*	1	0	0	100	Nocturnal
	Red Brocket Deer	*Mazama temama*	50	16	32	52	Cathermal
	Collared Peccary	*Pecari tajacu*	34	9	65	26	Mostly diurnal
	Paca	*Cuniculus paca*	138	5	30	64	Cathermal
	Nine-banded Armadillo	*Dasypus novemcitus*	20	10	25	65	Mostly nocturnal
	Common Opossum	*Didelphis marsupialis*	1	0	100	0	Diurnal
	White lipped peccary	*Tayassu pecari*	0	0	0	0	NA
	Lowland tapir	*Tapirus terrestris*	46	17	22	61	Cathermal
Romero	Jaguar	*Panthera onca*	33	12	33	55	Cathermal
	Puma	*Puma concolor*	37	8	16	76	Mostly nocturnal
	Agouti	*Dasyprocta punctata*	228	23	77	0	Diurnal
	Red Brocket Deer	*Mazama temama*	37	19	41	41	Cathermal
	Collared Peccary	*Pecari tajacu*	112	13	86	1	Diurnal
	Paca	*Cuniculus paca*	69	10	1	88	Nocturnal
	Nine-banded Armadillo	*Dasypus novemcitus*	3	0	0	100	Nocturnal
	Common Opossum	*Didelphis marsupialis*	16	13	0	88	Nocturnal
	White lipped peccary	*Tayassu pecari*	9	0	89	11	Diurnal
	Lowland tapir	*Tapirus terrestris*	52	4	6	90	Nocturnal
MLC	Jaguar	*Panthera onca*	29	14	48	38	Cathermal
	Puma	*Puma concolor*	35	6	26	69	Mostly nocturnal
	Agouti	*Dasyprocta punctata*	12	0	58	42	Cathermal

	Red Brocket Deer	*Mazama temama*	36	11	14	75	Mostly nocturnal
	Collared Peccary	*Pecari tajacu*	67	9	75	16	Mostly diurnal
	Paca	*Cuniculus paca*	71	13	21	66	Mostly nocturnal
	Nine-banded Armadillo	*Dasypus novemcitus*	49	0	6	94	Nocturnal
	Common Opossum	*Didelphis marsupialis*	13	8	15	77	Mostly nocturnal
	White lipped peccary	*Tayassu pecari*	16	13	81	6	Diurnal
	Lowland tapir	*Tapirus terrestris*	45	4	9	87	Nocturnal
Diamante	Jaguar	*Panthera onca*	33	12	12	76	Mostly nocturnal
	Puma	*Puma concolor*	55	5	44	51	Cathermal
	Agouti	*Dasyprocta punctata*	524	12	87	1	Diurnal
	Red Brocket Deer	*Mazama temama*	68	12	34	54	Cathermal
	Collared Peccary	*Pecari tajacu*	104	7	88	5	Diurnal
	Paca	*Cuniculus paca*	95	5	1	94	Nocturnal
	Nine-banded Armadillo	*Dasypus novemcitus*	12	8	0	92	Nocturnal
	Common Opossum	*Didelphis marsupialis*	66	14	0	86	Nocturnal
	White lipped peccary	*Tayassu pecari*	14	0	100	0	Diurnal
	Lowland tapir	*Tapirus terrestris*	73	12	10	78	Mostly nocturnal

Chapter 4 – Discussion

Anthropogenic disturbance has resulted in the loss of 239 million hectares of rainforest worldwide since 1990 (Staeck, 2022). This is a significant amount of destruction and has a harmful impact on the animals that live in these forests (Constantino, 2016). Behavioural changes in response to anthropogenic disturbance can have serious consequences for the health and well-being of individual animals and for the stability of whole ecosystems (Tuomainen and Candolin, 2011). In this sense, it is important to understand how animals alter their behaviour in response to anthropogenic disturbance in order to develop conservation strategies that minimise the impact of human activities on wildlife. The aim of this thesis has been to study the impact of anthropogenic disturbances on the behaviour of jaguars, pumas, and leaf cutter ants. This thesis has shown that **(Aim 1)** leaf cutter ants respond negatively to noise disturbance and **(Aim 2)** jaguars and pumas alter activity patterns across different disturbance histories.

Key Findings

Aim 1

This is the second study to directly investigate noise disturbance in foraging social insects. I found that the introduction of white noise decreased the speed of the ant, but the abundance was similar between treatments. The decreased speed under disturbance supports the notion that ants adapt behaviour. Interestingly, the results of this study were contradictory to Byrne et al., (2022). They found that ants increased speed under increased noise levels. The reason for this is not clear, however, a possible explanation could be colony personality. Previous studies have found that colonies of ants to have similar responses to environmental changes, but different behaviours. For example, *Pogonomyrmex occidentalis* colonies varied in the temporal pattern of foraging activity and also in the thermal range in which they forage (Cole et al., 2010). The black harvester ant colonies differed in speed and responsiveness to different foraging and disturbance situations (debris removal, response to alarm etc), however, their speed was similar in dry conditions (Pinter-Wollman et al., 2012).

Another important factor which could drive differences between the colonies used in Byrne et al., (2022) and the current study is the different noise treatment regimes. In our experiment, the ants were exposed to noise 75% of the time, while in Byrne et al., (2022) the ants were exposed 50% of the time. Our findings support the idea of colony personality by showing that colonies of the same species may respond differently to noise disturbance. However, additional research is needed, considering the length of time colonies are exposed to noise and the use of similar sound profiles. Furthermore, research should be carried out to determine whether different colonies of the same species that are strongly affected by one stimulus (e.g., noise) respond differently to another stimulus (e.g., predation), in order to determine whether personality is driving the changes.

Aim 2

Jaguars and pumas co-exist throughout the tropics and are under increasing pressure from anthropogenic disturbance. Both species are apex predators and have crucial roles in the shaping of the ecosystem. Understanding how they respond to disturbance is a crucial step toward developing effective conservation management plans that limit their decline. However, multiple studies have reported different behavioural patterns. For example, we found that jaguar cathermal diel activity was similar to other studies. However, at one site, the jaguars were predominantly nocturnal rather than cathermal. Puma's activity was consistent with other studies, but in those studies, Puma's activity was different. With cathermal and nocturnal diel activity reported. This highlights that generic patterns may not be useful when we look at different habitats and highlights the need for specificity when making generalisations about species behaviour so that conservation measures are made with the most accurate information possible. In addition, prey species have been suggested as a mechanism to explain the coexistence of these two predators and how they influence each other's activity patterns. We found that jaguars and pumas did not overlap with the same prey species at the same site, suggesting that they target different species to avoid conflict and coexist. However, a challenge to discern from our results is whether they were targeting specific prey or whether they were by chance. For example, in two of our site's puma activity was nocturnal, and it overlapped with that of its prey. However, it could be increased human activity that drove the change in activity rather than hunting prey. At the other sites, jaguar and puma showed cathermal activity. This behaviour increases the probability that they will encounter more prey and can facilitate avoidance strategies. As noted by the gamete of other studies, prey selection is the likely driver in the behavioural patterns of these predators. The study design is also a limitation in our study. Primarily, large cats use trails. However, if they are spooked or tracking a prey item, they could use any area of the forest. Therefore, large areas could go undetected. To ensure accurate assumptions can be made, full coverage of the study sites (on-off-the-trail) is required. I have shown that jaguars and pumas are adaptable to different study sites, which are likely driven by prey.

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