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Hunter territoriality creates refuges for threatened primates

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Summary

Unsustainable hunting threatens biodiversity in the tropics through the removal of key seed-dispersing frugivorous primates. Traditionally, hunting in the Amazon Basin was managed through hunter territoriality, with the threat of social sanctions for overexploitation. We examined hunter territoriality and differential prey selection as alternative hypotheses to central-place foraging. Territoriality occurred beyond common hunting grounds, which were on major rivers and immediately surrounding the community. Hunters displayed selectivity in prey choice, with 50% of hunters not hunting primates. The combination of hunter territoriality and differential prey selection means that over 22% of the hunted area of the Sucusari river basin could be considered primate refuge. Of the remaining hunted area, 16% was hunted relatively little by primate hunters. We suggest that the combination of territoriality and selection against primates creates refuges, mitigating the effects of sustained hunting pressure and contributing to the conservation of these species.

Introduction

The unparalleled biodiversity (Brown 2014) and productivity of Amazonian forests (Beer et al. 2010) are maintained in part by key ecosystem services provided by seed dispersers, such as frugivorous primates (Link & Fiore 2006, Arévalo-Sandi et al. 2018). The survival of many of these primate species, particularly large-bodied species that reproduce slowly (Mayor et al. 2017), is threatened by unsustainable hunting, resulting in large-scale loss of ecosystem services (Barrera Zambrano et al. 2008, Brodie et al. 2009). The sustainability of hunting is often modelled using assumptions based on the central-place foraging theory (Orians & Pearson 1979), in which hunters exploit resources near to the community or at other accessible points such as rivers first, producing a distance-based gradient of game abundance and availability (Charnov 1976, Winterhalder 2001, Venkataraman et al. 2017). In the absence of large source areas, primates may be extirpated from a region even with relatively light hunting pressure (Levi et al. 2009, 2011). The management of primate hunting is critical to the conservation of Amazonian biodiversity.

While primates have been hunted by Indigenous groups in the Amazon for millennia, recent evidence has shown that the protection of Indigenous lands and ways of life is intricately linked to the conservation of threatened primates (Estrada et al. 2022). Sparse human populations and traditional adaptive management systems (Gadgil 1998, Berkes et al. 2000, Colding & Folke 2001) may have contributed to the persistence of primates facing hunting pressure (Alvard 1995). One type of traditional management is territoriality of hunters (Dyson-Hudson & Smith 1978), where restraint from the exploitation of others' resources is governed by a fear of social sanctions. Territorial behaviour can be expected when game resources are moderate in density and evenly distributed and hunters can predict their location (Winterhalder 2001). These conventions spread out hunting pressure across the landscape, which increases sustainable harvest limits, and although widespread they are often employed without hunters acknowledging the role that territoriality plays in resource conservation (Gadgil et al. 1998). However, the erosion of traditional social systems may result in the abandonment of adaptive management practices, endangering species that were previously protected from overexploitation (Gadgil et al. 1998).

The Maijuna people are one of the most vulnerable Indigenous groups in Peru, with fewer than 600 individuals remaining in four communities (Gilmore et al. 2010). Their ancestral lands are currently threatened by a proposed highway development project, which would result in the destruction of both the ecosystem and the traditional culture and livelihoods of the Maijuna. Demonstrating ties between Maijuna culture and the conservation of natural resources, including wildlife, is critical to preserving the protected status of the region. This study aims to test whether the central foraging theory holds in the presence of territoriality among the

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Fig. 1. Diagrammatic map of the study site, the Maijuna community of Sucusari, the titled lands of the Sucusari community and the Maijuna–Kichwa Regional Conservation Area (MKRCA) in the north-eastern Peruvian Amazon.

hunters of the Maijuna community of Sucusari (Peru) and whether that territoriality, alongside partial prey preferences, could act as an adaptive management system for primate conservation. In this case, we describe territoriality as a passive strategy for spreading hunters across the landscape and maximizing the benefits from hunting, in which families willingly separate their hunting zones; we do not imply a defence of resources. We demonstrate that territoriality between families creates spatial heterogeneity in hunting pressure on primates across the landscape, but hunting was predicted to be heaviest surrounding the community, camps and major rivers and trails, following the central foraging theory. We found that large portions of the river basin may act as primate refugia due to the decision-making of individual hunters.

Methods

Study site

The Maijuna Indigenous community of Sucusari on the Rio Sucusari (Loreto, Peru; 72.92995° W, 3.24373° S; Fig. 1) is c. 120 km by river from the city of Iquitos, the commercial and political centre of Loreto. The titled land of the community encompasses 4771 ha and adjoins the Maijuna–Kichwa Regional Conservation Area (MKRCA), a 391 039.82-ha protected area collaboratively managed by Maijuna and Kichwa Indigenous communities and the regional government (El Peruano 2015). Sucusari has a population of 166 residents made up of monofamilial and plurifamilial households; 59% are ethnically Maijuna, 35% are mestizos and 6% are Kichwa (Roncal et al. 2018).

Subsistence strategies of community members include hunting, fishing, swidden-fallow agriculture and the gathering of various non-timber forest products (Gilmore 2010). Community members sell agricultural products and non-timber forest products such as game meat for income in the city of Iquitos, in towns surrounding their communities on the Napo River and in the market of Mazán (Gilmore 2010). Only men hunt in Sucusari (Roncal et al. 2018), hunting from canoes and on foot and at mineral lick sites located across the river basin (Gilmore et al. 2020). Hunters also hunt opportunistically from boats during travel when the hunter was not actively searching for prey but had a weapon available to them in the boat in case of a chance encounter with a game animal. All hunters hunt with shotguns or with machetes for slow-moving game species.

Data collection and analysis

We conducted weekly semi-structured interviews (Berg & Lune 2014) with 19 hunters (90.48% of all active hunters) in Sucusari to capture hunter territoriality and decision-making processes on prey selection and the economics of hunting for a 10-month period from September 2018 to June 2019. The mean age of hunters interviewed was 41 years old (range: 22–68 years). Of the 19 hunters interviewed, 10 were ethnically Maijuna, 8 were mestizo and 1 was Kichwa. If a hunter was not home when we visited his house, we made at least two more attempts to contact them during the days immediately following the initial visit. If a hunter was still not at home after three visit attempts, we gathered the data for that week during the following week's interview. During the interview, for each hunt we asked the hunter to draw the route they took on a provided base map, which included relevant landmarks such as rivers, streams, hunting camps and mineral licks, and to indicate which animals they encountered and if they had attempted to kill the animal (see Griffiths & Gilmore 2022, Griffiths et al. 2022). If they did not try to kill the animal, we asked why they chose not to. At the end of the study, to evaluate the degree to which hunters recognize differences in spatial use of the landscape, we asked questions about their preferred hunting locations and zones and why those locations were preferred. We also asked each hunter to indicate their hunting zone on the base map. Finally, we asked scenario-based questions about hunting zones, such as: 'If you wanted to, could you hunt in someone else's zone?'.

We digitized all hunter tracks in *ArcGIS* (ESRI 2018). To analyse the hunting zones of different families, we first grouped hunters into family groups. Only hunters who hunted more than 10 times during the study period were considered in the territory analyses ($n = 16$). Hunters that were linked by direct family ties (e.g., brothers or father/son) or direct marriage ties (e.g., married into a hunting family) were grouped together for family-level analyses based on data gathered from interviews showing that hunters in the same family hunted in the same zone. We used track data from interviews to calculate the zone of each family, excluding opportunistic hunts. Hunter tracks were converted to raster data in a 1 km × 1 km grid, a resolution chosen based on measured error in hunter reporting (Griffiths et al. 2021, 2023), where the value in each cell corresponded to the total number of kilometres walked by the family in that cell – a measure of hunting effort (Sirén et al. 2013). Hunting effort is used as a proxy for hunting pressure exerted by hunters on the grid cell. We summarized the overlap of territories by counting the proportion of cells that were only visited by one family throughout the study period. We then assessed the

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prevalence of common hunting grounds surrounding the community and along the two major rivers in the basin using a generalized linear model framework. We applied a generalized linear model with a Poisson distribution and response variable as the number of families that used each cell (n = 302). We used the distance from the centre of the cell to the community and whether or not the cell was located on one of the two major rivers (binary) as covariates, as well as the interaction between them. We used an information-theoretic framework for model selection (Burnham & Anderson 2002), comparing the Akaike information criterion (AIC) values of each unique covariate combination and choosing the model with the lowest AIC value as the optimal model. Covariates were checked for collinearity (Dormann et al. 2013) and full models were checked for overdispersion before proceeding with model selection.

As many hunters in Sucusari reported during interviews that they do not kill primates (Griffiths et al. 2022), we assessed the prevalence of primate refuges in the river basin. We calculated the proportion of the total hunting pressure in each grid cell that was contributed by hunters who do not kill primates. Cells that were only visited by hunters who do not kill primates (100% of contributed hunting pressure) were considered hunted primate refuges. We compared the area of primate refuge space and areas with relatively little hunting pressure on primates (<20% of total hunting pressure of the cell) to the total hunted area in the river basin.

To assess how the movement of primate hunters in Sucusari aligned with central foraging theory, we calculated predicted hunting pressure on primates using the distance-based model reported by Griffiths et al. (2021, 2023; cell size 1 km × 1 km). This generalized linear model assumes that hunters may radiate from four potential access points – the community, hunting camps, major rivers and major hunting trails – and that hunting pressure decreases with distance from these points. The model also takes into account movement cost associated with landscape factors such as elevation, slope and surface roughness (Griffiths et al. 2021, 2023). We divided each cell by the total predicted hunting pressure of all cells to yield a proportion of the total predicted hunting pressure in each cell. We then multiplied the predicted proportion of hunting pressure in each cell by 0.459 – the proportion of measured hunting pressure that came from primate hunters – to yield a predicted spatial spread of hunting pressure by primate hunters. We calculated the actual spatial spread of hunting pressure on primates by dividing the measured hunting pressure in each cell by the total hunting pressure exerted by primate hunters (total kilometres walked), so that each cell held a proportion of the total measured hunting pressure value. We visually compared maps of the predicted spread of hunting pressure on primates and the actual spread of hunting pressure on primates to examine how primate hunters conformed to central foraging theory.

Results

We conducted 780 interviews capturing data on 671 unique hunts, then another set of interviews with 19 hunters at the end of the study. All hunters stated in their interviews that they each had a hunting zone in the river basin where they would go to hunt and rarely entered others' zones, although they could if they chose to. Overall, 302 grid cells, or an area of 302 km^2, were hunted by the 16 hunters whose territories were assessed, who were grouped into six families. Upon calculating hunters' territories, 46% of cells were visited by only one family, 28% of cells were visited by two families

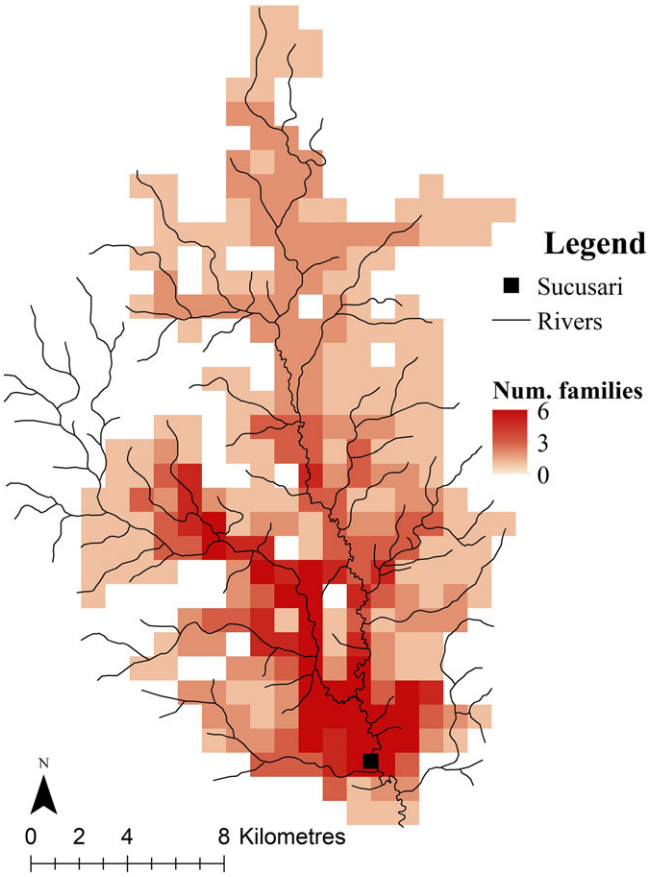


Fig. 2. Diagrammatic map showing the number of families that visited each hunted cell in the Sucusari river basin.

and 12% of cells were visited by three families during the study period (Fig. 2). When cells along the major rivers were excluded, 53% of cells were visited by only one family. The mean territory size for individual families was 103.83 km^2 (SD = 74.57, range = 38–224). The optimal model (df = 3, w = 0.59, explained deviance = 0.41) for predicting the number of families that visited each cell included covariates of distance from the community (coefficient = −0.039, SE = 0.0059) and the presence of a major river (coefficient = 0.53, SE = 0.091). One alternative model fell within 2 AIC points of the optimal model (ΔAIC = 0.76), which included river presence, distance from the community and their interaction; however, this model yielded the same trends as the optimal model. Model results showed that cells closer to the community and along rivers were visited by more families than those farther from the community and on land (Fig. S1).

We examined the spatial use of the landscape of primate hunters versus non-primate hunters. Overall, eight hunters out of the 16 analysed indicated that they do not hunt primates. On a family level, two families hunted primates, two families avoided primates and two families had individual hunters who either hunted or avoided primates. The map of the predicted spread of hunting pressure on primates differed from the measured spread of hunting pressure on primates (Fig. S2). Following central foraging theory and cost surfaces, hunting pressure on primates was predicted to be the heaviest immediately surrounding the community, hunting camps and major rivers and hunting trails. Hunting camps and points along rivers and trails that were closer to the community were predicted to experience heavier hunting

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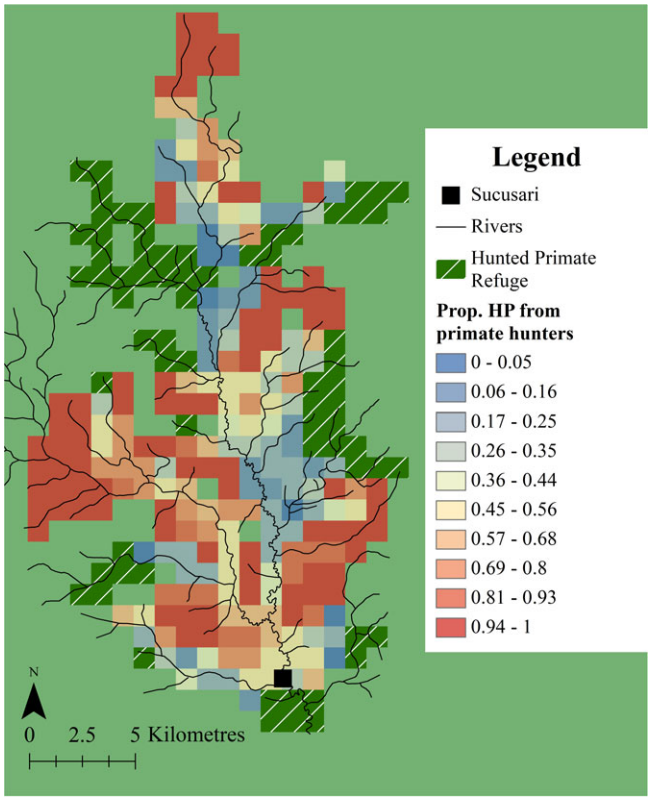


Fig. 3. Diagrammatic map of potential primate refuges in the Sucusari river basin, showing the cells that experienced no hunting (unhunted refuges, green), those that were hunted by non-primate hunters only (hunted primate refuges) and the proportion of each cell's total hunting pressure (HP) that came from primate hunters in every other hunted cell.

pressure than those further from the community. The map of actual hunting pressure on primates showed distinct areas in the eastern, north-western and north-eastern parts of the river basin, which experienced relatively little hunting pressure on primates in comparison (Fig. S2).

We examined these areas for the prevalence of primate refuges. Of the 302 km^2 that were hunted, 68 km^2 (23%) were hunted exclusively by hunters who do not kill primates (Fig 3). Within this area, 14 km^2 were constituted by fragments 1–5 km^2 in size. The mean refuge area was 6.18 km^2 (SD = 6.42) and the largest contiguous fragment was 22 km^2 (Fig. 3). Overall, 234 km^2 of the catchment area were hunted either exclusively by hunters who do kill primates or by both groups of hunters (Fig. 3). Within this area, 38 km^2 (16% of cells) had at least 80% of their hunting pressure attributed to hunters who do not kill primates, and 155 km^2 (66% of cells) had at least 50% of their hunting pressure attributed to hunters who do not kill primates. Hotspots of hunting pressure on primates also occurred, with several cells only being hunted by hunters who target primates.

Discussion

All hunters recognized a distinct zone as their own hunting territory and indicated that they do not enter others' zones, although they could if they chose to. The high level of agreement on these questions indicated that there was territoriality (Berkes et al. 2000) surrounding resource use. Areas near to the community and along the two major rivers in the Sucusari basin acted as common areas and were visited by almost all hunters, while areas farther from the community formed more distinct territories between families. It is probable that the use of hunter tracks to calculate territories overestimates the overlap among families, as hunters frequently travel through other zones on their way to their own (e.g., using the same river as an access point; Griffiths et al. 2022). Therefore, while our results showed c. 54% overlap among the zones hunters entered, including the common areas near to the community and rivers, it is probable that spatial partitioning of the landscape is even more distinct between families. Territoriality among hunters may also be a traditional practice for the Maijuna, resulting in differential use of resources across the landscape (Gilmore et al. 2020).

Even though there seemed to be consensus on how hunting zones are used, there are no formalized or written community-wide regulations surrounding their use. In this case, the consensus probably indicates the presence of social norms in the community that may be acting as a resource management system in which rules are unwritten but still very closely adhered to (St John et al. 2011). The partitioning of space limits the hunting pressure that each area is subject to and spreads the hunting pressure more evenly across the landscape. These social norms mean that some hunters solely hunt far away from the community, challenging the idea that hunters are central-place foragers and that hunting pressure decreases continuously as hunters move farther from the community. The partial preferences for primates exhibited by hunters create an even more fractured mosaic of hunting pressure on primates, resulting in refuges. Over 22% of the hunted area of the river basin could be considered refugia for primates, with another 16% of the remaining area being hunted for primates relatively little (<20% of the area's total hunting pressure). In the northern Congo, heterogeneity in landscape features created small sources scattered throughout the landscape that distributed animals into sink areas (Mockrin et al. 2011). In Sucusari, similar heterogeneity is created by hunter territoriality and prey preferences, and the effects on species distributions are probably similar. In this case, the partitioning of space by social and cultural norms could have effects similar to changes in habitat and accessibility. This may be particularly true for species that have a small home range, such as the red howler monkey (Crockett & Eisenberg 1987).

The conservation and sustainability implications of this adaptive management system are far-reaching. On the surface, hunters in Sucusari appear to be central-place foragers: they live in a community and travel to hunting grounds via rivers. However, a more detailed analysis of hunting reveals that hunting pressure is not only highly variable spatially, but also changes based on the game species in question. It should be noted that hunters in Sucusari hunt in both their community titled lands and in the MKRCA to the north, to which they have hunting rights. While we have never observed a difference in behaviour of hunters who are hunting in the titled lands versus the MKRCA, it is probable that hunters and communities without titled lands (and without access to a large conservation area) behave quite differently. It is possible that the continued protected status of their lands (and the food security that this status brings) is the only thing that allows these passive management practices to flourish. Hunters who are more food insecure (without access to large source areas) are likely to be less selective about prey items and about hunting zones.

This study provides evidence that an understanding of local norms and hunter preferences is essential when assessing the impacts of hunting on mammal populations, and that these social

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and cultural conventions are critical to providing an accurate understanding of hunting in local communities. The presence of local refuges may impact the overall sustainability of hunting and contribute to the conservation of ecologically important species (Gadgil et al. 1998). These refuges create resilience in the hunting system, ensuring the conservation of key seed-dispersing primates that maintain diversity and ensure the survival of even more species of plants and animals. Our results demonstrate the complexity of wild game management in Amazonia, where socio-cultural and ecological factors interact to influence conservation and sustainability, and these factors should be considered before management decisions are made. Furthermore, the erosion of traditional adaptive management practices could be detrimental to the sustainability of hunting in rural areas.

Supplementary material. For supplementary material accompanying this paper visit https://doi.org/10.1017/S0376892923000061.

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Competing interests. The authors declare none.

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